

Sediment heterogeneity affects variability of resuspension-induced CO₂ production

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Abstract. Demersal fishing is a major anthropogenic disturbance to marine sediments, with global implications for benthic carbon cycling and greenhouse gas emissions. Resuspension of sediment organic carbon during bottom trawling enhances oxic mineralisation, converting stored organic matter into aqueous CO₂ and reducing the long-term carbon storage potential of the seafloor. Sediment heterogeneity likely plays a role in the vulnerability of sedimentary organic carbon to resuspension, but spatial estimates of trawling-induced CO₂ release from resuspended sediment rarely account for this heterogeneity. ~~In this study, we~~ We conducted a large-scale survey in the Hauraki Gulf, New Zealand, to assess how sediment characteristics affect resuspension-induced CO₂ production (RCO_2P). Using a resuspension assay at 57 sites, we quantified RCO_2P ~~and~~ ~~accompanied with~~ by measurements of sediment grain size, organic matter content and quality, and phytopigments. ~~Boosted regression tree modelling revealed that organic matter content has the strongest influence, with a non-linear relationship to RCO_2P and interaction effects with water depth and medium sand content. Vulnerability to CO₂ release was highest in sediments with > 3 % organic matter and < 27 % medium sand, particularly at depths between 55—95 m. Our results demonstrate that sediment heterogeneity must be accounted for in regional assessments of seafloor carbon storage and disturbance impacts. For this, the resuspension assay offers a practical tool to empirically assess carbon storage vulnerability and can complement model based approaches to inform spatial management of demersal fisheries.~~ Boosted regression tree analysis revealed that organic matter content has the strongest influence on RCO_2P variability, followed by coarse grained sand content and water depth. Non-linear relationships with RCO_2P further indicate context-dependent mechanisms controlling RCO_2P and allowed for the identification of three clusters with differing levels of vulnerability to resuspension impacts and different environmental conditions influencing this vulnerability. Overall, risk of resuspension-induced CO₂ release was moderate to very high in sediments with > 3 % organic matter, < 8 % coarse grained sand, and at depths > 56 m, comprising 73% of our sampling sites. Multiple “hotspot” locations were found in the Hauraki Gulf, likely driven by an interplay of organic matter bioavailability and hydrodynamic conditions. Our results demonstrate that accounting for sediment heterogeneity in resuspension impact assessments will create more realistic and ecologically relevant estimates of C vulnerability over regional scales to inform spatial fisheries management.

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1 Introduction

35 ~~Marine anthropogenic activities are a major disruption for the seafloor and its ecological functioning. The most prominent disturbance is demersal fishing; a method whereby weighted gear is dragged over the marine sediment to catch bottom-dwelling fish and benthic shellfish. Approximately 21.9 Gt of sediment are resuspended with this fishing technique globally each year (Oberle et al., 2016), which destroys benthic habitats (Thrush and Dayton, 2003), and alters benthic carbon (C) cycling processes (Bradshaw et al., 2021; Polymenakou et al., 2005; Pusceddu et al., 2005). Globally, bottom trawling is estimated to cause a loss of stored organic C to aqueous CO₂ of 0.58 Gt per year (Sala et al., 2021), with 55–60% released back to the atmosphere, highlighting the considerable contribution of demersal fishing to greenhouse gas production (Atwood et al.,~~
40 ~~2024). However, little regulatory action has been taken to account for the vulnerability of marine sediment C storage to disturbance (Porz et al., 2024). Spatial fisheries management that incorporates seafloor C storage could sustain natural C sinks which would not only support the mitigation of anthropogenic CO₂ emissions but also help stabilize the Earth's climate and sustain marine biodiversity (Hiddink et al., 2023; Matthews et al., 2022; Thrush and Dayton, 2003). With the climate crisis progressing, humanity is in urgent need for undisturbed natural ecosystems to help stabilize the Earth's climate. Coastal and shelf seas hereby play a pivotal role by functioning as carbon (C) sinks as these highly productive systems build up large organic C stocks and high C burial rates in their sediments (Bianchi et al., 2018; Najjar et al., 2018). However, marine anthropogenic activities are a major disruption to the seafloor and its C sink functioning. The most prominent disturbance is demersal fishing whereby weighted gear is dragged over marine sediment to catch bottom-dwelling fish and benthic shellfish. Approximately 21.9 Gt of sediment are resuspended globally by this technique each year (Oberle et al., 2016), destroying~~
45 ~~benthic habitats and altering benthic C cycling processes (Bradshaw et al., 2021; Polymenakou et al., 2005; Pusceddu et al., 2005a; Thrush and Dayton, 2003).~~

55 ~~Large organic C stocks are found in the sediments of coastal and shelf seas (Bianchi et al., 2018; Najjar et al., 2018), which at the same time are highly impacted by demersal fishing (Oberle et al., 2016). These productive marine systems span a wide range of environmental settings covering water depths of up to 200 m, different hydrodynamic regimes, light availabilities, temperatures, productivity and proximity to land—all influencing sediment characteristics and biophysico-chemical conditions in the sediment thus creating sediment heterogeneity. Sediment heterogeneity plays an important role for the reactivity of organic C and thus how much of it is mineralised or buried (Arndt et al., 2013; Burdige, 2007; Middelburg, 2018; Snelgrove et al., 2018). When sediment organic C is resuspended, it becomes exposed to oxygen which can change its reactivity and stimulate heterotrophic processes that convert organic C to aqueous CO₂ (Bianchi et al., 2016; Ståhlberg et al., 2006). Not only fresh labile organic matter, but also older refractory components were found to be remineralised to aqueous CO₂ when re-introduced to oxygen (Hulthe et al., 1998). This causes organic C mineralisation rates often being higher in resuspended sediments compared to undisturbed sediments (Almroth-Rosell et al., 2012; Bartl et al., 2025; Polymenakou et al., 2005;~~

65 Ståhlberg et al., 2006) affecting the proportion of organic carbon that can be buried long-term. Benthic C cycling is controlled
by complex interactions of physical, chemical and biological processes. For example, the interplay of hydrodynamics, light
availability, temperature, oxygen exposure, pH, grain size, permeability, redox state and benthic community structure and
activity (fauna, algae, microbes) all affect organic matter reactivity which eventually determines how much of the organic C
70 is naturally mineralised or buried (Arndt et al., 2013; Burdige, 2007; Middelburg, 2018;). Sediment resuspension influences
this interplay by mixing organic matter from a certain sediment layer into the water column, thereby likely removing any redox
gradients or physical protections that preserved the organic matter within the sediment (Burdige, 2007; Kleber et al., 2021;
Mayer, 1994). As a result, the resuspended organic matter is a mixture of dissolved and particulate organic C of different
concentrations, bioavailability, composition, and structure altering its overall reactivity (Arndt et al., 2013). Resuspension
75 changes the abiotic conditions, most prominently oxygen exposure which can alter degradation rates of refractory and labile
organic matter (Hulthe et al., 1998). Also the response of microbial community structure and activity to resuspension and
priming can alter organic C mineralisation (van Nugteren et al., 2009; Pusceddu et al., 2005b). As a result, sediment
resuspension experiments often report higher mineralisation rates in resuspended than in undisturbed sediments (Almroth-
Rosell et al., 2012a; Bartl et al., 2025; Polymenakou et al., 2005; Ståhlberg et al., 2006), suggesting that the resuspension
impact on physical, chemical and biological drivers stimulates organic C mineralisation thus reducing the fraction of organic
80 C that can be buried long-term.

Based on the concept of resuspension stimulating organic C mineralisation, modelling studies estimated that bottom trawling
causes a release of stored organic C as aqueous CO₂ of 1.7 – 493 t CO₂ km⁻² yr⁻¹ (Luisetti et al., 2019; Muñoz et al., 2023; Porz
85 et al., 2024; Sala et al., 2021) (Sala et al., 2021). Such estimates differ by up to two orders of magnitude as they rely on different
first-order degradation rate constants and different assumptions about organic C lability. Different rate constants are applied
across oceanic regions (Muñoz et al., 2023; Sala et al., 2021) or to C pools of varying lability (Porz et al., 2024; Zhang et al.,
2019), along with assumptions that either all organic C (Luisetti et al., 2019) or only the labile fraction (Atwood et al., 2024,
90 Sala et al., 2021) is mineralised once resuspended. The used degradation constants and model assumptions have been critically
debated around their applicability for the spatially highly variable marine sediments (Atwood et al., 2023; Epstein et al., 2022;
Hiddink et al., 2023). Marine sediments display large spatial diversity of sediment properties formed by physical, chemical
and biological processes as well as their interactions (Holland and Elmore, 2008; Snelgrove et al., 2018). While the role of
varying sediment properties for undisturbed organic C mineralisation and burial is known, the resuspension impact on this
process is less clear as experiments often use only one to three sediment types (Almroth et al., 2009; Almroth-Rosell et al.,
95 2012b; Lønborg et al., 2024; Ståhlberg et al., 2006). Measuring resuspension effects across wider ranges of sediment properties,
i.e. across sediment heterogeneity, will provide new and spatially detailed insights on potential impacts on the C storage
function. Modelling estimates of organic C mineralisation to CO₂ in trawled sediments quantify rates using first order
degradation rate constants and assumptions on organic C reactivity as empirical measurements on resuspension induced CO₂

100 production are limited (Atwood et al., 2024; Muñoz et al., 2023; Porz et al., 2024; Sala et al., 2021). Different rate constants
are used for different oceanic regions (Muñoz et al., 2023; Sala et al., 2021), or different organic C labilities (Porz et al., 2024;
105 Zhang et al., 2019) alongside assumptions that either all organic C (Luisetti et al., 2019) or only the labile fraction of organic
C (Sala et al., 2021) is mineralised once resuspended. This results in estimations differing by up to two orders of magnitude
(Luisetti et al., 2019; Muñoz et al., 2023; Porz et al., 2024; Sala et al., 2021) with limited integration of sediment heterogeneity.
This generates uncertainty in these quantifications, particularly at regional scales (Atwood et al., 2024; Epstein et al., 2022).
110 Recent trawling impact assessments have therefore used alternative qualitative and semi-quantitative approaches to evaluate
the vulnerability of the seafloor C storage to demersal fishing and the risk of CO₂ production in resuspended sediments (Black
et al., 2022; Epstein et al., 2025). However, rates of resuspension induced organic C mineralisation to CO₂ are crucial
quantifications to assess the CO₂ footprint of demersal trawling and the loss of C storage function along with its climatological
consequences. Simple and efficient empirical measurements of sediment heterogeneity and resuspension induced CO₂
115 production can provide a practical solution to enable assessments of the vulnerability of C storage to resuspension (Bartl et al.,
2025). This will not only complement geospatial modelling approaches but also open opportunities to find solutions to
sustainably manage the seafloor's carbon storage function.

To empirically quantify variability of resuspension impacts across sediment heterogeneity, we have recently developed a
115 measure of C storage vulnerability through a resuspension assay (Bartl et al. 2025). The assay quantifies potential rates of
resuspension-induced organic C mineralisation, and its simple design allows for high sampling resolution within one region.
In this study, we conducted a survey in the Hauraki Gulf (New Zealand), a heterogeneous shelf system impacted by dredging
and bottom trawling, where we applied the resuspension assay across 57 sites spanning wide ranges of sediment characteristics
and water depths. Surface sediment grain size fractions, organic matter content and freshness, and phytopigments were used
120 as indicators of sediment heterogeneity, and we analysed their influence on resuspension-induced CO₂ production using
boosted regression tree modelling. Our results provide detailed insights into the relationships between sediment heterogeneity
and sediment resuspension impacts on C storage, contributing to discussions around sustainable spatial management of
demersal fisheries in shelf sea regions.

~~To address the key question of how sediment heterogeneity affects resuspension induced CO₂ production (RCO₂P), we
125 conducted a survey in the Hauraki Gulf (New Zealand), a heterogeneous marine coastal system that experiences anthropogenic
impacts including dredging and bottom trawling. Working in heterogeneous systems requires a large sample size of empirical
measurements and we therefore applied a resuspension assay at 57 sampling sites arrayed across a range of sediment types.
We used surface sediment grain size fractions, organic matter content and quality, and phytopigments as measures of sediment
heterogeneity and analysed their influence on RCO₂P using boosted regression tree modeling. With our results we aim to
130 contribute to discussions on the spatial management of demersal fisheries in coastal and shelf seas such as the Hauraki Gulf.~~

2 Methods

2.1 Study site and sampling

135 The Hauraki Gulf is a semi-enclosed, oligotrophic shelf sea up to 150 m deep, located northeast of New Zealand's North Island. Its seafloor comprises diverse volcanic and alluvial sediments ranging from coarse calcareous sand and gravel to fine sands and silts rich in clay (Manighetti and Carter, 1999). Water circulation and sediment transport are dominated by the south-eastward flowing East Auckland Current and strong tidal currents (Manighetti and Carter, 1999; Sharples, 1997; Zeldis et al., 2004). Terrestrial organic C input is limited and mainly confined to the Firth of Thames, while in the inner and outer Gulf, sediment organic matter derives from both terrestrial and marine sources (Sikes et al., 2009). Anthropogenic impacts have affected the Gulf for decades, including bottom trawling, dredging, and sand mining (Hauraki Gulf Forum, 2020, 2023).
140 Bottom trawling generally occurs at depths > 50 m (Fig. S1) while commercial scallop dredging took place in shallower areas (< 50 m) but has been banned since 2022 (Hauraki Gulf Forum, 2020, 2023).

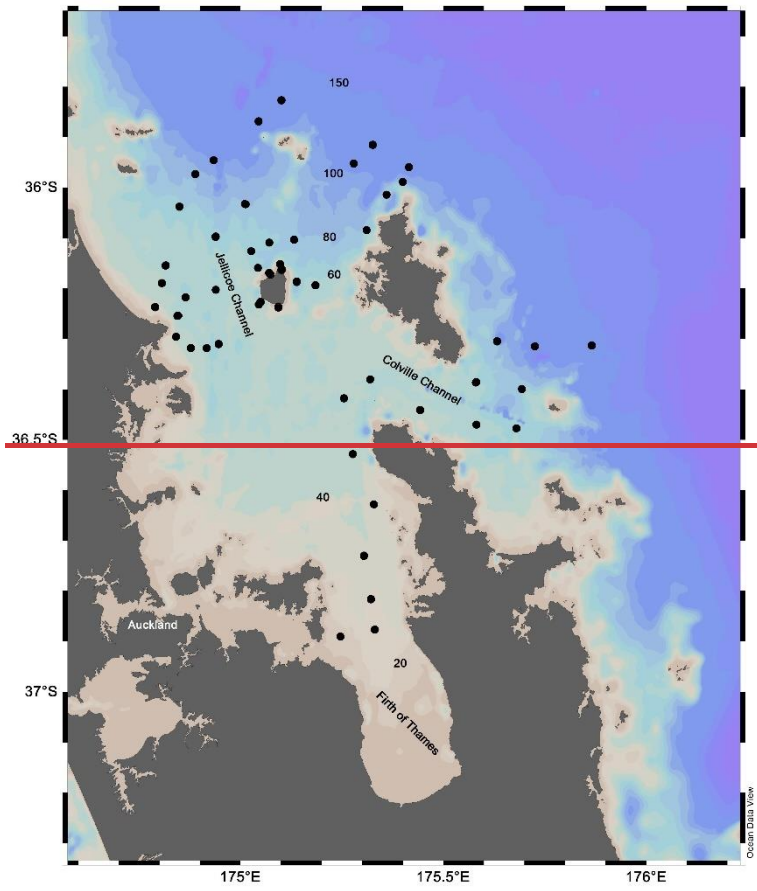
The Hauraki Gulf is a semi-enclosed, oligotrophic shelf sea of up to 150 m water depth in the northeast of the North Island, New Zealand. The seafloor consists of a large variety of volcanic and alluvial sediments ranging from coarse, calcareous sand and gravel to fine sands and silts with high clay content (Manighetti and Carter, 1999). The south-eastward flowing East Auckland Current and tidal currents dominate the water circulation and sediment transport in the Gulf (Manighetti and Carter, 145 1999; Sharples, 1997; Zeldis, 2004). Terrestrial organic C input is low and confined to the Firth of Thames, while in the inner Gulf sediment organic matter is a mixture of terrestrial sources and marine primary production and at the outer gulf marine primary production dominates (Sikes et al., 2009).

150 In February and March 2024, 57 sites were sampled aboard the R/V *Te Kaihōpara* (Fig. 1). Sediments were collected using a HAPS corer (KC Denmark, 14 cm diameter), with three replicate cores taken per site. Subsamples from the surface sediment (0–3 cm) were collected for characterisation using acid-cleaned (10 % HCl) polypropylene syringes with cut-off tips, while paired small sediment cores were taken for the resuspension assay using acid-cleaned acrylic core liners (inner diameter = 3.4 cm, height = 14 cm). Sediment characterisation samples were immediately transferred to acid-cleaned polypropylene 155 containers, kept on ice, and frozen at –20 °C at the end of each sampling day. The small intact cores were stored with open tops in dark seawater tanks at ambient bottom-water temperature (± 2 °C), and resuspension assay incubations were conducted within two hours of sampling.

In February and March 2024, 57 sites were visited in the Hauraki Gulf and outer shelf with the R/V *Te Kaihōpara* (Fig. 1). Sites were chosen to encompass the widest range of seafloor characteristics. Sediments were sampled using a HAPS corer (KC 160 Denmark, 14 cm diameter) and three HAPS cores were taken at each site. Subsamples for surface sediment (0–3 cm) characterisation were taken using acid-cleaned (10 % HCl) plastic syringes (Polypropylene) with cut off tips, and subsamples for the resuspension assay were taken in pairs of small sediment cores in acid-cleaned acrylic core liners (inner diameter = 3.4 cm, core liner height = 14 cm). Subsampled cores that contained large macrofauna were discarded from use for the re-

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~~suspension assay. The sediment characteristics samples were immediately transferred to acid-cleaned polypropylene containers, stored in ice and frozen at 20 °C at the end of a sampling day. The small cores for the assay were stored with open tops in dark seawater tanks at ambient bottom water temperature (± 2 °C) and assays were conducted within 2 hours of sampling.~~



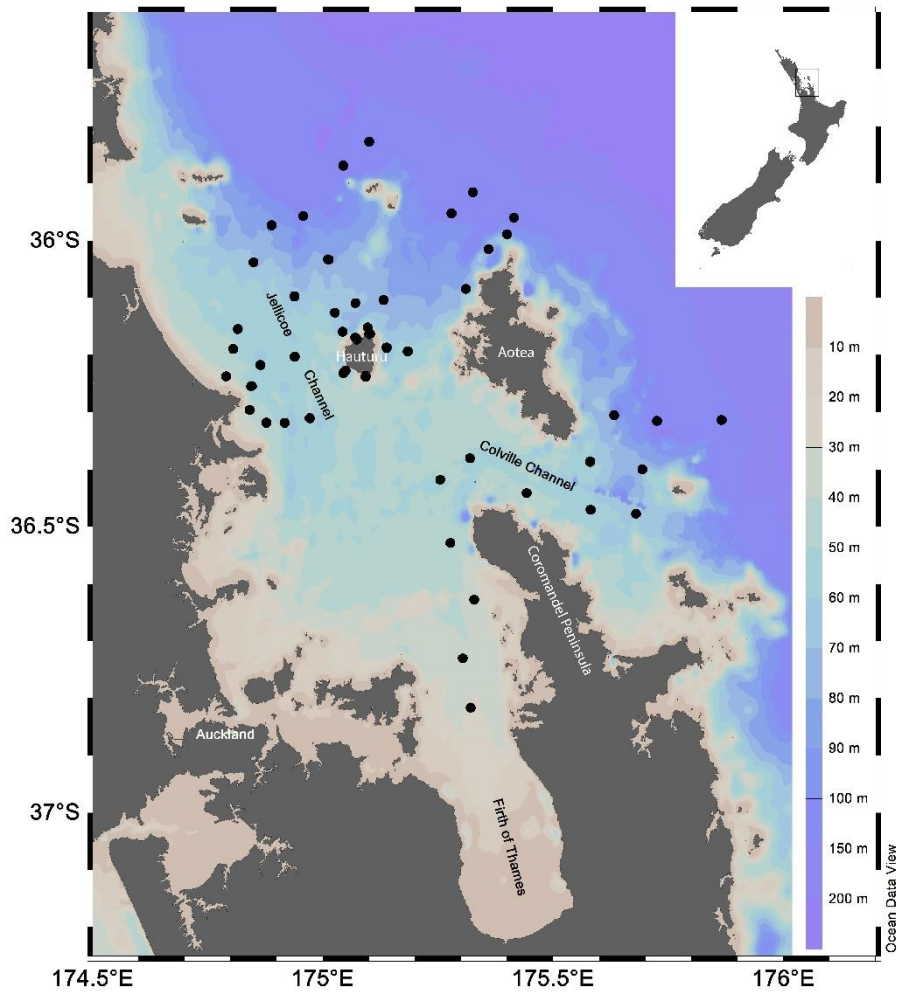


Figure 1: Study sites in the Hauraki Gulf, New Zealand (black dots). Coloured shading represents bathymetry.

Figure 1: Study sites in the Hauraki Gulf (black dots). Brown to blue shading represents bathymetry with depths (m) shown by numbers.

2.2 Resuspension assay

To quantify aqueous CO_2 production in resuspended sediments, we conducted resuspension assays following Bartl et al. (2025). The assay incubates undisturbed sediments in small cores and resuspended sediments in glass bottles, measuring temporal changes in oxygen concentration to determine sediment oxygen demand (SOD). For both treatments, the upper 3 cm of sediment - typically disturbed by trawling and dredging (Hiddink et al., 2017) - were incubated. Optimal sediment-to-water ratios to maintain oxic conditions were 1:8 for sandy sediments (250-mL bottles) and 1:17 for muddy sediments (500-mL bottles). For the resuspension treatment, sediment was added to glass bottles pre-filled with filtered seawater and the sediment

was resuspended by gentle inversion for 30 s. In both undisturbed cores and resuspension treatments, SOD ($\text{mmol m}^{-2} \text{h}^{-1}$) was calculated from oxygen concentrations measured at the start and end of the 4 – 6 h incubations (OXROB10 probe and FireSting GO_2 meter, Pyroscience, Germany). Values were normalised to incubation time and sediment surface area. Linear decline in oxygen, a requirement for this calculation, was validated through preliminary tests (Bartl et al., 2025). At each site, three pairs of control cores and resuspension treatments were incubated in the dark at ambient bottom-water temperature, conditions were monitored with loggers (Hobo Pendants, USA). Incubations showing > 30 % oxygen decrease between initial and final measurements, or before and after shaking, were discarded (Bartl et al., 2025). Organic C mineralisation to CO_2 was estimated from SOD using a respiratory quotient (RQ) of 0.9 for inner-shelf sites (< 50 m depth) and 0.85 for outer-shelf sites (50–200 m; Jørgensen et al., 2022). Resuspension-induced CO_2 production (RCO_2P) was calculated as the difference in CO_2 production between resuspended and undisturbed samples. The factor increase in CO_2 production was obtained by dividing resuspended values by undisturbed values. RCO_2P serves as a proxy for the vulnerability of sediment organic C to severe resuspension, with higher RCO_2P indicating greater vulnerability.

To quantify the production of aqueous CO_2 through enhanced organic C mineralisation in resuspended sediments, we conducted the resuspension assay according to Bartl et al. (2025). The assay incubates undisturbed sediments in cores and resuspended sediments in glass bottles and measures the change in oxygen concentration through time to determine the sediment oxygen demand (SOD). SOD ($\text{mmol m}^{-2} \text{h}^{-1}$) was calculated from oxygen concentration measurements (OXROB10 probe and FireSting GO_2 oxygen meter, Pyroscience, Germany) at the start and end of the incubation period and normalised to incubation time and area of the sediment core. At each site three pairs of control cores and resuspension treatments were incubated in the dark for 4–6 h at ambient bottom-water temperatures. From SOD, organic carbon mineralisation to CO_2 was estimated using a respiratory quotient of 0.9 for inner shelf sediments (Jørgensen et al., 2022). Resuspension induced CO_2 production (RCO_2P) was then calculated as the difference of CO_2 production in the resuspension treatment and the undisturbed sediment of each sample pair. The factor increase in CO_2 production in the resuspension treatment was calculated by dividing it with the CO_2 production from the undisturbed core. RCO_2P will be used as a proxy for the vulnerability of sediment organic C to resuspension with higher RCO_2P rates indicating higher sediment OC vulnerability.

2.3 Sediment characteristics

Organic matter content was determined by loss on ignition, burning dried sediments (60 °C for 7 d) at 450 °C for four hours. For grain size analysis, sediments were digested with 10 % H_2O_2 for six weeks to remove organic matter, washed with deionised water, and dispersed in 5 % sodium hexametaphosphate before laser diffraction analysis using a Malvern Mastersizer-3000 (Malvern, UK). Four grain size classes were used in data analysis: coarse sand (500–2000 μm), medium sand (250–500 μm), fine sand (63–250 μm), and mud (< 63 μm). This grouping reflects the bimodal grain size distributions observed in most samples while keeping the number of grain size factors in data analysis manageable. Shell hash and gravel were quantified by wet sieving and weighing two dried fractions: > 2 mm (shell hash and gravel) and < 2 mm (remaining sediment). Phytopigments (chlorophyll a and phaeophytin) were extracted from 1 g of homogenised, freeze-dried sediment using 3 mL of 90 % aqueous

acetone over 24 h (Buffan-Dubau and Carman, 2000; Sun et al., 1991). Pigment absorbances were measured before and after acidification with a spectrophotometer (Duetta, Horiba Scientific), and concentrations were calculated following Lorenzen et al. (1967). Chlorophyll a concentration was used as an indicator of algal biomass, while the ratio of organic matter content to total phytopigment concentration (Chl.a + phaeophytin) served to characterise short-term organic matter freshness (Miatta and Snelgrove, 2021). Total phytopigment concentration was used rather than Chl.a because both photosynthetic Chl.a and its degradation product represents labile organic matter components (Pusceddu et al., 2010). Lower ratios indicate fresher, less degraded material.

Sediment characterisation involved analysis of organic matter content, grain size and phytopigment concentration in the top 3 cm surface sediments. Sediment samples were homogenised, and subsamples (5 mL) were dried at 60 °C for seven days. Subsequently, sediment organic matter content was determined through weight loss on ignition by burning the dried sediment samples at 450 °C for 4 hours. For sediment grain size distribution, sediments were digested with 10 % H₂O₂ for six weeks to remove organic matter, washed using DI water and dispersed using 5 % sodium hexametaphosphate before laser diffraction analysis using a Malvern Mastersizer 3000 (Malvern, UK). The following grain size classes were used in data analysis: coarse sands (500—2000 µm, covering size classes of coarse and very coarse sand), medium sand (250—500 µm), fine sands (63—250 µm, covering size classes of fine and very fine sand), and mud (< 63 µm). Shell hash/ gravel was quantified via wet sieving and weighing of two dried size classes, > 2 mm (shell hash and gravel) and < 2mm (remaining sediment). Only one site contained actual gravel, all other sites had only shell hash in the > 2mm size class. The phytopigments chlorophyll a and Phaeophytin were extracted from homogenized, freeze dried sediment samples (1 g) over 24 hours using 3 mL 90% aqueous acetone (Buffan Dubau and Carman, 2000; Sun et al., 1991). Pigment absorbances were measured before and after acidification using a spectrophotometer (ThermoFisher Scientific, Type 1530, Finland) and concentrations were calculated according to Lorenzen et al. (1967). The chlorophyll a (Chl.a) concentration serves as an indicator of algal biomass whereas the total phytopigment concentration (Chl.a + Phaeophytin) was used to characterise the freshness of organic matter in the sediment, by calculating the mass ratios of organic matter content to phytopigment concentration (Pusceddu et al., 2010). Lower ratios indicate fresh, less degraded organic matter while higher reflect older, more degraded organic matter.

2.4 Data analysis

A total of 171 samples were analysed for each sediment characteristic alongside 171 resuspension assays. After quality assessment of the assay data (lost cores, > 30 % oxygen decline, or large macrofauna), two sites (6 data points) and 21 additional data points were removed. Two Chl.a values were interpolated as the mean of the remaining site replicates, resulting in a complete dataset of 144 samples. To identify relationships between sediment heterogeneity and RCO₂P, we applied supervised machine learning using boosted regression trees (BRTs; (Friedman, 2001). BRTs are ensemble models that sequentially build decision trees, with each tree correcting errors from the previous iteration, improving predictive performance. They capture non-linear relationships and interactions, making them suitable for analysing complex ecological datasets while maintaining strong predictive power (Lucas, 2020; Rubbens et al., 2023). BRTs have been widely applied for

250 predicting species distributions, fishing effort, ecosystem services (Cimino et al., 2020; Lohrer et al., 2020; Soykan et al., 2014) and linking biogeochemical variables to environmental factors (Panaïotis et al., 2025; Rijkenberg et al., 2011).

255 Our dataset included the following variables indicative of sediment heterogeneity: water depth (Depth), shell hash and gravel content (S/G), coarse sand (C-Sand), medium sand (M-Sand), fine sand (F-Sand), mud (Mud), organic matter content (OM), and the organic matter-to-total phytopigment ratio (OM:Phyto). The response variable was resuspension-induced CO₂ production (RCO₂P). Mud, M-Sand, and OM were highly collinear ($r > |0.8|$; Fig. S2). While multicollinearity does not affect BRT predictions, it complicates interpretation of feature importance and interactions (Boulesteix et al., 2012; Dormann et al., 2013; Lucas, 2020). We therefore excluded Mud and M-Sand, retaining OM as it is the substrate for C mineralisation. Replacement tests using Mud and M-Sand instead of OM produced similar BRT results (Table S1). To perform BRT the data set was split into a training set (75 % of the samples) and a testing set (25 % of the samples). Hyperparameters were tuned via

260 grid search and 4-fold cross-validation: number of trees = 1000, maximum depth = 3, minimum samples per leaf = 3, learning rate = 0.005, and subsampling = 0.8. To ensure robustness, 50 BRT iterations were run. Model interpretation employed SHAP (SHapley Additive exPlanations) values to assess feature importance, interactions, and feature relationships to modelled RCO₂P (Li, 2022; Lundberg et al., 2018; Lundberg and Lee, 2017). Mean absolute SHAP values were used to derive overall feature and interaction importance. SHAP dependence plots visualised how modelled RCO₂P increased (positive SHAP values)

265 or decreased (negative SHAP values) across feature values. Feature importance rankings and dependence plots were then used to identify clusters with differing RCO₂P. Within each cluster, Pearson correlation analysis was used to determine relationships between features and RCO₂P. All analyses were conducted in Python (v3.12.7) using the packages *scikit-learn* (v1.6.1; Pedregosa et al., 2011) and *SHAP* (v 0.47.1; Lundberg et al., 2017, 2020).

270 A total of 171 samples were collected and analysed for each sediment characteristic alongside 171 resuspension assays. 34 data points of the resuspension assay were removed from data analysis after thorough data quality assessment (lost samples, > 30 % oxygen decline, or large macrofauna in samples, see Bartl et al., 2025). Two Chlorophyll *a* datapoints were interpolated as average of the other two site replicates to yield a complete data set with 137 samples spread capturing the ranges of water depth and sediment characteristics of our sampling sites. To understand how the sediment heterogeneity affects RCO₂P, and which sediments are most vulnerable to releasing CO₂ when resuspended, we conducted supervised gradient boosting machine

275 learning using boosted regression trees (Friedman, 2001). Boosted regression tree models (BRT) build ensembles of decision trees sequentially where each new tree attempts to correct the errors made by the previous ensemble. BRT captures both, non-linear relationships of environmental factors with the response variable and factor interactions, making it suitable to understand ecological processes from heterogeneous environmental data while maintaining strong predictive power (Lucas, 2020; Rubbens et al., 2023). In our BRT, we included the following environmental factors as features: water depth (Depth), shell

280 hash content (Shell hash), coarse sand content (C Sand), medium sand content (M Sand), fine sand content (F Sand), mud content (Mud), organic matter content (OM), and the mass ratio of organic matter to total chlorophyll (OM:Phyto). The response variable is resuspension induced CO₂ production (RCO₂P). To perform BRT the data set was split into a training set

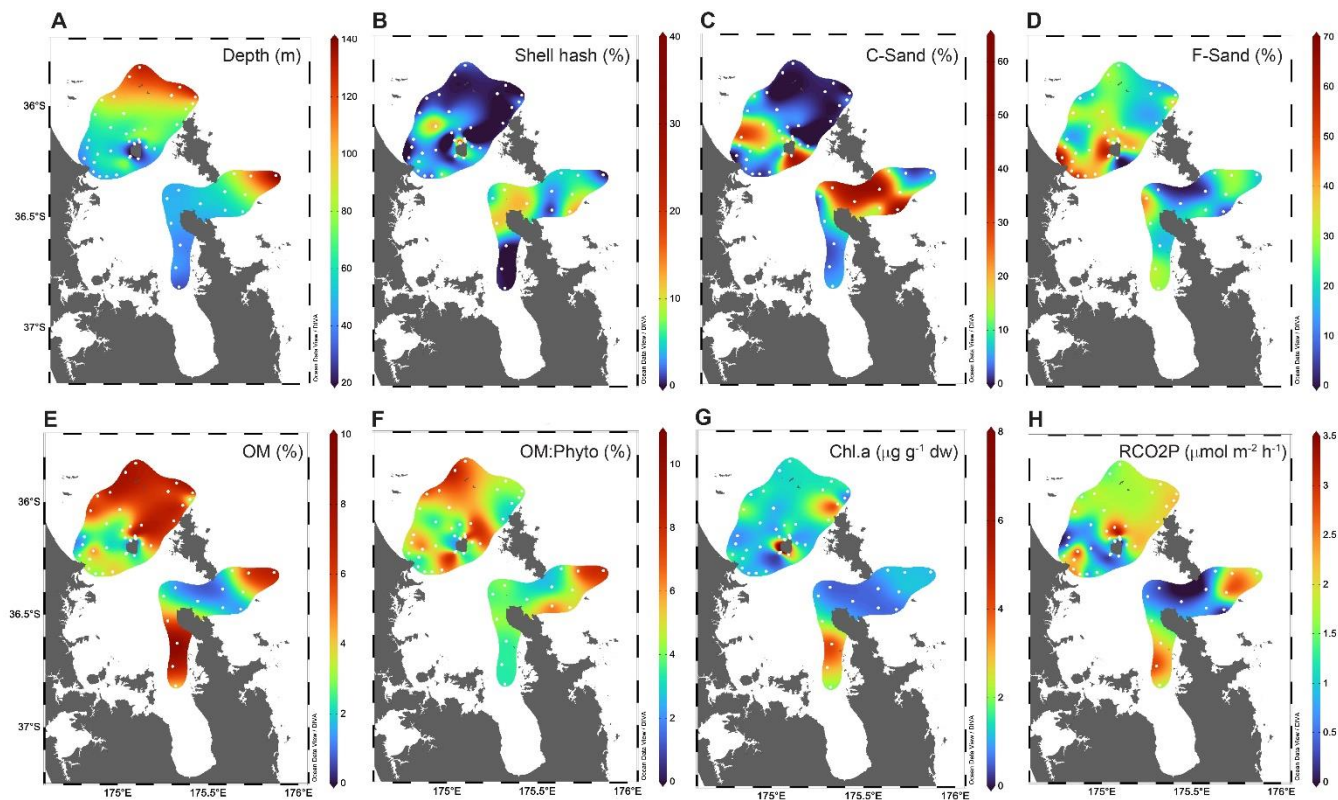
(75 % of the samples) and a testing set (25 % of the samples). The following hyperparameters, i.e. the settings for BRT, were tuned using the gridsearch function and a 4 fold cross validation: number of trees = 500, maximum tree depth = 3, minimum number of samples in final leaf = 4, learning rate = 0.05, and subsampling = 0.8. To create a robust model for interpretation we ran 50 BRT iterations with 50 different splits of training and testing data and will report mean diagnostic metrics. To identify the importance of single features, the impact of feature interactions and the relationship between features and RCO₂P, we used the SHAP values which assigns a contribution score to each feature through which the feature's impact on the modelled RCO₂P can be quantified (Li, 2022; Lundberg et al., 2018; Lundberg and Lee, 2017). Feature importance and feature interaction importance will be represented by mean absolute SHAP values to provide an insight into which environmental variable is most influential for modelled RCO₂P. To account for collinearity in our features, we used the tree based SHAP algorithm and performed SHAP cluster analysis to identify correlating features. All analyses were performed using Python (Jupyter Notebook, v 7.2.2) and the packages scikit.learn and SHAP (Lundberg et al., 2017, 2020; Pedregosa et al., 2011).

3 Results

3.1 Distribution of sediment characteristics and resuspension-induced CO₂ production ~~Sediment characteristics affecting resuspension induced CO₂ production~~

The sampled sites covered a wide range of sediment types and depths, with S/G, C-Sand, M-Sand, F-Sand, and Mud contents ranging from 0–40 %, 0–62 %, 1–54 %, 2–68 %, and 1–84 %, respectively. Grain size was spatially variable: coarser sediments dominated channels and areas around Hauturu (Figure 2A–C; Figure S3), while finer sands and mud prevailed near the coast and at deeper outer-shelf sites (Figure 2D; Figure S3). OM content ranged from 0.9 – 9.6 %, with highest values at outer-shelf sites and inner-shelf areas west of Coromandel Peninsula (Figure 2E). OM freshness varied widely irrespective of OM content or water depth (OM:Phyto = 1.2 – 16.1; Figure 2F). Algal biomass, indicated by Chl.a, was mainly concentrated at shallow inner-shelf sites, reaching up to 8 µg g⁻¹ dw (Figure 2G). Notably, Chl.a of 2 – 4 µg g⁻¹ were also detected at several sites deeper than 50 m, suggesting either microphytobenthos presence or substantial sedimentation of algal material. CO₂ production rates were 1.4 – 19.5 times higher in resuspended sediments than in undisturbed sediments (Figure S4). RCO₂P (0.1 – 3.5 mmol CO₂ m⁻² h⁻¹) showed strong spatial variability, with elevated rates observed at multiple shallow and deep sites (Figure 2H).

The sampled sites covered a large variety of sediment grain sizes as well as organic matter quantities and qualities (Table 1, Fig. S1 and S2) confirming that the selection of our sampling sites is a solid representation of sediment heterogeneity in the Hauraki Gulf. CO₂ production rates determined via the resuspension assay were 1.4 – 19.4 times higher in the resuspended sediments compared to undisturbed sediments and RCO₂P strongly varied from 0.1 to 3.7 mmol CO₂ m⁻² h⁻¹ (Table 1).



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Figure 2: Environmental features water depth (A), shell hash/gravel (B), coarse grained sand (500 – 2000 μm , C), fine grained sand (63 – 250 μm , D), organic matter content (E), ratio of organic matter and phytopigments (F), and Chlorophyll a content (G) as well as resuspension-induced CO_2 production rates (H) in the Hauraki Gulf, New Zealand. For better visualisation, data were spatially interpolated from the sampling sites (white dots) using DIVA in Ocean Data View (Schlitzer, 2025).

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Table 1: Sediment characteristics and CO_2 production rates determined through the resuspension assay. Values shown are average \pm standard deviation and ranges from minimum to maximum values. Undisturbed CO_2 production was measured from incubation of undisturbed sediment cores while resuspension-induced CO_2 production (RCO2P) was determined from incubation of a resuspension treatment. OM:Phyto is the mass ratio of organic matter content and Phytopigments and Phaeo:Chla is the mass ratio of Phaeopigments and Chlorophyll. Both represent measures of organic matter freshness with lower ratio reflecting higher freshness.

Sediment characteristic	Average \pm Std	Range
Shell hash (%)	3.7 ± 5.7	0–39.8
Coarse sand (%)	10.8 ± 12.9	0–62.0
Medium sand (%)	22.7 ± 14.1	1.4–53.9
Fine sand (%)	30.0 ± 13.7	1.7–67.7
Mud (%)	36.4 ± 24.8	0.6–84.0
Organic matter (%dw)	4.0 ± 2.1	0.9–9.6

Chl.a ($\mu\text{g g}^{-1}\text{-dw}$)	1.8 ± 1.5	0.3—8.0
OM:Phyto (mass)	5.2 ± 2.7	1.2—16.1
Resuspension assay		
Undisturbed CO_2P ($\text{mmol m}^{-2}\text{h}^{-1}$)	0.3 ± 0.1	0.1—1.0
RCO_2P ($\text{mmol m}^{-2}\text{h}^{-1}$)	1.6 ± 0.9	0.1—3.7
Factor increase of RCO_2P	6.9 ± 3.9	1.4—19.4

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3.2 Most important features and relationships

The 50 BRT model iterations performed well in predicting RCO_2P , with an R^2 of 0.58 ± 0.11 and a root mean squared error of $0.54 \pm 0.07 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, indicating good performance for highly variable environmental data. OM was the most important feature, showing the highest mean absolute SHAP value and ranking first across all 50 model runs (Table 1). C-Sand was the second most important feature, with a mean absolute SHAP value 3.6 times lower than that of OM. Depth and F-Sand had similar SHAP importances (~ 0.1), consistently ranking third and fourth, while Chl. a and S/G were least influential (Table 1). The most significant feature interactions were OM – C-Sand and OM – Depth, which had higher SHAP values than Chl. a and S/G but remained lower than the top four individual features. Overall, RCO_2P variability was primarily driven by the individual effects of OM, C-Sand, Depth, and F-Sand, with only minor contributions from interactions.

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Table 1: Feature importance of individual features and interacting features based on mean absolute SHAP values. Higher values indicate higher influence of feature on modelled RCO_2P . Values in brackets are the 95% confidence intervals from the 50 model iterations.

<u>individual feature</u>	<u>mean SHAP feature importance</u>	<u>Rank stability</u>	<u>interacting features</u>	<u>mean SHAP interaction importance</u>
OM	0.47 (0.010)	1.0 (0.00)	OM + C-Sand	0.061 (0.005)
C-Sand	0.13 (0.008)	2.5 (0.23)	OM + Depth	0.056 (0.006)
Depth	0.10 (0.008)	3.6 (0.31)	F-Sand + Depth	0.033 (0.003)
F-Sand	0.09 (0.006)	3.7 (0.29)	OM + F-Sand	0.029 (0.003)
OM:Phyto	0.07 (0.006)	4.6 (0.29)	OM + Chl.a	0.025 (0.002)
Chl.a	0.04 (0.003)	6.1 (0.20)	C-Sand + Depth	0.023 (0.002)
S/G	0.04 (0.005)	6.5 (0.26)	Other interaction pairs	<0.023

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The 50 iterations of the BRT model performed well in predicting RCO_2P with an R^2 of 0.57 ± 0.1 and a root mean squared error was $0.56 \pm 0.1 \text{ mmol CO}_2 \text{ m}^{-2} \text{ h}^{-1}$, a strong result for highly variable environmental data. SHAP values from the BRT model show how much each feature (sediment characteristics and water depth) contributes to an increase (positive SHAP values) or decrease (negative SHAP values) of modelled RCO_2P which is used to evaluate feature importance and

relationships. Organic matter content was by far the most influential factor on modelled RCO₂P, followed by water depth and the sand fractions (Fig. 3A). Interestingly, the freshness of organic matter measured via OM:Phyto had low feature importance for RCO₂P (Fig. 2A). SHAP cluster analysis showed that there were strong correlations ($r > 0.7$, i.e. cluster distance < 0.3) among 8 out of the 9 features particularly between organic matter and mud content (Fig. 2A). This clustering suggests that correlating features carry similar information for the prediction of modelled RCO₂P and that a reduction of features could be tested when using the model for prediction. SHAP interaction scores revealed two strong interactions (OM and MSAND: 0.049, OM and DEPTH: 0.021, Fig. 2B) suggesting that the most important features also have interaction effects on RCO₂P. Partial dependence plots for the three most important features revealed a predominance of non-linear relationships between modelled RCO₂P and features (Fig. 2C-E). Along the concentration range of organic matter, there is a strong shift from negative to positive SHAP values at 3% OM, indicating that RCO₂P are highest in sediments with an OM of $> 3\%$ (Fig. 2C). Similarly, sediments with lower fractions of medium sand ($< 27\%$) and from water depths of > 55 m are linked to high RCO₂P (Fig. 2D, E). Interestingly, SHAP values peaked at water depths between 55–95 m before levelling off at greater depths (Fig. 2D). Overall, the BRT results revealed that organic matter contributes most to the variability of RCO₂P, and their non-linear relationship suggests context dependent influences of OM through interactions with water depth and medium sand. SHAP dependence plots revealed predominantly non-linear relationships between modelled RCO₂P and features (Figure 3). Across the OM gradient, SHAP values shifted from negative to positive at $\sim 3\%$ OM, indicating highest RCO₂P in sediments containing 3–10% OM (Figure 3A). Similarly, sediments with C-Sand below 8% and from depths of 56 – 100 m exhibited positive SHAP values, linking these conditions to higher RCO₂P (Figure 3B, C). Although less influential overall, F-Sand and OM:Phyto showed more linear relationships with RCO₂P, with highest SHAP values at F-Sand $> 27\%$ and OM:Phyto < 4.7 , suggesting that greater CO₂ production corresponds to higher F-Sand content and fresher organic matter (Fig. 3D, E). No clear relationships were observed for Chl.a or S/G (Figure 3F, G).

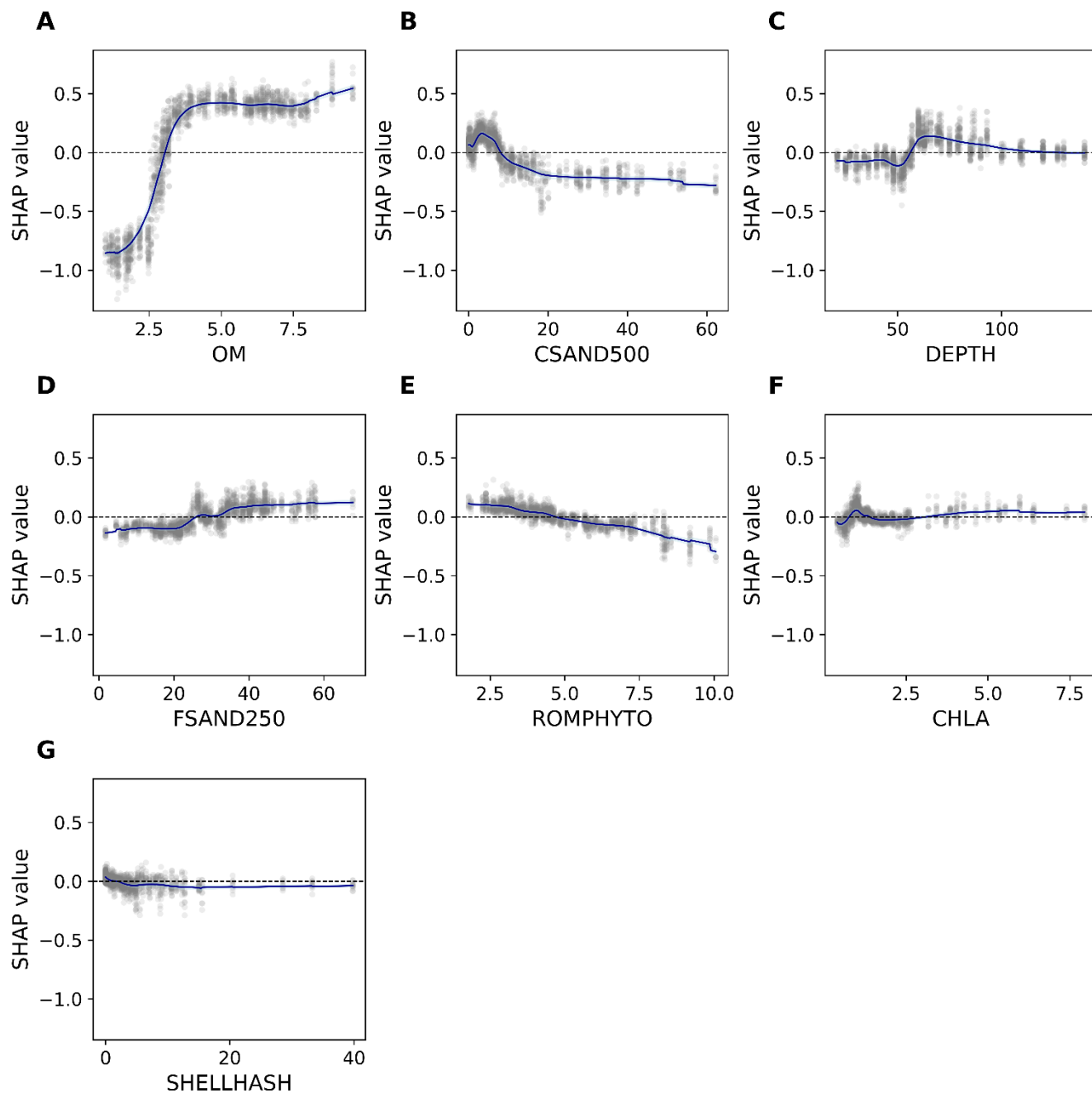
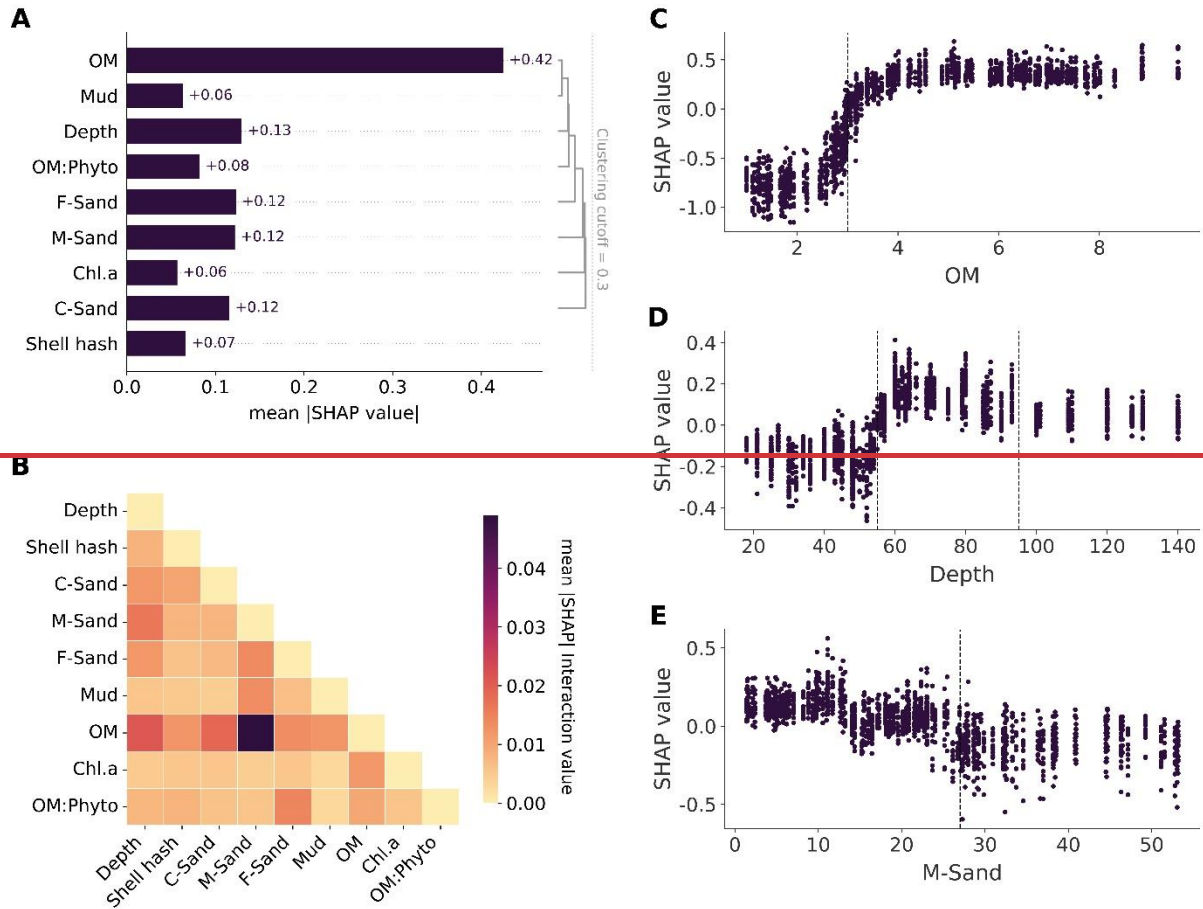


Figure 3: Partial-dependence-plots showing the relationship between SHAP values and features. Positive SHAP values reflect a positive contribution of the feature-value to model output, i.e. to higher RCO₂P than average, and vice versa. Lowess smooth function was applied for each of the 50 model iterations and its mean and 95% confidence interval are shown as dark blue solid line and light blue shading, respectively. The shape of the scatter shows non-linear relationships between SHAP values and features, with strong shifts (across SHAP = 0) at OM = 3 %, C-Sand = 8 %, and Depth = 56 m.



375 **Figure 2: Results from the BRT model: (A) Feature importance and (B) Feature Interaction Importance based on mean absolute SHAP values. Higher values indicate higher influence of feature on modelled RCO₂P. (C–E) Partial dependence plots showing the relationship between SHAP values and predictors organic matter content (OM), water depth (Depth), and medium sand content (M-Sand). Positive SHAP values represent a positive impact and thus higher RCO₂P than average, vice versa for negative SHAP values. The shape of the scatter shows non-linear relationships between SHAP value, i.e. modelled RCO₂P, and features, with strong shifts along the concentration gradient of OM and M-Sand at 3% and 27%, respectively, and at 55 m and 95 m water depth (vertical dashed lines).**

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385 **3.23 Clusters with different levels of RCO₂P and differing relationships** ~~Sediment types and areas with highest vulnerability to resuspension-induced CO₂ release~~

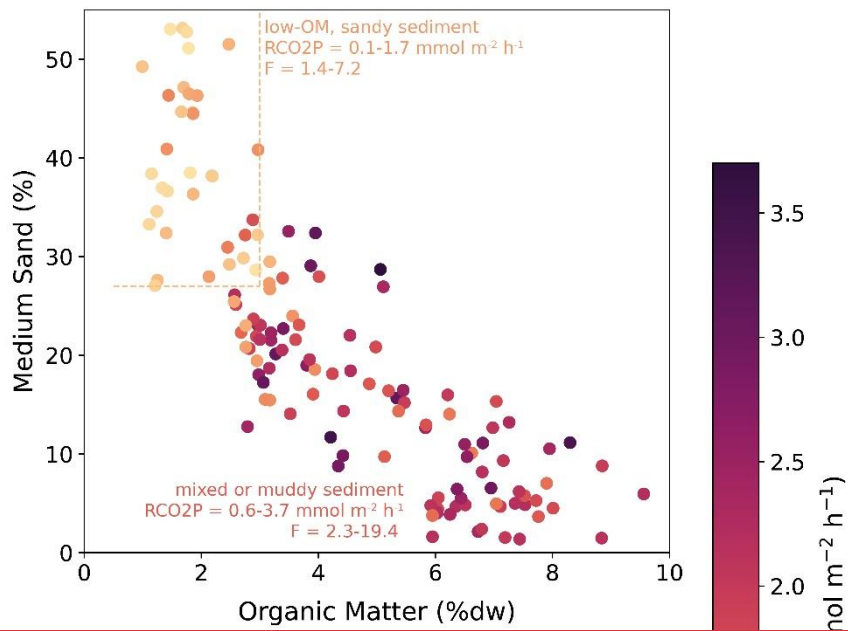
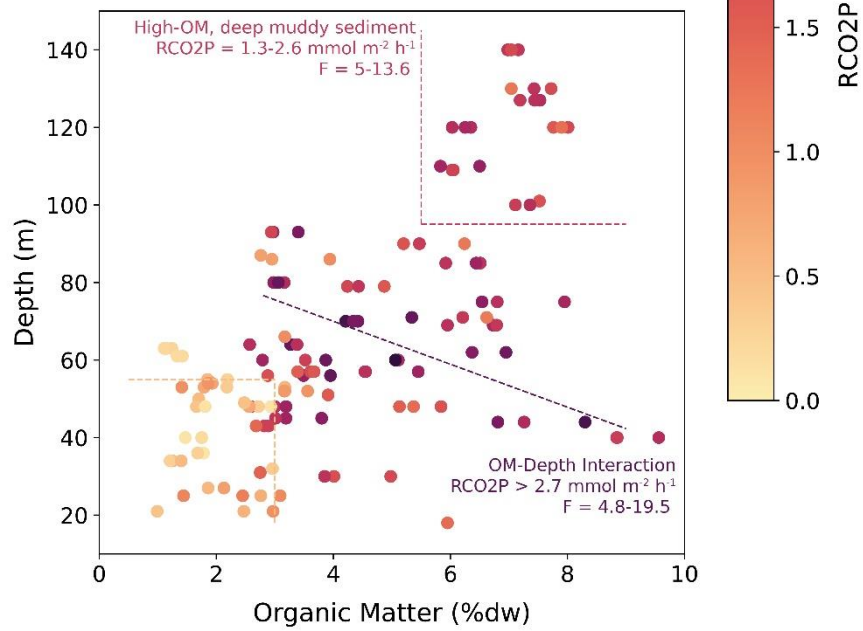
To visualise which sediment types are most vulnerable to CO₂ release upon resuspension, we produced scatter heat maps from the original dataset and used BRT results to identify clusters (Figure 4, Table 2). Lowest RCO₂P rates ($0.5 \pm 0.3 \text{ mmol m}^{-2} \text{ h}^{-1}$) occurred in sandy sediments (> 8 % C-Sand, > 27 % F-Sand) with low organic matter (< 3 %) and shallow depths (< 56

m), forming a distinct OM-poor cluster (Figure 4A, B). Sediments in this cluster are from the Colville and Jellicoe Channels and around Hauturu and show a low to moderate risk of CO₂ release (Figure 2H, Table 2). Within this cluster, RCO₂P correlated positively with OM and F-Sand but negatively with C-Sand, indicating stronger resuspension-driven mineralisation where OM and finer fractions are higher (Figure 4C). At depths ≥ 100 m, both OM content and RCO₂P were high and relatively uniform, with RCO₂P about four times higher than in the OM-poor cluster (Table 2). This deep cluster showed negative correlations between RCO₂P and OM, and slightly higher rates at lower OM:Phyto ratios, reflecting fresher organic matter (Figure 4E).

Mixed sediments from intermediate depths (56 – 100 m, > 3 % OM, < 8 % C-Sand) formed a mixed cluster with RCO₂P ranging from 0.8 – 3.5 mmol m⁻² h⁻¹, equivalent to 3 – 19.5 times higher CO₂ release than in undisturbed sediments (Figure 4A, B, Table 2). No clear correlations were found here (Table 2, Figure 4D). The mixed cluster contained the highest 10 % of RCO₂P values (> 2.6 mmol m⁻² h⁻¹) which occurred along interactions between OM and C-Sand (C-Sand = 270.08 × OM^{-2.93}, R² = 0.51, p = 0.003) and OM and Depth (Depth = -4.97 × OM + 87.45, R² = 0.32, p = 0.029; Fig. 4A,B). Together, the Mixed and Deep cluster cover 73 % of the sampled sites and are moderately to very highly vulnerable to releasing CO₂ when disturbed (Table 2, Figure 2 H).

Based on the most important features (Fig. 2A, B) and the shifts in SHAP values along the concentration range of these features (Figs. 2C-D), we created scatter heatmaps using our full dataset to visualize which sediment types are most vulnerable to CO₂ release when resuspended (Fig. 3). Lowest RCO₂P rates of 0.54 ± 0.4 mmol m⁻² h⁻¹ occur in coarser grained (> 27 % medium sand) sediments with low organic matter content (< 3 %) from shallow depths (< 55 m) creating a distinctive cluster (Fig 3A, B). This indicates a low to moderate vulnerability of these sediment types and corresponds to sampled areas in the Colville and Jellicoe Channel (Fig. 4). Sediments containing > 3 % OM and < 27 % medium sand span RCO₂P rates from 0.6–3.7 mmol m⁻² h⁻¹ corresponding to 2.3–19.5 times more CO₂ released compared to undisturbed sediments. This means that in the Hauraki Gulf, a considerable range of sediment types and a considerable portion of the sampled sites (73 %) in the Hauraki Gulf are moderately to highly vulnerable to releasing CO₂ when disturbed (Fig. 3A, Fig. 4).

Within the cluster of highly vulnerable sediments, two interesting patterns emerge from organic matter—depth interactions. Firstly, at sites deeper than 95m, both organic matter content of 6.9 ± 0.7% and RCO₂P rates of 2 ± 0.33 mmol m⁻² h⁻¹ are relatively constant, with RCO₂P around 4 times as high as in the shallower, low OM cluster (Fig 3B). Secondly, the highest 10 % of RCO₂P (> 2.7 mmol m⁻² h⁻¹) can be found along a linear interaction between depth (44–95 m) and OM (3–9 %, linear regression: Depth = -5.54 × OM + 92.15, R² = 0.47, p = 0.007, Fig. 3B). This means that highest RCO₂P rates can be found, both, at deeper sites with lower OM and at shallower sites with higher OM with those hotspots being located landward and seaward to the low RCO₂P areas in Colville and Jellicoe Channel (Fig. 4). These two patterns suggest that the deep muddy sediments of the Hauraki Gulf display a consistently high vulnerability to releasing CO₂ when disturbed while highest vulnerability is linked to an interaction of water depth and organic matter content.

A**B**

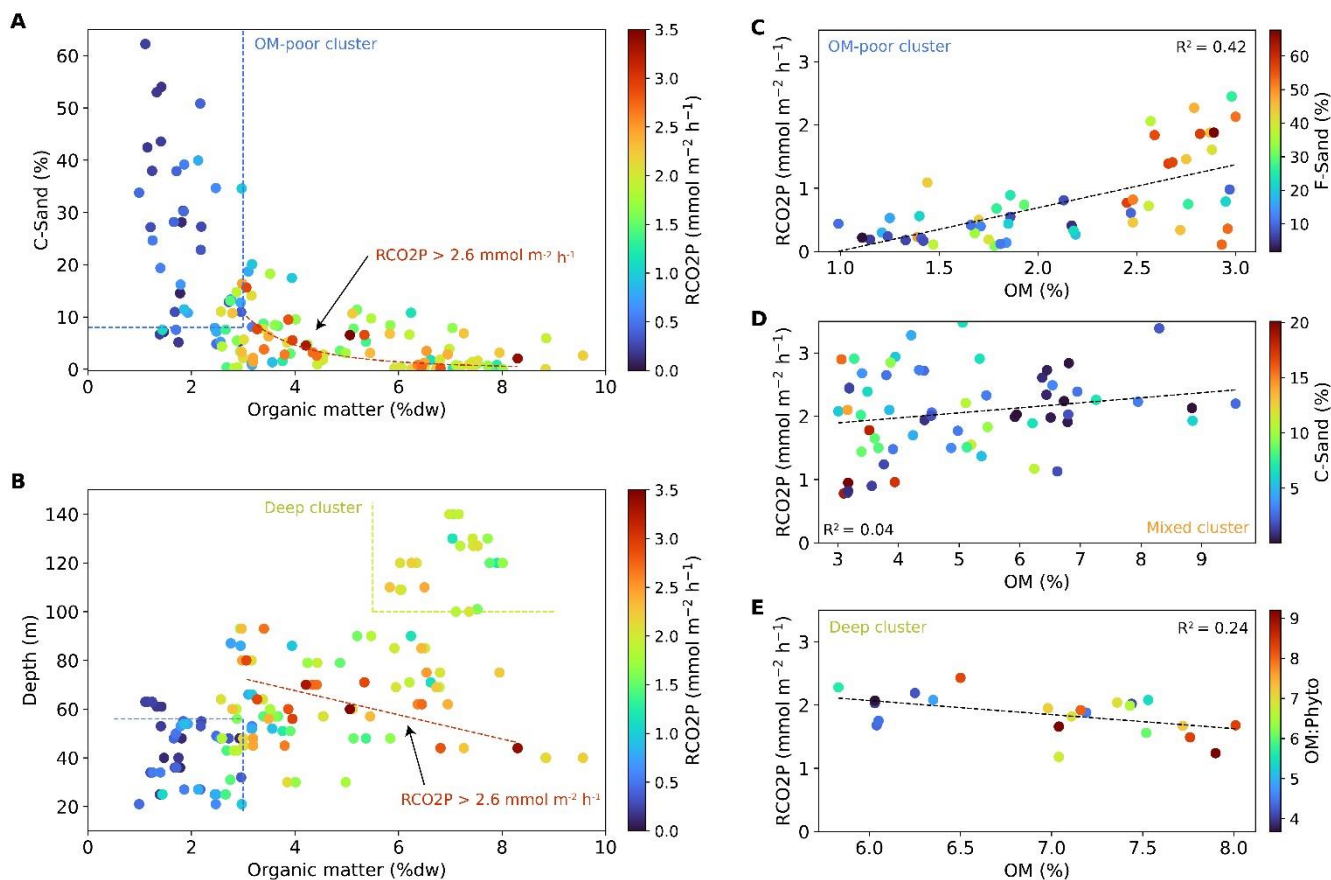
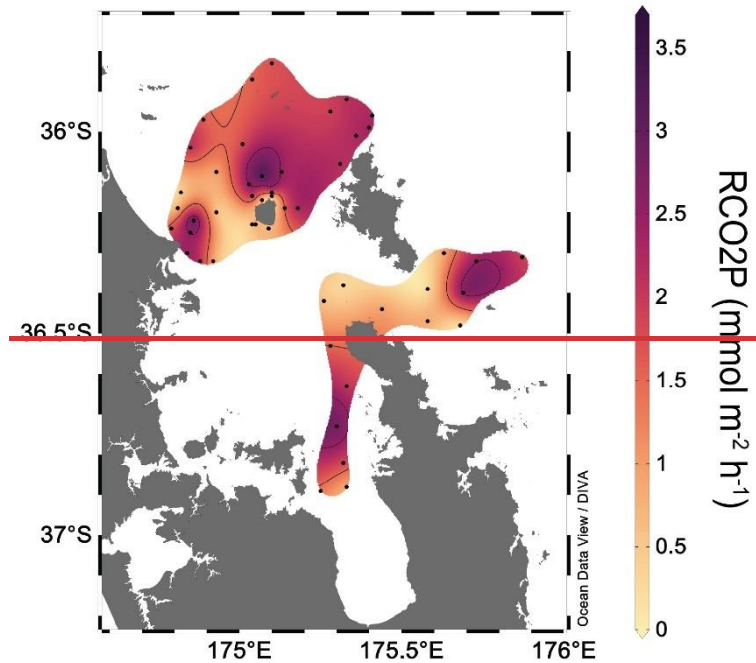


Figure 4: Scatter heatmaps showing the resuspension-induced CO₂ production (RCO₂P, colour gradient) over organic matter content and C-Sand (A), and over organic matter content and water depth (B). Blue dashed lines represent the OM-poor cluster, the green dashed line represents the deep-cluster, and the red dashed line shows the interactions of organic matter and C-Sand ($y=270.08x^{-2.93}$, $R^2=0.51$, $p=0.003$) and organic matter and water depth ($y = -4.97x + 87.45$, $R^2=0.32$, $p=0.029$) along which the 90th quantile of RCO₂P rates align. Panels C-E show relationships of environmental variables with RCO₂P in the OM-poor cluster (C), the Mixed cluster (D), and the Deep-cluster (E). Ranges and correlation coefficients are given in Table 2.

Figure 3: Heatmaps showing the resuspension-induced CO₂ production (RCO₂P, colour gradient) related to (A) organic matter content (x-axis) and medium sand content (y-axis), and (B) organic matter content (x-axis) and water depth (y-axis). Yellow dashed lines represent the thresholds determined from the partial dependence plots from the BRT model (see Fig. 3), red dashed lines represent the cut-off to deep-water sites (>95 m) and the purple dashed line shows the linear regression between organic matter and water depth ($y = -5.54x + 92.15$, $R^2=0.47$, $p=0.007$) for the 90th quantile of RCO₂P rates indicating an interaction effect of both features on RCO₂P rates > 2.7 mmol m⁻² h⁻¹.



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Figure 4: Surface map of resuspension-induced CO₂ production (RCO₂P) rates. Contour lines are RCO₂P at 1.7 mmol m⁻² h⁻¹ (solid) representing the low RCO₂P cluster and at 2.7 mmol m⁻² h⁻¹ (dashed) representing RCO₂P hotspots. Values were spatially interpolated using DIVA gridding in Ocean Data View (Schlitzer, 2025).

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Table 2: Average (Avg), standard deviation (Std) and ranges of environmental features and risk of CO₂ release in the three clusters identified through BRT analysis. Pearson correlation coefficients (R) are provided for relationships of RCO₂P and individual features in each cluster. Correlations (R ≥ 0.4) in bold are significant at p < 0.05, and in italic at p < 0.1. C storage vulnerability levels are based on RCO₂P rates and the factor increase relative to CO₂ production from undisturbed sediments cores.

Cluster	Features						C storage vulnerability		
	Metric	OM	C-Sand	Depth	F-Sand	OM:Phyto	RCO ₂ P	Factor increase	level
OM-poor cluster (n=53)	Avg ± Std	2.1 ± 0.6	20.1 ± 16.0	45.7 ± 16.1	30.0 ± 18.5	4.4 ± 1.9	0.7 ± 0.7	3.9 ± 2.5	low - moderate
	Range	1.0 – 3.0	0.2 – 62.2	21.0 – 87.0	1.8 – 67.7	1.8 – 9.9	0.1 – 2.5	1.4 – 12.5	
	R	0.651	-0.472	0.156	0.516	<i>-0.258</i>			
	p	<0.001	<0.001	0.264	<0.001	0.062			
Deep cluster (n=23)	Mean ± Std	7.0 ± 0.7	1.3 ± 2.1	120 ± 12.4	22.2 ± 5.4	6.3 ± 1.8	1.9 ± 0.3	9.6 ± 2.3	High to very high
	Range	5.8 – 8.0	0.0 – 7.9	100 – 140	14.3 – 32	3.7 – 9.2	1.2 – 2.4	5.0 – 13.6	
	R	-0.493	0.153	<i>-0.134</i>	<i>-0.253</i>	<i>-0.393</i>			
	p	0.017	0.486	0.541	0.245	0.064			
Mixed cluster (n=53)	Mean ± Std	5.0 ± 1.7	5.3 ± 5.0	62.6 ± 15.5	31.5 ± 9.2	4.6 ± 1.6	2.1 ± 0.7	8.2 ± 3.9	moderate to very high
	Range	3.0 – 9.6	0.1 ± 20.1	30.0 – 93.0	16.4 – 55.9	2.3 – 10.1	0.8 – 3.5	3.0 – 19.5	
	R	0.203	<i>-0.239</i>	<i>-0.042</i>	0.101	<i>-0.087</i>			
	p	0.110	0.059	0.741	0.431	0.496			

4 Discussion

445 Our results show that resuspension of the 3-cm surface sediment strongly enhances organic C mineralisation producing up to 20 times more CO₂ compared to undisturbed surface sediments in the Hauraki Gulf. Sediment heterogeneity, based on organic matter content, sand content and water depth played an important role explaining the variability of resuspension-induced CO₂ production and their non-linear relationships indicate context-dependent controls and allowed us to identify three clusters with different levels of C storage vulnerabilities.

450 ~~The broad range of water depths and sediment characteristics of Hauraki Gulf sediments allowed us to investigate the effects of sediment heterogeneity on resuspension-induced CO₂ production. Our results show that in these heterogeneous sediments, organic matter content, sand content and water depth played important and interactive roles explaining the variability of RCO₂P. Both, non-linear relationships of RCO₂P with organic matter content, water depth, and sand content and interaction effects of these three features allowed us to identify that any sediment with less than 27 % medium sand and more than 3 % organic matter had a moderate to high risk of releasing CO₂ when resuspended, making 73 % of our sampled sites at high risk to lose their C storage function when disturbed.~~

4.1 Spatial variability of resuspension-induced CO₂ production driven local environmental settings

460 The stimulation of organic C mineralisation through sediment resuspension can involve multiple physical, chemical and biological mechanisms (Hulthe et al., 1998; Kleber et al., 2021; van Nugteren et al., 2009; Pusceddu et al., 2005b) which in sum contribute to the RCO₂P rates that we measured. While we expected variability of RCO₂P due to sampling across substantial sediment heterogeneity, the extent of variability and the location of apparent hotspots was surprising. Variability of RCO₂P was partitioned into three clusters of C storage vulnerability in which RCO₂P appears to be regulated by differing environmental conditions. Firstly, low to moderate vulnerability in the shallow, coarse-grained sediments around Hauturu and in the channels is likely linked to strong tidal and residual currents that winnow fine organic particles and/or naturally enhance organic matter turnover resulting in a smaller resuspension impact (Boudreau et al., 2001; Manighetti and Carter, 1999). The positive relationship of RCO₂P with organic matter quantity and finer grained sand content suggests that substrate availability and strong (less F-Sand) vs. calm (more F-Sand) hydrodynamic conditions were controlling the magnitude of the resuspension impact. At the other end of the spectrum, deep, muddy, OM-rich sediments showed high to very high C storage vulnerability likely due to the consistently high pool of OM that accumulates in the deep outer shelf area of the Hauraki Gulf. Interestingly, here RCO₂P was ~10 % higher when OM was fresher, suggesting that quality of the resuspended organic matter influences mineralisation when the substrate is abundant.

475 We could not derive mechanistic explanations of RCO₂P variability in the mixed sediment cluster based on our sediment data. This suggest that there may be other environmental variables that could explain the spatial variability of resuspension impacts

480 in these sediments. Measures of organic matter quality or bioavailability are likely to influence RCO₂P and may have been underrepresented in our set of features. While the use of simple and cost-effective proxies (e.g. loss-on-ignition OM and OM:Phytopigment ratio) enables broad applicability (Bartl et al., 2025) it may overlook important compositional nuances of OM. Incorporating additional measures, such as C:N ratios, δ¹³C signatures, or n-alkane signatures (Sikes et al. 2009), may help resolve spatial RCO₂P patterns. RCO₂P variability could also be linked to the concentration and quality of dissolved organic matter that is resuspended with the sediment and can contain a considerable fraction of readily degradable compounds that could enhance microbial mineralisation (Kujawinski, 2010; Lengier et al., 2024; Reader et al., 2019). Lastly, the composition and activity of the microbial community and their response to being resuspended could influence RCO₂P irrespective of the amount, composition or biochemical quality of organic matter (DesRosiers et al., 2022). On a broader scale, 485 spatially variable OM supply from benthic or pelagic primary production or lateral transport by cross-shore bottom currents could also drive the spatial pattern of RCO₂P in the Hauraki Gulf (Chang et al., 2003; Zeldis et al., 2004). Since we can only speculate about potential underlying mechanisms of resuspension impacts in mixed sediments, future targeted experiments on the role of organic matter bioavailability and the microbial response to resuspension in mixed sediment types will shed more light on underlying mechanisms of resuspension-induced organic C mineralisation.

490 **4.2 Sediment heterogeneity as predictor of sediment C vulnerability?**

Our BRT model explained ~ 58 % of variability in RCO₂P forming a strong basis for using BRT models like ours to predict C storage vulnerability from spatial patterns of sediment characteristics. Sediment grain size and organic matter data often have high spatial resolution and thus represent useful surrogates to quantify large-scale sediment C vulnerability. Improving the performance of our BRT model to capture more of the currently unexplained variability (~40 %) can perhaps be achieved through integrating more nuanced features as discussed above (see section 4.1). Additionally, history or intensity of trawling can influence both the long-term concentration and reactivity of OM as well as how it is mediated through benthic faunal communities (Hale et al., 2017; Pusceddu et al., 2014; Tiano et al., 2022; Zhang et al., 2024). As a result, RCO₂P could be partly driven by the sampling site's trawling disturbance history. However, incorporating a measure of historical disturbance frequency may only improve assessments if the data on trawling activity is collected at the resolution necessary to link it to local sampling coordinates. Compared to first-order model estimations that rely on assumptions of degradation constants and organic C lability (Atwood et al., 2024; Luisetti et al., 2019; Muñoz et al., 2023; Sala et al., 2021), predictions from a BRT model approach are based on empirical measurements of sediment characteristics, resuspension-induced organic C mineralisation rates and the relationships and interactions that they form. This makes it a powerful tool that integrates environmental variability making predictions more realistic and detailed at the regional scale offering opportunities for 505 meaningful regulatory actions for trawling.

4.3 Methodological considerations of resuspension assay quantifications

510 The resuspension assay provides a simple measure of oxic organic C mineralisation in the top 3 cm of sediment, offering insight into the vulnerability of seafloor C storage. Porz et al. (2024) used a similar approach in their model, defining sediment organic C vulnerability in the top 10 cm as the maximum potential oxic organic C remineralization rate. Their modelled rates (0.1 – 100 mmol C m⁻² d⁻¹) align with our empirical RCO₂P measurements (2 – 88 mmol C m⁻² d⁻¹). Other experiments investigating the immediate impact of sediment resuspension reported mineralisation rates to be 1.1 – 4.7 times higher in resuspension treatments compared to controls (Almroth-Rosell et al., 2012a; Niemistö et al., 2018; Ståhlberg et al., 2006). This
515 is comparable but at the lower end of the range of our measurements where RCO₂P was 1.4–19.5 times higher in resuspended sediments. The difference may be attributable to a thicker sediment layer being resuspended in our assay (3 cm) compared to the other experiments (0.3 µm to 1 cm) and the different methodological approaches (e.g. in situ chamber vs. bottle incubations). Overall, the comparability of our measurements to both model and experimental studies supports the assay’s relevance for resuspension impact assessments.

520 Two methodological aspects of the assay need to be considered when linking the assay to trawling impacts and organic C mineralisation. Firstly, the assay determines potential CO₂ production after severe resuspension through shaking up sediment in a bottle and therefore may not reflect the true mechanical impact of individual trawling gear and trawling technique (O’Neill and Ivanović, 2016; Rijnsdorp et al., 2021). However, the high sampling frequency that is possible with the assay enhances
525 our spatial understanding of sediment C vulnerability and thus where trawling would be most impactful. Secondly, the assay converts sediment oxygen demand to CO₂ production using respiratory quotients (see section 2.2). This quantification may overestimate CO₂ production if reduced species are oxidised alongside organic C. We incubated the surface sediments from an oligotrophic system where oxygen and nitrate penetration depths (O₂: 3–6 mm, nitrate: 12 mm) and total-to-diffusive oxygen uptake ratios (TOU/DOU = 2.4) indicate strong macrofaunal influence on redox conditions and minimal accumulation of
530 reduced species in both sandy and muddy sediments (30–128 m depth; Cheung et al., 2024). This aligns with findings of low acid volatile sulfide concentrations (AVS) in non-impacted Hauraki Gulf sediments (0 – 1 µmol g⁻¹ ww) compared to higher AVS levels in sediments impacted by a mussel farm (2 – 12 µmol g⁻¹ ww, Wilson and Vopel, 2015). Future use of the resuspension assay, particularly in more reduced or eutrophic sediments, should include a validation of the SOD approach by measuring changes dissolved CO₂ or DIC during the incubations.

535 Our resuspension assay offers a simple and practical measure of oxic organic C mineralisation in the top 3 cm of sediment, providing insight into the vulnerability of seafloor C storage. Porz et al. (2024) presented a similar approach in their modelling study, defining sediment organic C vulnerability in the top 10 cm of the sediment as the maximum potential oxic organic C remineralization rate, based on three different degradation constants (k) for labile, semi-labile and refractory organic C. The
540 range of modelled remineralisation rates reported by the authors (0.1–100 mmol C m⁻² d⁻¹) is similar to our measurements (2

—88 mmol C m⁻² d⁻¹), supporting the assay's applicability for resuspension assessments. First-order kinetics imply that reactive organic carbon decomposes at a rate (k) directly proportional to its concentration (Middelburg, 1989). However, the non-linear relationship between RCO₂P and OM content in our data suggests that the conversion of organic C to CO₂ changes disproportionately along the OM gradient. The resuspension process likely alters the reactivity of the resuspended OM pool and how bacteria metabolize it (Arndt et al., 2013; LaRowe et al., 2020). Using different rate constants for different organic C labilities may partly account for that, but the minor influence of OM lability (OM:Phyto ratio) on RCO₂P in our sediments suggests that other physical, chemical and biological properties of the surrounding environment influence reactivity of resuspended organic matter. In this context, the importance of median sand content and OM depth interaction in explaining variability of RCO₂P suggest that other environmental factors play a role for the reactivity of sediment OM and thus RCO₂P. The spatial distribution of larger grain sizes and OM along depth gradient can be a result of physical forces such as the Gulf's circulation and tidal currents (Black et al., 2000; Manighetti and Carter, 1999; Zeldis et al., 2004). This may indicate that physical transport and deposition pathways of OM within the Hauraki Gulf are important factors for RCO₂P, though this hypothesis warrants further exploration. Broad classifications of degradation rate constants in models may overlook non-linear and interactive dynamics like the ones we found for the Hauraki Gulf. Our approach captured the sediment heterogeneity without relying on predefined categories, thus embracing variability in sediment characteristics as information, not noise. While our findings are specific to the Hauraki Gulf, they highlight the value of integrating continuous sediment heterogeneity data into regional trawling assessments for a real-world understanding of spatial patterns.

Our BRT model explained ~57 % of RCO₂P variability, a strong result given the variability of sediment characteristics in the dataset. However, a substantial portion of variability remains unexplained, suggesting that additional drivers may be at play. One possibility is the respiration of small macrofauna and meiofauna within the incubated surface sediment. While samples with visibly large macrofauna were excluded, the presence of smaller macrofauna and meiofauna was observed by small worm burrows. These benthic species may alter their respiration in response to resuspension stress, potentially influencing RCO₂P depending on their abundance and biomass. Such animal effects would also influence CO₂ production when the animals are disturbed by trawls or dredges. Including faunal abundance or biomass data could help clarify these effects in a diverse system would add substantially to the analytical time and likely restrict replication across a sampling region. Another factor influencing RCO₂P is the history of trawling disturbance, which can influence both the concentration and reactivity of OM as well as how it is mediated through benthic faunal communities (Hale et al., 2017; Pusceddu et al., 2014; Tiano et al., 2022; Zhang et al., 2024). Incorporating a measure of historical disturbance frequency could improve assessments of RCO₂P vulnerability if the data on trawling activity is collected at the level of precision necessary to link it to our sampling sites. Overall, our results clearly demonstrate that integrating sediment heterogeneity in resuspension assessments advances our spatial understanding of potential trawling impacts.

4.4 Seafloor protection based on C vulnerability

575 As our understanding of sediment C storage vulnerability grows, its integration into spatial management of demersal fisheries becomes inevitable. In the Hauraki Gulf, recent discussions on confining trawling pressures focused on protecting reef-forming species and habitats (Bennion et al., 2024), while sediment C storage vulnerability was not considered. Trawling remains allowed in areas deeper than 50 m (Newsroom, 2025), which, based on our results, includes nearly all sediments at high to very high risk of CO₂ release when disturbed. This leaves Hauraki Gulf sediments at risk to lose their climate-stabilizing C

580 storage function and will contribute to the green-house gas emission of the NZ fisheries industry. By integrating sediment heterogeneity and the resulting spatial variability of resuspension impacts, highly vulnerable areas can be identified and protected. In a recent modelling study, Porz et al. (2024) compared different seafloor protection scenarios in the North Sea and found that protection based on C vulnerability was most efficient for preserving organic carbon and maintaining benthic macrofauna biomass. This highlights that seafloor carbon protection generates benefits not only for organic C storage, but also

585 for benthic species and habitats ultimately maintaining the undisturbed functioning of seafloor ecosystems. Recent discussions around confining trawling pressures focused on reducing the impact on benthic habitats and reef forming benthic species (Bennion et al., 2024; Smith et al., 2023). As our understanding of the vulnerability of sediment C storage to demersal fishing grows, it underlines the need to integrate it into the spatial management of the demersal fishery. Porz et al. (2024) identified a model scenario of seafloor carbon protection to be the most efficient in sediment organic carbon

590 preservation and maintaining benthic macrofauna biomass for the highly impacted North Sea. It highlights that integrating seafloor carbon protection into spatial planning benefits sediment organic C sequestration and storage as a key climate function, reducing the CO₂ footprint of demersal fishing practices and protecting benthic species and habitats. Considerations of sediment carbon vulnerability are lacking in recent suggestions for ‘trawling corridors’ in the Hauraki Gulf (Fisheries New Zealand, 2023). We hope our empirical assessment of C storage vulnerability using the resuspension assay will provide relevant

595 information to be included in the spatial management of demersal fishing in the Hauraki Gulf.

5 Conclusion

The risk of CO₂ release from the sediment as a consequence of resuspension is not something we can ignore as we seek to limit emissions and meet climate obligations. Our findings show that the variability of resuspension-induced CO₂ release is linked to sediment characteristics resulting in local environmental conditions controlling resuspension impacts. Using

600 measures of sediment heterogeneity and the resuspension assay offers localised insight into where carbon storage is most vulnerable to disturbance, and where management efforts could be focused. Our results support the inclusion of seafloor carbon protection in regional planning, particularly in areas like the Hauraki Gulf where sediment heterogeneity and fishing pressure intersect. Moving forward, combining our empirical assessment with more nuanced data on organic matter quality, physical and biological organic matter inputs, and disturbance history will enhance our ability to estimate human impacts on the seafloor

605 and sustain natural C sinks that contribute to global climate stabilisation.

610 The risk of CO₂ release from the sediment as a consequence of resuspension is not something we can ignore as we seek to limit emissions and meet climate obligations. Our findings underscore the importance of accounting for sediment heterogeneity when assessing the vulnerability of seafloor carbon storage to anthropogenic disturbance. The resuspension assay provided a robust empirical measure of oxic organic carbon mineralisation in resuspended sediments, revealing that organic matter content, water depth, and sediment grain size interact and drive variability in resuspension-induced CO₂ production. These interactions highlight that sediment characteristics cannot be considered in isolation, and that context dependent relationships are key to understanding carbon loss from marine sediments. The identification of sediment types and areas in the Hauraki Gulf with high RCO₂P rates offers localised insight into where carbon storage is most at risk, and where management efforts could be focused.

615 By embracing sediment heterogeneity, our approach complements model based assessments and provides a pathway for refining regional scale predictions of carbon disturbance. As global efforts to reduce the carbon footprint of demersal fishing intensify, integrating sediment carbon vulnerability into spatial fisheries management becomes increasingly critical. Our results support the inclusion of seafloor carbon protection in regional planning, particularly in areas like the Hauraki Gulf where sediment heterogeneity and fishing pressure intersect. Moving forward, combining empirical assessments with improved data on faunal activity, organic matter reactivity, and disturbance history will enhance our ability to sustain natural C sinks in sediments and contribute to climate mitigation strategies.

Data and code availability

625 Data and software code will be published upon acceptance of the manuscript but are made available to the reviewers of this manuscript.

Author contributions

SF and IB developed the resuspension assay and planned the campaign; IB conducted the sampling campaign, performed the measurements and analysed the data; IB wrote the manuscript draft; SF reviewed and edited the manuscript.

Competing Interests

630 The authors declare that they have no conflict of interest.

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