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1 **Acute impacts of bottom trawl gears on benthic metabolism and** 2 **nutrient cycling**

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12

13 **Abstract**

14 Research on the environmental impacts of bottom fishing gears has focused mainly on benthic fauna
15 and the physical characteristics of the seafloor. This study assesses the benthic biogeochemical
16 consequences associated with tickler chain beam trawl and electric PulseWing trawl gears. In June
17 2017, professional fishermen trawled experimental transects with both types of gears in the Frisian
18 Front area of the North Sea. Box core sediment samples and *in-situ* landers were used to evaluate
19 biogeochemical fluxes and sediment characteristics in untrawled and trawled areas (samples taken 3.5
20 – 70 h after fishing). A reduction of sedimentary chlorophyll *a* was observed, which was larger
21 following tickler chain (83%) compared to PulseWing trawling (43%). This displacement of surface
22 material caused significant decreases in the sediment oxygen consumption in tickler chain (41%) and
23 PulseWing trawled samples (33%) along with a deeper penetration of oxygen in the sediment (tickler
24 chain: 3.78 mm, PulseWing: 3.17 mm) compared to untrawled areas (2.27 mm). Our research implies

25 that bottom trawl disturbance can lead to immediate declines in benthic community metabolism with
26 tickler chain trawling exhibiting greater and less variable alterations than PulseWing trawling on
27 benthic biogeochemical processes.

28

29 **Keywords:** biogeochemistry, ecosystem functioning, oxygen dynamics, nutrients, beam trawling,
30 pulse trawling, organic carbon, Frisian Front

31

32 **Introduction**

33 Concerns over the ecological impacts of bottom trawl fishing have dated back since its inception in
34 the 14th century (Collins, 1887). This form of fishing has since gained widespread use and we find
35 ourselves asking the same questions about its environmental effects as during its commencement.
36 Current worldwide criticism of bottom trawling and the introduction of the experimental method of
37 “electric pulse fishing” in the North Sea once again brings this topic to the limelight. While we have
38 knowledge of the mechanical (Depestele *et al.*, 2016; Eigaard *et al.*, 2016; O’Neil and Ivanovic, 2016)
39 and ecological (Bergman and van Santbrink, 2000; Kaiser *et al.*, 2006; Hiddink *et al.*, 2017; Sciberras
40 *et al.*, 2018) impacts of bottom trawling on the marine ecosystems, only limited information is
41 available on its effects on benthic biogeochemistry (Kaiser *et al.*, 2002). Furthermore, no research has
42 been conducted on the potential side-effects of electric pulse trawling on geochemical fluxes or
43 benthic ecosystem functioning (Soetaert *et al.*, 2015).

44 Traditional beam trawls are rigged with tickler chains or chain matrices and scrape the seabed in order
45 to mechanically stimulate and catch flatfish. This can lead to a direct release of nutrients from the
46 sediments which can enhance primary production in the water column (Duplisea *et al.*, 2001; Dounas
47 *et al.*, 2006; Dounas *et al.*, 2007; Couceiro *et al.*, 2013) and may also release contaminated material if
48 present (Bradshaw *et al.*, 2012). Benthic trawling has been linked to reduced oxygen concentrations in
49 the water column (Riemann and Hoffman, 1991), the homogenisation of benthic nutrient profiles (van

50 de Velde *et al.*, 2018) and alterations of the sediment redox layer (Depestele *et al.*, 2018). The
51 potential for towed gears to remove and kill benthic fauna (Bergman and Hup, 1992; Bergman and
52 van Santbrink, 2000) can indirectly alter habitat dynamics with the loss of important bioturbators
53 and/or ecosystem engineers (Duplisea *et al.*, 2001; Olsgard *et al.*, 2008). Bottom trawling, dredging or
54 other types of human disturbance has been linked to both the fining (Trimmer *et al.*, 2005; De Backer
55 *et al.*, 2014) and coarsening of the bottom material (Palanques *et al.*, 2014; Depestele *et al.*, 2018),
56 both of which can induce changes to the whole benthic community (De Backer *et al.*, 2014).

57 The controversial introduction of pulse trawling changed the behaviour and activity of fisherman in
58 the North Sea (Sys *et al.*, 2016). With this method, tickler chains are being replaced by electrodes to
59 electrically stimulate flatfish out of the sediment. Reduced fuel consumption (up to 50%) from lower
60 towing speeds/decreased drag through the seafloor (van Marlen *et al.*, 2014), reductions and increased
61 survivorship of discards (van Marlen *et al.*, 2014; Batsleer *et al.*, 2016; Reijden *et al.*, 2017) provided
62 evidence for pulse fishing as an environmentally friendly alternative to traditional tickler chain beam
63 trawling. Its popularity amongst the Dutch fishing fleet (Haasnoot *et al.*, 2016), however, was met
64 with international criticism due to increased competition between fishermen (Sys *et al.*, 2016) and
65 ecological concerns over animal welfare (de Haan *et al.*, 2016; Soetaert *et al.*, 2016a; Soetaert *et al.*,
66 2016b).

67 Compared to traditional tickler chain trawl gears, pulse trawls show reduced alterations to seabed
68 bathymetry (Depestele *et al.*, 2016; Depestele *et al.*, 2018). It may be speculated that the reduced
69 mechanical disturbance will also lead to a lower impact on benthic biogeochemistry. Nonetheless,
70 concrete knowledge about the potentially negative side-effects of pulse trawling on characteristics
71 such as sediment community metabolism and benthic pelagic coupling is lacking. Further research in
72 these areas is therefore needed to fully understand the environmental effects of different bottom trawl
73 gears.

74 Our research investigates the impact of both conventional (tickler chain) beam trawl and electric
75 PulseWing trawl gears on benthic biogeochemistry. Along with the mechanical effects from
76 PulseWing and tickler chain trawling, Depestele *et al.* (2018) explored changes in biogeochemical

77 redox conditions associated with the two methods. Here we build upon this knowledge and present the
78 first study with pulse trawling focusing on benthic metabolism and nutrient cycles. We originally
79 aimed for a full BACI (Before-After-Control-Impact) design to allow the comparison of trawled
80 experimental areas and an untrawled reference area before and after the tickler chain and PulseWing
81 fishing disturbances. Due to unforeseen logistic constraints and a severe summer storm which took
82 place at the end of the campaign, a balanced design using all experimental equipment (i.e. *in-situ*
83 mooring/landers, box cores) could not be achieved. Our untrawled “control” samples, therefore, come
84 from the experimental trawl areas before the fishing disturbance (T0) as well as one sampling period
85 in an adjacent reference area.

86

87 **Materials and Methods**

88 **Study site**

89 Experimental fishing and sampling were carried out within a one kilometre radius of 53.6816° N and
90 4.4565° E at a water depth of 34 m in the area of the North Sea known as the Frisian Front (Figure 1).
91 This area provided a promising location for our study due in part to its high productivity and
92 homogeneity. The Frisian Front is a transitional zone between coarser sandy sediments in the
93 Southern Bight to the south and the siltier Oyster Grounds to the north. It exhibits fine muddy sand
94 with an organic carbon percentage between 0.28-1.0 (Upton *et al.*, 1993; Gehlen *et al.*, 1995; Lohse *et al.*
95 *et al.*, 1995; Slomp *et al.*, 1997; Boon and Duineveld, 1998). These sediments are subject to faunal
96 induced mixing with the presence of burrowing organisms such as *Callianassa subterranea* and
97 *Upogebia deltaura* (Rowden *et al.*, 1998; Dewicke *et al.*, 2002). Previous research has shown that the
98 area is biologically diverse and relatively high in benthic biomass (Dauwe *et al.*, 1998; Dewicke *et al.*,
99 2002; Duineveld and Boon, 2002), biological activity (Duineveld *et al.*, 1990; Duineveld *et al.*, 1991),
100 and chlorophyll *a* (Chl *a*) influx to the sediments (Boon *et al.*, 1998) compared with adjacent North
101 Sea habitats. Moreover, areas with these characteristics (muddy sediment/high biomass) are known to
102 be more vulnerable to trawling activity than sandy dynamic habitats (Duplisea *et al.*, 2001; Kaiser *et*

103 *al.*, 2006; Queirós *et al.*, 2006, Allen and Clarke, 2007; Sciberras *et al.*, 2016). These environmental
104 conditions paired with the extensive historical data on the site made the Frisian Front an ideal location
105 to measure the impact of bottom trawl fishing. Vessel monitoring system (VMS) data was used to
106 estimate the likelihood of bottom trawl disturbance within one year prior to the study using the
107 method shown in van Denderen *et al.*, (2014).

108 **Experimental design**

109 To experimentally determine the biogeochemical impact of tickler chain and PulseWing trawl gears,
110 commercial trawlers were instructed to fish specified areas in the Frisian Front. Information was
111 collected before and after fishing and at a nearby reference location (Figures 1 and 2). Intact sediment
112 samples were brought on-board to obtain information on Chl *a*, particle size analysis, organic
113 carbon/nitrogen, oxygen microprofiles, porewater nutrients and oxygen/nutrient fluxes while *in-situ*
114 data for benthic fluxes and water column parameters was also obtained. We looked at short term
115 effects (<24 hr) and longer-term effects >24 hr in the case of the tickler chain trawler. A summer
116 storm took place during the afternoon of 6 June, which modified the surface sediment due to storm-
117 induced sediment resuspension and mixing. Hence, we decided to discard all samples taken after the
118 storm event (Figure 2).

119 Two rectangular 80 m by 1000 m treatment areas were specified for experimental fishing by either
120 beam trawl (“tickler”) or pulse trawl (“pulse”) gears. A non-fished reference area was chosen south of
121 the treatment areas (Figure 1). The areas were spaced 400 m apart and aligned parallel but not directly
122 adjacent to each other in order to minimize interference from resuspended sediment caused from the
123 experimental trawling (Figure 1). To ensure full “coverage” of the seafloor being fished in the
124 treatment areas, both vessels conducted 7 trawl passes in parallel yet slightly overlapping trajectories
125 over the treatment areas. Given the widths and the space between the trawl gears, this led to a fishing
126 intensity of 150 to 200% within the middle portion of the treatment areas (modelled after the
127 procedures conducted in Bergman and van Santbrink, 2000 and Depestele *et al.*, 2016).

128 *Experimental fishing*

129 On the 1st of June 2017 (8h30 – 10h) the tickler treatment was carried out by the HD 29 commercial
130 vessel which towed its gear at ~ 6 knots. Conventional 12 m wide beam trawl gears (a shoe located at
131 both ends of the beam) were towed at both sides of the ship, each rigged with 8 tickler chains and 10
132 net ticklers. Following the experimental fishing, a side-scan sonar was used to observe changes in
133 bathymetry caused from tickler chain trawling.

134 The pulse treatment was carried out by the UK 227 commercial vessel on the 6th of June 2017 (7h30 –
135 10h). This vessel trawled at a speed of ~ 5 knots and towed a 12 m wide “HFK PulseWing” at either
136 side of the boat. With the PulseWing, the traditional beam is replaced with an aero foil shaped ‘wing’
137 without shoes at the ends but with one “nose” located in the middle of the front section of the gear.
138 The wing creates lift as it is towed through the water similar to an aeroplane wing. It is designed to
139 skim above the seabed with a standard beam trawl net behind it. To stimulate the flatfish from the
140 seabed the tickler chains are replaced by electrodes which use a pulsed bi-polar current. This type of
141 alternating current is used to minimize the effects of electrolysis which would cause corrosion of the
142 electrodes (H.K. Woolthuis, designer of HFK PulseWing, pers. comm). Each pulse wing gear was
143 rigged with 28 electrodes lined up parallel to the fishing direction (0.42 m apart) and worked with a
144 voltage of 50 V at the electrodes at 80 pulses per second. More details on the fishing gears and
145 electric parameters used, can be found in van Marlen *et al.*, (2014) and de Haan *et al.*, (2016).

146 **Data collection**

147 *Water column plume dynamics*

148 To investigate the effect of PulseWing trawling on the water column characteristics, a mooring was
149 deployed (4 to 8 June 2018) 100 m north of the experimental area. The location of the mooring was
150 chosen based on the predicted direction of the current during the experimental fishing operation. The
151 mooring was equipped with an Aanderaa SeaGuard recorder, suspended at 3.5 m above the sediment
152 (29 m depth) which featured a turbidity sensor which measured suspended particulate matter (SPM),
153 an oxygen optode and doppler current sensor. The logistic and time constraints mentioned earlier did
154 not allow for the planned deployment of this mooring during tickler chain trawling.

155 *Box core sampling*

156 All sampling equipment was deployed from the R.V. *Pelagia*. A cylindrical NIOZ box corer with an
157 internal diameter of 30 cm and a height of 55 cm, collected intact sediment samples up to 40 cm deep
158 into the seafloor. Tickler samples were taken one hour before fishing (T0, 2 box cores, 4 incubations)
159 and 6 h (T1, 2 box cores, 4 incubations), 30 h (tickler T2; 2 box cores/incubations) and 75 h (tickler
160 T3; 3 box cores/incubations) after trawl disturbance (Figure 2). In the pulse treatment area, samples
161 were taken 3 days before trawling (T0, 3 box cores/incubations) and 3.5 hours after trawling (T1, 4
162 box cores, 7 incubations). For the “control” variable used to compare with trawled conditions, the T0
163 samples from tickler and pulse areas were combined with additional data (2 box cores/incubations)
164 taken from the reference area on 3 June 2017.

165 *Dry sediment parameters and chlorophyll a*

166 All sediment samples were freeze dried and sieved (1 mm) prior to analysis. Laser diffraction was
167 used to measure particle size analysis (PSA) parameters with a Malvern Mastersizer 2000 (McCave *et al.*,
168 1986). Organic carbon (OC), was measured by removing carbonate from the total carbon (TC)
169 concentration (with 0.1N HCl) and calculating the difference (Nieuwenhuize *et al.*, 1994). TC, OC
170 and total nitrogen (TN) content were determined using an Interscience Flash 2000 organic element
171 analyser. Samples for chl *a* analysis were collected from the top 1 cm of sediment from each box core
172 and were immediately placed in a -80 °C freezer for storage. Sediment phytopigments were extracted
173 with acetone and measured using HPLC methods (Zapata *et al.*, 2000). Subsamples for
174 carbon/nitrogen (C/N) and PSA were taken with 3.5 cm diameter sediment cores and were sliced at
175 2.5 cm intervals down to 12.5 cm.

176 *On-board measurements: Benthic profiles and fluxes*

177 From the box cores, “incubation” sediment cores (14 cm diameter) with overlying water were
178 subsampled for oxygen microprofiling and subsequent oxygen consumption/nutrient flux incubations
179 (hereafter referred to as “on-board incubations” to distinguish between *in-situ* lander incubations).
180 During the on-board incubations, overlying water in the cores was continually mixed with a central

181 stirring mechanism which ensured homogenous concentrations of nutrients and O₂ but without
182 resuspending the sediment. All incubations were run in a climate-controlled chamber which
183 maintained a constant temperature of 12°C representative of the bottom water.

184 Clark-type O₂ micro-electrodes (100 µm tip size, Unisense) were used to make oxygen-depth profiles
185 in the cores immediately after collection (Revsbech, 1989). In each incubation core, 3 replicate
186 profiles were taken from different areas of the sediment. For each profile, readings were taken at 100-
187 µm intervals, starting approximately 10000 µm (10 mm) above the sediment water interface (100%
188 O₂ saturation) to the depth in the sediment at which all oxygen was depleted (i.e. the oxygen
189 penetration depth [OPD]). A two point calibration was conducted prior to measurements using 100%
190 and 0% oxygen saturated seawater to represent water column and anoxic O₂ concentrations
191 respectively.

192 The incubation cores used for oxygen profiling were subsequently placed in a 12°C water bath and
193 sealed for up to 12 h in order to obtain sediment community oxygen consumption (SCOC) estimations
194 in the dark. The oxygen concentration during the incubation period was measured with optode sensors
195 (FireStingO2, Pyroscience) using a measurement interval of 30 seconds. The cores were opened, re-
196 aerated and kept for an additional 24-36 h to take samples for nutrient flux measurements.

197 Ammonium (NH₄⁺), nitrogen oxides (NO_x), phosphate (PO₄³⁻) and silicate (SiO₂) fluxes (mmol m⁻²d⁻¹)
198 were determined by fitting a linear regression over the concentration change in the overlying water
199 over time and multiplying the regression coefficient with the height of the water column. For this
200 regression, water samples were taken at 0, 8, 16, 22, 36, and 48 hours after the start of the incubation
201 with a syringe and filtered (0.45 µm) into a 10 mL polystyrene vial for nutrient analysis (NH₄⁺, NO_x,
202 PO₄³⁻ and SiO₂) and stored frozen (-20°C). Upon thawing, samples were analysed by a SEAL
203 QuAAtro segmented flow analyser (Jodo *et al.*, 1992; Aminot *et al.*, 2009). If the fitted regression was
204 not statistically significant (Pearson correlation, $p > 0.05$), it was interpreted as a zero flux.

205 Box cores were further subsampled for porewater nutrients using 10 cm diameter sub-cores with
206 vertical sampling ports. These were used in combination with rhizon samplers (Rhizosphere Research
207 Products) to collect water samples at 0, 1, 2, 3, 5, 7, and 10 cm depth (Seeberg-Elverfeldt *et al.*, 2005;

208 Dickens *et al.*, 2007; Shotbolt, 2010). Porewater nutrients were stored and analysed using the same
209 methods as the incubation water samples.

210 *In-situ SCOC and nutrient fluxes*

211 Two ALBEX landers (Autonomous Landers for Biological Experiments) Duineveld *et al.*, 2004;
212 Witbaard *et al.*, 2000) were used to obtain *in-situ* rates of oxygen and nutrient fluxes from the
213 sediment. The landers were deployed in tickler (1 June 2017) and pulse (6 June 2017) trawled areas
214 within 3 h after fishing concluded. The exact position inside the tickler trawled area was verified by
215 using a side scan sonar (Kongsberg PULSAR) which was used in conjunction with the Kongsberg
216 EM302m MBES (Multibeam Echosounder) mounted on the RV Pelagia (Figure 3). To gather
217 information from an untrawled location, the landers were positioned inside the pulse treatment area on
218 4 June 2017 before fishing as the control deployment.

219 Each lander held 3 measurement chambers enclosing a surface area of 144 cm². For deployment, the
220 landers were carefully lowered on a cable until they reached the seafloor. After descent, each
221 measurement chamber was autonomously driven into the sediment by a hydraulic mechanism. The *in-*
222 *situ* incubations lasted 5 h and began shortly after deployment.

223 The decrease in oxygen concentration in the headspace of each chamber was measured every 30
224 seconds using JFE-ALEC rinko optodes. Water in the chamber was stirred with a magnetic stirrer
225 mounted to the lid. At pre-set time intervals, a 30 ml water sample was taken from the headspace of
226 each chamber. At the first (and last) sampling moment, a simultaneous sample from the outside water
227 was taken. In this way a sequence of water samples were taken. Upon retrieval, water samples were
228 immediately frozen and analysed similar to the other nutrient samples. At the end of the incubation, a
229 sliding lid closed the underside of the measurement chamber and the entire sample including the
230 incubated sediment was brought back on board with the lander.

231 **Data analysis and statistics**

232 Shapiro-Wilk and Levene's tests were conducted to determine if data was normally distributed and/or
233 displayed homogeneity of variances. If assumptions for parametric testing were violated, data was

234 normalised using a log-transformation. Differences in depth, biogeochemical parameters (benthic O₂
235 and nutrient fluxes, OPD, Chl *a*, porewater nutrients, OC, TN), and sediment characteristics (% silt, %
236 fine sand, D50, D10) between T0 samples from the tickler chain, PulseWing and reference areas (i.e.
237 untrawled areas) were tested for by applying a one-way analysis of variance (ANOVA). A one-way
238 ANOVA was used to investigate significant differences in biogeochemical and sediment parameters
239 between tickler T1, tickler T2, tickler T3, pulse T1 and untrawled samples. If significant differences
240 were detected by the ANOVA, a Tukey HSD post hoc test was applied to perform pairwise
241 comparisons between specific treatments. To quantify the relationship between water column oxygen
242 and SPM concentrations, a linear regression was performed. All statistical analyses were performed
243 using R (R Core Team, 2013).

244

245 **Results**

246 **Study site characteristics**

247 Data from the echosounder showed no significant differences in depth between sample locations in
248 tickler, pulse, or reference areas (ANOVA, $p > 0.05$). Additionally, untrawled sediment from tickler
249 T0, pulse T0 and reference box core samples did not show significant differences between O₂/nutrient
250 fluxes, porewater nutrients, chl *a*, OC, TN, measurements or grain size characteristics (ANOVA, $p >$
251 0.05). Therefore, for the rest of the analyses, data from the T0 (pulse and tickler) and reference
252 samples were pooled to act as the control treatment representing the untrawled situation. Estimates of
253 trawl disturbance using VMS data suggested that in the year leading up to the study, the fishing effort
254 within the treatment areas was minimal with little to no beam trawling occurring, however, the
255 analysis also suggested a possibility (0.25 – 1.25 h fished) of pulse trawling conducted in part of the
256 reference area.

257 Our personal observations confirmed that both tickler chain and PulseWing commercial trawlers
258 made 7 trawl passes through the designated treatment areas. The effect of tickler chain trawling was
259 also verified by using side-scan sonar, which showed the mechanically disturbed seabed across the

260 planned treatment area (Figure 3). Furthermore, the sonar images revealed that the benthic landers
261 were placed inside the disturbed area (Figure 3). Unfavourable weather conditions prevented us from
262 using the side scan sonar following PulseWing trawling. As a result, we relied on the visual tracking
263 of the pulse trawler using its AIS (Automatic Identification System) from the RV Pelagia.

264 **Effect of the PulseWing on sediment plume dynamics**

265 The turbidity sensor on the mooring logged a notable increase in the suspended particulate matter
266 (SPM) concentration, including distinct peaks with each passage of the PulseWing trawl (Figure 4).
267 SPM concentrations ranged from 4.0 to 23.2 mg L⁻¹ and increased rapidly whenever the pulse trawler
268 passed through its designated treatment area. The peaks in SPM coincided with dips in the dissolved
269 oxygen concentration (Figure 4a). Linear regression analysis showed that 73% of the variation in
270 oxygen concentration was accounted for by the variations in turbidity during experimental pulse
271 fishing demonstrating an inverse relationship ($p < 0.001$; Figure 4b). Data from the SeaGuard showed
272 that at the time of trawling, the current was northward and in the direction of the mooring and with a
273 current velocity between 3 and 15 cm/s.

274 **Fishing effects on sediment characteristics**

275 *Physical sediment parameters*

276 Box core sediment samples collected after beam trawling (tickler T1, tickler T2) exhibited a fluffy
277 layer of fine sand at the surface which was not present in control samples. Tickler samples also
278 appeared visibly “flatter” in topography, while control samples displayed superficial sand ripples.
279 These characteristics (finer sediment layer/flat topography) were present in some but not all sediment
280 samples taken after pulse trawling (pulse T1).

281 Deeper sediment layers (2.5 – 12.5 cm) did not exhibit any significant differences for physical
282 sediment characteristics between treatments or surface sediment (ANOVA, $p > 0.05$). The following,
283 therefore only documents the changes found in the upper sediment layers (0 – 2.5 cm). Table 1 shows
284 results from the grain size measurements in control, tickler chain, and PulseWing trawled box core
285 samples. Smaller mean silt (<63 μm) fractions were found for tickler T1 and tickler T2 compared to

286 control and pulse T1 and tickler T3 samples (Table 1). This was significant for tickler T2 versus
287 control (HSD, $p < 0.001$), pulse T1 (HSD, $p < 0.01$), and tickler T3 (HSD, $p < 0.001$) sediments. Fine
288 sand (62.5-125 μm) fractions in tickler T2 were significantly higher than control (HSD, $p < 0.05$),
289 pulse T1 (HSD, $p < 0.05$), and tickler T3 (HSD, $p < 0.05$) samples while fine sand fractions in tickler
290 T1 were significantly higher compared to only the pulse T1 sediments (HSD, $p < 0.05$). For D10
291 values (10% of the sample particles are smaller than this value), tickler T1 and tickler T2 were
292 significantly higher than control (HSD, $p < 0.05$, $p < 0.0001$), pulse T1 (HSD, $p < 0.001$, $p < 0.0001$),
293 and tickler T3 (HSD, $p < 0.001$, $p < 0.0001$) samples showing coarsening after beam trawl fishing
294 (tickler T1/T2), followed by the reestablishment of ambient sediment characteristics (tickler T3). For
295 all grain size measurements, control, tickler T3 and pulse T1 samples displayed similar values which
296 were not statistically different from each other (ANOVA, $p > 0.05$; Table 1).

297 Table 2 documents organic carbon and total nitrogen in surface sediments (0 – 2.5 cm). OC and TN
298 displayed similar patterns to the silt content. Average organic carbon in surface sediments was highest
299 in pulse T1 samples but was only significantly higher than tickler T2 (HSD, $p < 0.05$; Table 2). Total
300 nitrogen content in these sediments was significantly lower in tickler T2 samples compared with
301 control (HSD, $p < 0.05$) and pulse T1 (HSD, $p < 0.01$) values (Table 2).

302 *Chlorophyll-a in surface sediments*

303 Figure 5 illustrates the relationship between average levels of surface chlorophyll *a* amongst control,
304 tickler T1 and pulse T1 treatments. Control samples had an average chl *a* concentration of 3.01 ± 0.68
305 $\mu\text{g chl } a \text{ g}^{-1}$, while fished samples decreased to $0.51 \pm 0.17 \mu\text{g chl } a \text{ g}^{-1}$ for tickler T1 and 1.76 ± 0.91
306 $\mu\text{g chl } a \text{ g}^{-1}$ for pulse T1. The acute impact from both fishing methods caused a significant decrease in
307 surface chl *a* compared with the control areas, however, the effect of the tickler chain trawl (tickler
308 T1; HSD, $p < 0.0001$) was more pronounced and less variable than the effects of the PulseWing trawl
309 (pulse T1; HSD, $p < 0.05$; Figure 5). Surface chl *a* in tickler T2 samples remained significantly lower
310 than in control samples ($0.71 \pm 0.29 \mu\text{g chl } a \text{ g}^{-1}$, HSD, $p < 0.001$). Compared to tickler T2, tickler T3
311 samples showed an increase (though not significantly different than T1 or T2) in chl *a* at 1.50 ± 0.61
312 $\mu\text{g chl } a \text{ g}^{-1}$, though this was still significantly lower than control samples (HSD, $p < 0.05$).

313 Fishing effects on oxygen and nutrients

314 Porewater NH_4^+ profiles in control samples exhibited a depth gradient with $<15 \mu\text{mol}$ at the surface
315 that steadily increased down to $40 \mu\text{mol}$ at 10 cm depth (Figure 6). Following tickler and pulse
316 trawling, average NH_4^+ concentrations in the upper 3 cm of the box cores were significantly elevated
317 for tickler T1 (HSD, $p < 0.01$) and pulse T1 (HSD, $p < 0.05$) treatments compared with control
318 samples (Table 3). Tickler T1 samples in particular, had a more homogenous depth profile of NH_4^+
319 compared with the control samples (Figure 6a). NH_4^+ found in the top 3 cm of the tickler T2 samples
320 remained higher than the control sediments, albeit not significantly (Table 3). Control samples in the
321 upper 3 cm exhibited the highest average concentrations of porewater NO_x and SiO_2 as well as the
322 lowest values for PO_4^{3-} compared to trawled (tickler T1, tickler T2, pulse T1) samples, though the
323 differences were not statistically significant (Table 3). Deeper (5 – 10 cm) sediment layers showed no
324 significant patterns between porewater nutrients in control, tickler or pulse samples (ANOVA, $p >$
325 0.05). No porewater samples were collected for Tickler T3.

326 The average oxygen penetration depth after tickler chain trawling (tickler T1) was $3776 \pm 731 \mu\text{m}$. In
327 comparison, pulse T1 cores had an oxygen penetration depth of $3166 \pm 1808 \mu\text{m}$. These were both
328 deeper than the OPD's found in the control cores which measured $2250 \pm 565 \mu\text{m}$ though the
329 difference was only significant between the control and tickler T1 treatments (HSD, $p < 0.001$; Figure
330 7). Accurate OPD measurements for tickler T2 could not be obtained, because of variability created
331 from macrofaunal burrows near the sediment water interface. However, the OPD in tickler T3
332 samples were not significantly deeper than control profiles ($2972 \mu\text{m} \pm 935$; HSD, $p < 0.05$).

333 Table 4 shows the average O_2 and nutrient flux values between on-board and *in-situ* incubations (note:
334 O_2 "fluxes" in the table are denoted as negative to be consistent with the nutrient flux data, while in-
335 text O_2 "consumption" data are positive by definition). Sediment community oxygen consumption
336 (SCOC) was significantly higher in the control incubations compared to both tickler T1 (HSD, $p <$
337 0.001) and pulse T1 (HSD, $p < 0.05$) treatments (Table 4, Figure 8). SCOC in tickler T2 and T3
338 samples remained significantly lower than the control (HSD, $p < 0.05$) measurements (Table 4). *In-*

339 *situ* oxygen consumption measured by the ALBEX landers was lowest after tickler chain trawling,
340 and highest after PulseWing trawling though the differences were not significant (Figure 8b, Table 4).
341 Nutrient fluxes from the on-board incubation cores showed no significant differences between fished
342 or control treatments (ANOVA, $p > 0.05$, Table 4). Phosphate fluxes from on-board incubations were
343 close to zero with the highest flux coming from Pulse T1 samples ($0.002 \pm 0.02 \text{ mmol m}^2 \text{ d}^{-1}$) and the
344 lowest showing an influx from the control sediments ($-0.003 \pm 0.02 \text{ mmol m}^2 \text{ d}^{-1}$). NH_4^+ fluxes ranged
345 from $0.35 \pm 0.41 \text{ mmol m}^2 \text{ d}^{-1}$ at tickler T1 to $0.10 \pm 0.25 \text{ mmol m}^2 \text{ d}^{-1}$ in tickler T2 samples.

346 *In-situ* incubations yielded lower NO_x fluxes after tickler chain and PulseWing trawling compared to
347 the control deployment which was statistically significant for the tickler treatment (HSD, $p < 0.05$).
348 No other significant differences were found in nutrient fluxes between control, tickler or pulse lander
349 deployments, however, *in-situ* estimates for PO_4^{3-} and SiO_2 fluxes were markedly higher than in the
350 on-board incubations (Table 4). It is noted that data from only one of the landers could be used after
351 PulseWing trawling. Storm induced water currents created a build-up of sediment which partially
352 buried the incubation chambers of one of the landers (which was evidenced upon retrieval) and
353 seemed to create irregular measurements. Data was, therefore, used only from the lander which
354 showed a range of flux data comparable to historical information from the Frisian Front.

355

356 Discussion

357 In this study we compared the effects of conventional tickler chain trawling and electric pulse fishing
358 on benthic biogeochemical functioning and water column processes in the Frisian Front, an area
359 located 50 km off the Dutch Coast characterised by fine sandy sediments. Despite unfortunate
360 methodological constraints, we were able to effectively capture and assess the acute effects of bottom
361 trawl activity on the biogeochemical functioning of North Sea sediments. In particular, our results
362 show that trawling resulted in clear differences between chl *a* (labile organic material), and oxygen
363 dynamics in trawled and untrawled sediments. Here, we discuss the effect of bottom fishing on water

364 column properties, followed by sedimentary organic and inorganic solid particles, to end with the
365 impact on benthic oxygen and nutrient dynamics.

366 **Effects in the water column**

367 The mooring, deployed during PulseWing trawling, showed increased turbidity after each pass of the
368 fishing vessel (Figure 4), indicating resuspension of sediments to the overlying water. This data
369 supports the findings of Depestele *et al.*, (2016) who recorded sediment resuspension from both
370 tickler chain and pulse trawled gears. Concurrent with the increased turbidity, we observed prominent
371 drops in water column oxygen concentrations (Figure 4a). A similar decrease in water column O₂ was
372 documented by Riemann and Hoffman, (1991) after mussel dredging in the Limfjord. The release of
373 low oxygenated porewater and reoxidation of reduced substances resuspended from the sediment may
374 be the primary cause for the increased water column O₂ uptake (Almroth *et al.*, 2009; Almroth-Rosell
375 *et al.*, 2012).

376 The sediment data are consistent with these water column observations. The decrease of silt,
377 chlorophyll and organic carbon in the upper sediment layers after fishing suggests resuspension of
378 these substances to the water column. Furthermore, the reduction in sediment oxygen uptake that we
379 found after fishing suggests that part of the metabolic activity, due to removal of labile organic matter
380 and loss of reduced compounds, is displaced from the sediment to the overlying water.

381 **Removal of surficial sediment**

382 We observed an overall coarsening in surface sediments due to trawl activity (Table 1), which is in
383 agreement with Depestele *et al.*, (2018), Mengual *et al.*, (2016) and Palanques *et al.*, (2014). The
384 appearance of finer particles on the sediment surface after tickler chain trawling, however, suggests
385 that two processes are occurring: 1) the smallest sediment fraction (silt) is winnowed and reallocated
386 away from the trawl track, while 2) the heavier sand fractions resettled or remained on the trawl track
387 leaving finer particles (but not the finest silt fraction) sorted on the surface with heavier particles
388 underneath. As sedimentary organic carbon and nitrogen are strongly associated to the abundance of
389 fine sediment, the winnowing of the upper silt fraction led to decreases in OC, TN as well as chl *a*.

390 Tickler T3 samples showed reintegration of silt particles in the upper sediment layers along with OC
391 and TN (Tables 1 and 2). This relatively fast “recovery” of sediment parameters may have occurred
392 through bioturbation activity as infaunal organisms such as *Upogebia deltaura* and *Callianassa*
393 *subterranea* rebuild their burrows after disturbance and are known to expel large amounts of
394 sediments from depth (Rowden *et al.*, 1998).

395 Our study was conducted after the spring bloom (April/May), which provides an annual influx of chl
396 *a* from the water column onto the sediment surface of the Frisian Front (Boon and Duineveld, 1996;
397 Boon and Duineveld, 1998). Both trawl types induced large reductions of sediment chl *a* (83% -
398 tickler T1, 45% - pulse T1; Figure 4), implying that trawling physically removed the top sediment
399 layer along with the labile organic material within it, lowering benthic food quality (Watling *et al.*,
400 2001). The observed reductions in sedimentary OC and chl *a* are in agreement with Brylinsky *et al.*,
401 (1994) and Watling *et al.*, (2001), who documented significant losses of phytopigments shortly after
402 towing bottom trawl gears in shallow (<15 m) sediments. The loss of chl *a* is expected if an acute
403 mechanical stressor, such as bottom trawling, is able to displace the surface sediment, however,
404 longer-term effects on sediment phytopigments and organic material may vary.

405 Pusceddu *et al.*, (2014) sampled chronically trawled versus untrawled deep sea (500 – 2000 m)
406 sediments and reported reduced chl *a* and OC concentrations due to bottom trawling. In shallower (10
407 – 70 m) environments Pusceddu *et al.*, (2005) and Palanques *et al.*, (2014), however, associated
408 increased OC with greater annual trawl intensities. Sciberras *et al.*, (2016) related higher chl *a* with
409 long-term trawl disturbance. In the Bay of Fundy, Brylinsky *et al.*, (1994) detected an increase in
410 sediment chl *a* occurring 80 days after an initial depletion of phytopigments caused from experimental
411 trawling. Enhanced OC and chl *a* production after bottom trawl disturbance may come as a delayed
412 response due to the loss of microbial (Watling *et al.*, 2001) or macrofaunal (Bergman and Hup, 1992;
413 Bergman and van Santbrink, 2000; Tanner, 2003) biomass leading to reduced grazing activity and/or
414 the eventual settling of silt particles (Palanques *et al.*, 2014). Watling *et al.*, (2001) saw an 88%
415 decline in surface chl *a* immediately after scallop dredging in shallow (15 m) water but reported only
416 a 4% difference in chl *a* from disturbed and adjacent areas four months after the fishing. Deep sea

417 environments lack the biological and physical mechanisms to recover quickly from disturbance, thus
418 leaving OC and pigment levels in their depleted state for longer periods of time.

419 **Effect on biogeochemical profiles and fluxes**

420 The significant increase in porewater NH_4^+ after tickler chain and PulseWing trawling (tickler
421 T1/pulse T1) in the top 3 cm sediment suggest a physical disturbance in the upper sediment layer
422 (Table 3, Figure 5). As it can take several months for NH_4^+ to reach a new steady state after sediment
423 disturbance (van de Velde *et al.*, 2018), these altered profiles probably show transient effects,
424 reflecting the removal of the upper sediment layer and/or the homogenisation of the sediment column.
425 Oxygen, in contrast will more quickly reach its steady state in the sediment.

426 Decreased labile organic material and the removal of reduced compounds will lower SCOC and
427 increase O_2 concentrations in the sediment, thereby increasing the OPD (Gundersen and Jorgensen,
428 1990). Our results demonstrate this pattern as fishing disturbance led to deeper OPD's in addition to
429 the reduction in SCOC (Figures 7 and 8) and chl *a* (Figure 5). The OPD's in our study were 40%
430 deeper in the tickler T1 and 29% deeper in pulse profiles in comparison with control samples (Figure
431 7). These results are supported by Allen and Clarke, (2007)'s prediction of a deeper sediment oxic
432 layer following bottom trawl disturbance.

433 Sediment community oxygen consumption (SCOC) can be used as a measure for total (oxic and
434 anoxic) sediment metabolism, as it represents the collective respiration of microbial, meiofaunal and
435 macrofaunal communities residing in the sediment, as well as chemical reoxidation processes of
436 reduced compounds (Glud 2008). Historical data from the Frisian Front shows seasonal variation in
437 O_2 consumption from $5 \text{ mmol O}_2 \text{ m}^2\text{d}^{-1}$ during winter months to its peak in August at around 50 mmol
438 $\text{O}_2 \text{ m}^2\text{d}^{-1}$ (van Raaphorst *et al.*, 1992; Nedwell, *et al.*, 1993; Upton *et al.*, 1993; Boon *et al.*, 1998;
439 Boon and Duineveld, 1998). From the month of June, O_2 consumption ranges between 15 to 36 mmol
440 $\text{O}_2 \text{ m}^2\text{d}^{-1}$ (Upton *et al.*, 1993; Boon *et al.*, 1998; Boon and Duineveld, 1998), which is comparable
441 with the SCOC rates from our study before trawling.

442 Although the differences in O₂ consumption from the *in-situ* lander incubations were not statistically
443 significant, the results are complimentary to the data from our on-board incubations, implying that
444 fishing with tickler chains is more likely to cause reductions in SCOC than PulseWing trawling. The
445 reduction of SCOC rates and deepening of the OPD after trawl disturbance is consistent with the
446 removal of the reactive top layer of sediment, as demonstrated by the loss in chlorophyll and organic
447 matter. This top layer typically also holds high abundances of microbial (Watling *et al.*, 2001) and
448 macrofaunal (Dauwe *et al.*, 1998) organisms. Thus, removal of this layer likely decreased the overall
449 biological activity and carbon mineralisation in these sediments.

450 To our knowledge, we are the first to report significantly decreased SCOC rates and increased O₂
451 penetration in marine sediments following bottom trawling. Trimmer *et al.*, (2005) found no
452 significant changes in oxygen uptake between trawled (various bottom gear types) and untrawled
453 sandy sediments in the southern North Sea. Sciberras *et al.*, (2016) did not find a significant effect of
454 bottomfishing (scallop dredge/otter trawl) on OPD in sandy and muddy sediments in the Irish Sea. In
455 the soft sediments of Galveston Bay Texas, Warnken *et al.*, (2003) found inconsistent results in their
456 oxygen flux measurements leading them to conclude that O₂ consumption was not affected by shrimp
457 trawling. Our results contrast with the findings of van de Velde *et al.*, (2018) who reported, a drastic
458 increase in total carbon mineralisation rates after anthropogenic caused mixing in carbon rich muddy
459 sediments off the coast of Belgium. The increase was attributed to the re-exposure of previously
460 buried organic material to oxic conditions. The sediments in their study, however, are extremely
461 eutrophic and therefore not representative for most North Sea sediments. In comparison, Frisian Front
462 sediments are less metabolically active, contain significantly less carbon, and have much higher
463 macrofaunal activity.

464 Nutrient fluxes measured in sediment cores and *in-situ* were quite variable both in the control and
465 trawled areas. The ammonium fluxes (0.10 – 0.61 mmol m² d⁻¹) were lower than the maximum
466 summertime values recorded in previous studies, but were well within the range of annual fluctuations
467 in NH₄⁺ flux (-0.1 – 1.7 mmol m² d⁻¹) in this area (van Raaphorst *et al.*, 1992; Nedwell, *et al.*, 1993;
468 Lohse *et al.*, 1995). NO_x fluxes in the Frisian Front can reach a value around 0.3 mmol m² d⁻¹ in

469 summer, however, van Raaphorst *et al.* (1992) found that NO_x fluxes in June remained closer to 0.1
470 mmol m² d⁻¹ which is comparable to the fluxes found in our study (Table 4). Whereas the NH₄⁺ fluxes
471 between treatments in our study were not significantly different, we found a 50% decrease between
472 *in-situ* lander NO_x fluxes from control and tickler trawled incubations. The Frisian Front exhibits
473 distinct porewater NO_x maxima near the sediment surface (Lohse *et al.*, 1995), which is consistent
474 with the nitrate fluxing out of the sediment (Table 4). The removal of the top sediment layer may have
475 weakened the diffusive gradient between NO_x and the overlying water, therefore reducing fluxes from
476 the sediment.

477 In-situ lander flux estimates were consistently higher for oxygen, phosphate and silicate compared
478 with on-board incubations (Table 4). Cores used for the on-board incubations held 22 cm of sediment
479 at most, and so the fluxes recorded in the on-board incubation cores, measure the results of processes
480 occurring within this space. The *in-situ* landers have no such limitation and measure fluxes over a
481 deeper sediment layer. Bioturbating infauna in the North Sea are known to contribute to significant
482 releases of silicate from the sediment (Olsgard *et al.*, 2008). A prominent mud shrimp in the Frisian
483 Front, *C. subterranea*, has burrows extending down to 81 cm, and water in its burrows can hold
484 higher concentrations of phosphate and ammonium compared to the overlying water (Witbaard and
485 Duineveld, 1989, Rowden and Jones, 1995). Macrofaunal burrows were frequently seen in our
486 sediment samples, several of which extended beyond the bottom of the incubation cores. We therefore
487 infer that processes occurring deep in the sediment are the primary cause for the discrepancy in fluxes
488 measured in our *in-situ* landers compared with the on-board incubations, where the former includes
489 the impact of deep dwelling organisms, and the latter does not. Wave-induced advective transport
490 may have also played a role in our *in situ* lander results if waves were able to pump burrow water into
491 the measurement chambers. The impermeable muddy sand in the Frisian Front, however, would
492 prevent this process from occurring through advective porewater transport.

493 **Implications**

494 Previous research has shown that different bottom gear types can cause variable effects on benthic
495 fauna (Kaiser *et al.*, 2006; Hiddink *et al.*, 2017; Sciberras *et al.*, 2018). Moreover, severe bottom

496 trawling may potentially induce long-term impacts on benthic biogeochemical cycles in certain
497 sediments (Pusceddu *et al.*, 2014; van de Velde *et al.*, 2018). Our study adds the ability for bottom
498 trawl gears to slow down overall benthic metabolism, at a time scale of several days at the least. The
499 lowering of benthic oxygen consumption and the simultaneous increase in oxygen demand from the
500 water column, provides evidence that trawling displaces part of the benthic activity into the overlying
501 water. Given the global scope of bottom trawl fishing, this has widespread implications for carbon
502 mineralization and nutrient cycling. The significant loss of labile organic matter (in the form of chl *a*)
503 from the sediments after trawl disturbance and consequent lowering of the food quality may also
504 affect benthic lifeforms on longer time scales.

505 Finally, this study demonstrated the greater and less variable impact of tickler chain beam trawl gears
506 on biogeochemical functioning when compared with PulseWing trawling. Information gained from
507 this research has implications for bottom trawl fisheries management and provides concrete evidence
508 linking lower mechanical disturbance in fishing gears to a reduced impact on benthic marine
509 ecosystems.

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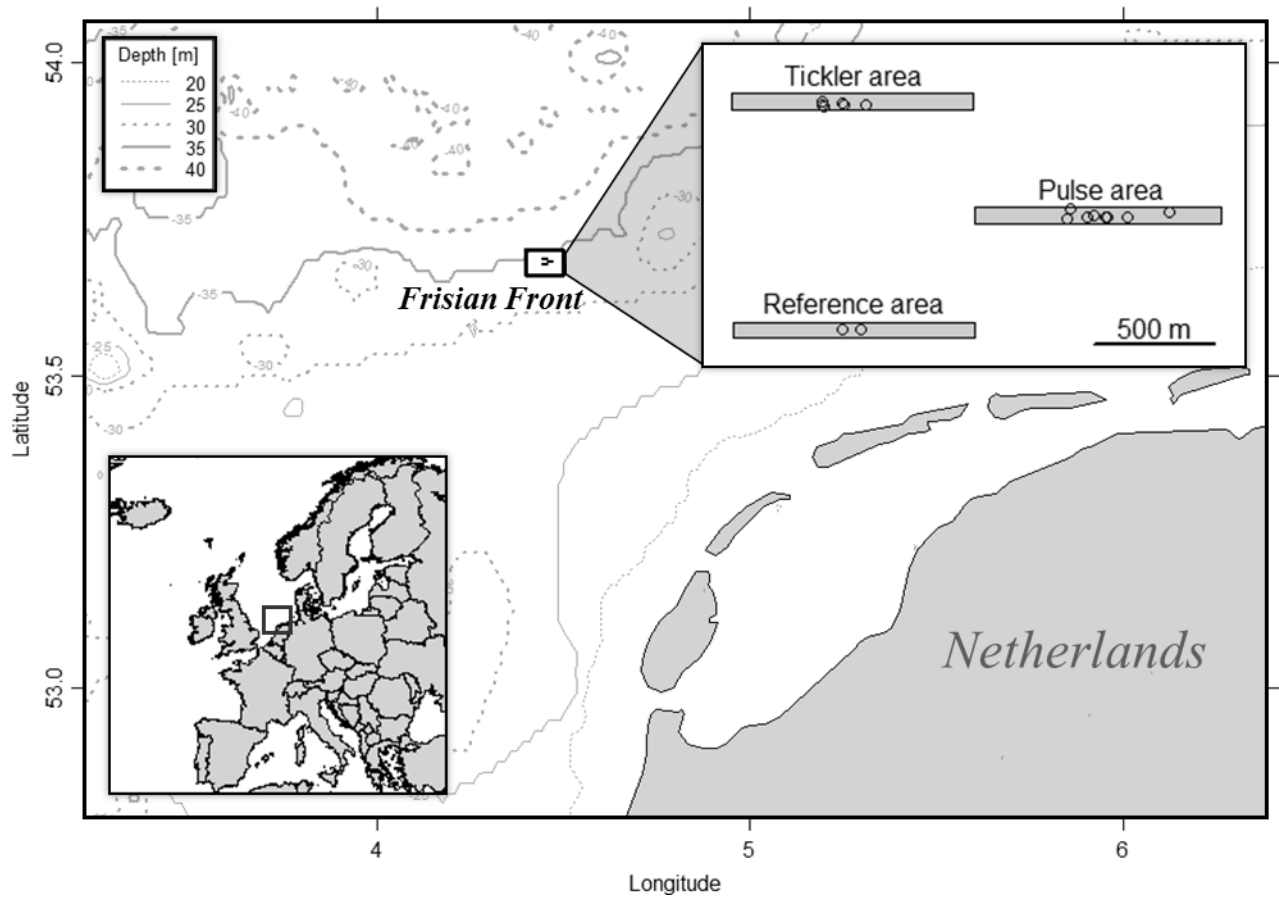
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Figures



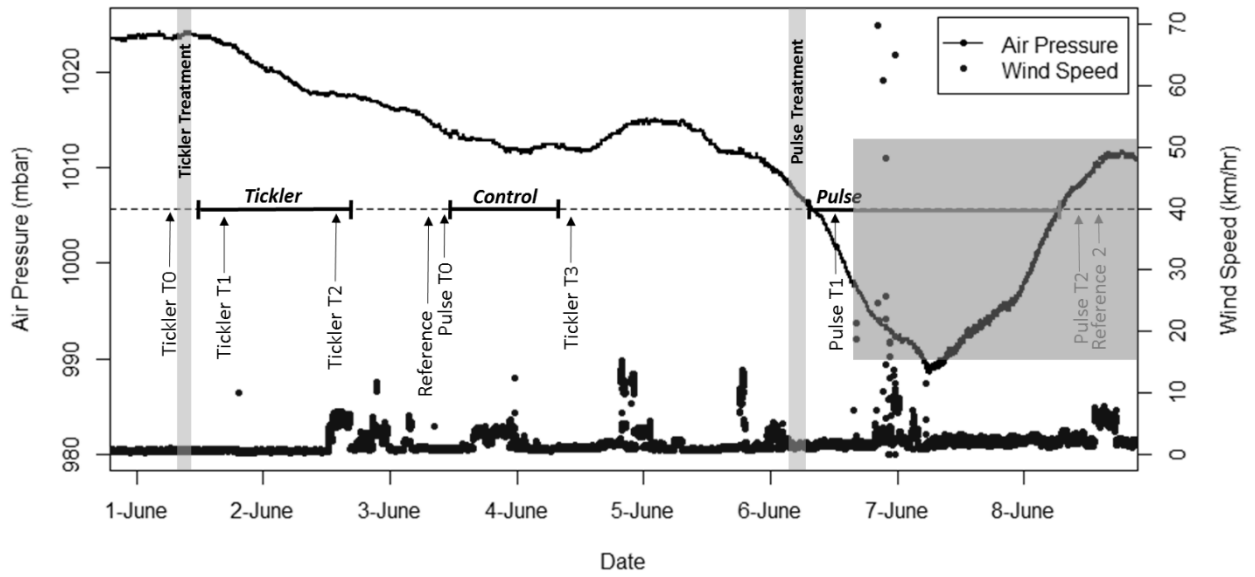
722

723 **Figure 1.** Map of the study site. The inset shows the positions of the experimental areas and box cores

724 taken from the tickler treatment to the north, the pulse treatment to the east and the reference area in

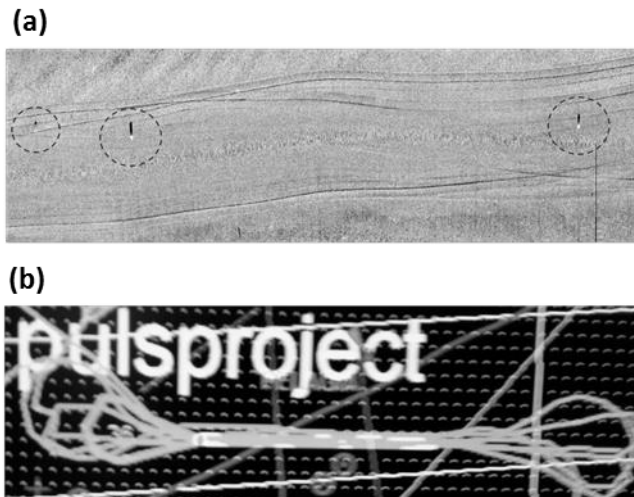
725 the south.

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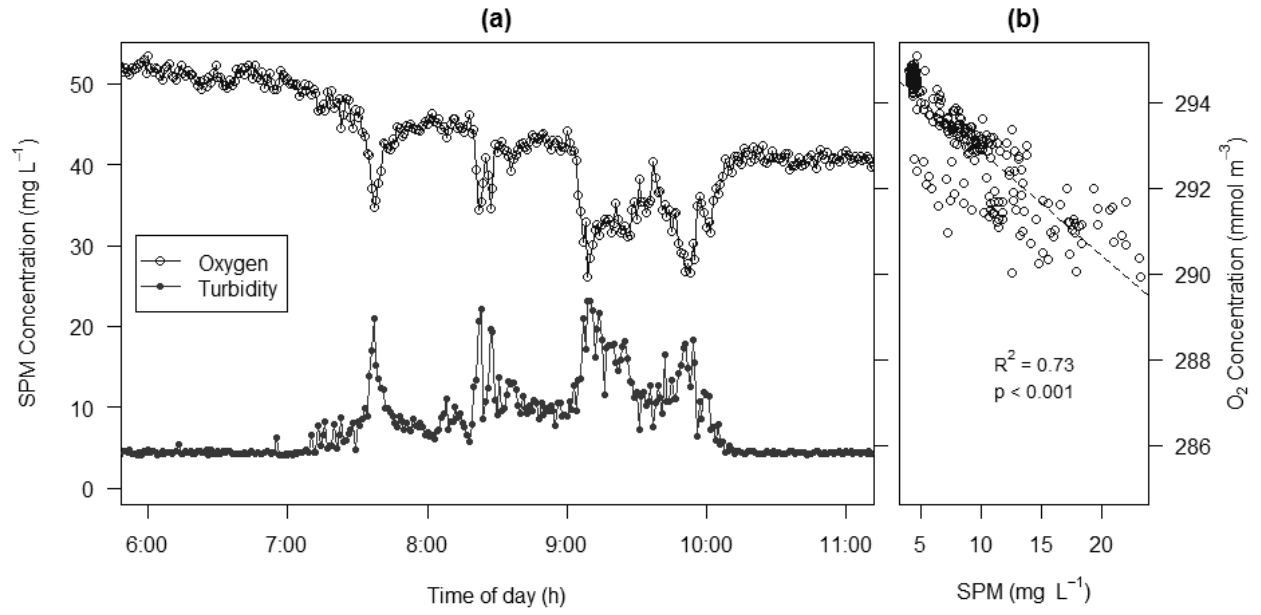
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728 **Figure 2.** Sequence of events and weather conditions. Box core sediment samples (arrows), *in-situ*
 729 lander deployments (brackets) and experimental fishing treatments (shaded columns) are shown.
 730 Samples taken in the shaded region on the right were not included in the analysis due to storm
 731 induced sediment disturbance.



732

733 **Figure 3.** (a) A side-scan sonar image of the tickler trawled area. In addition to the evidence of
734 bottom disturbance, images of 2 benthic ALBEX landers and an additional oxygen sensing lander can
735 be seen within the disturbed portion of the seafloor. (b) Tracking of PulseWing trawl coordinates
736 showing the path taken by the fisherman while fishing the experimental (pulse) area.



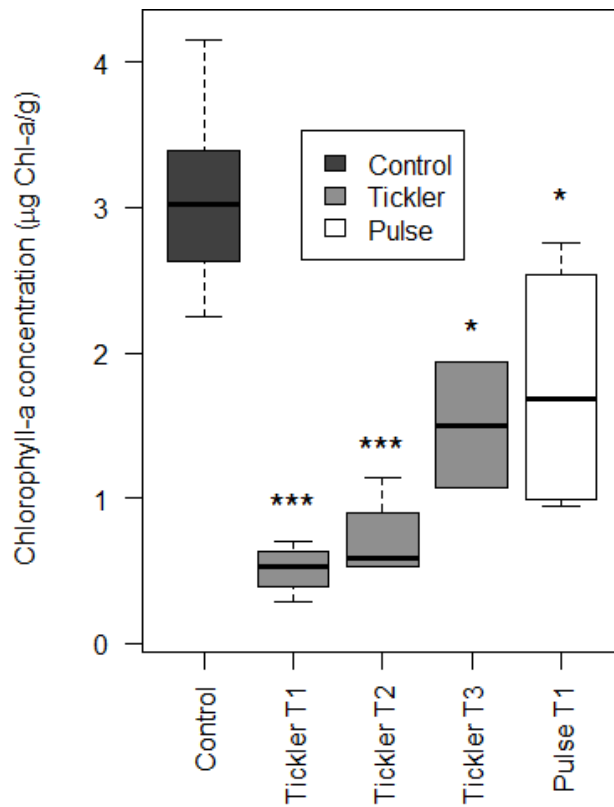
737

738 **Figure 4.** (a) PulseWing facilitated resuspension effects on SPM (mg L⁻¹) and O₂ (mmol m⁻³)

739 concentrations. Data was taken from 3.5 m above the sediment surface. (b) The relationship between

740 SPM (x-axis) and O₂ concentration (y-axis) in the water column during pulse fishing.

741

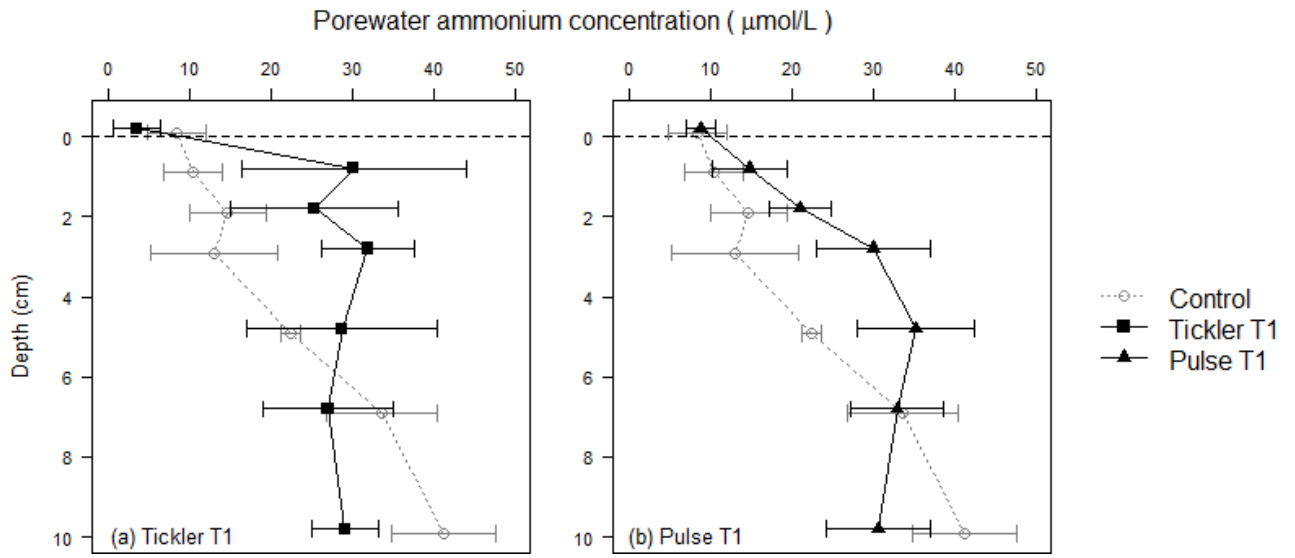


742

743 **Figure 5.** Surface chlorophyll-*a* concentrations in control, tickler T1, tickler T2, tickler T3 and pulse

744 T1 sediments. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ significant differences compared to control

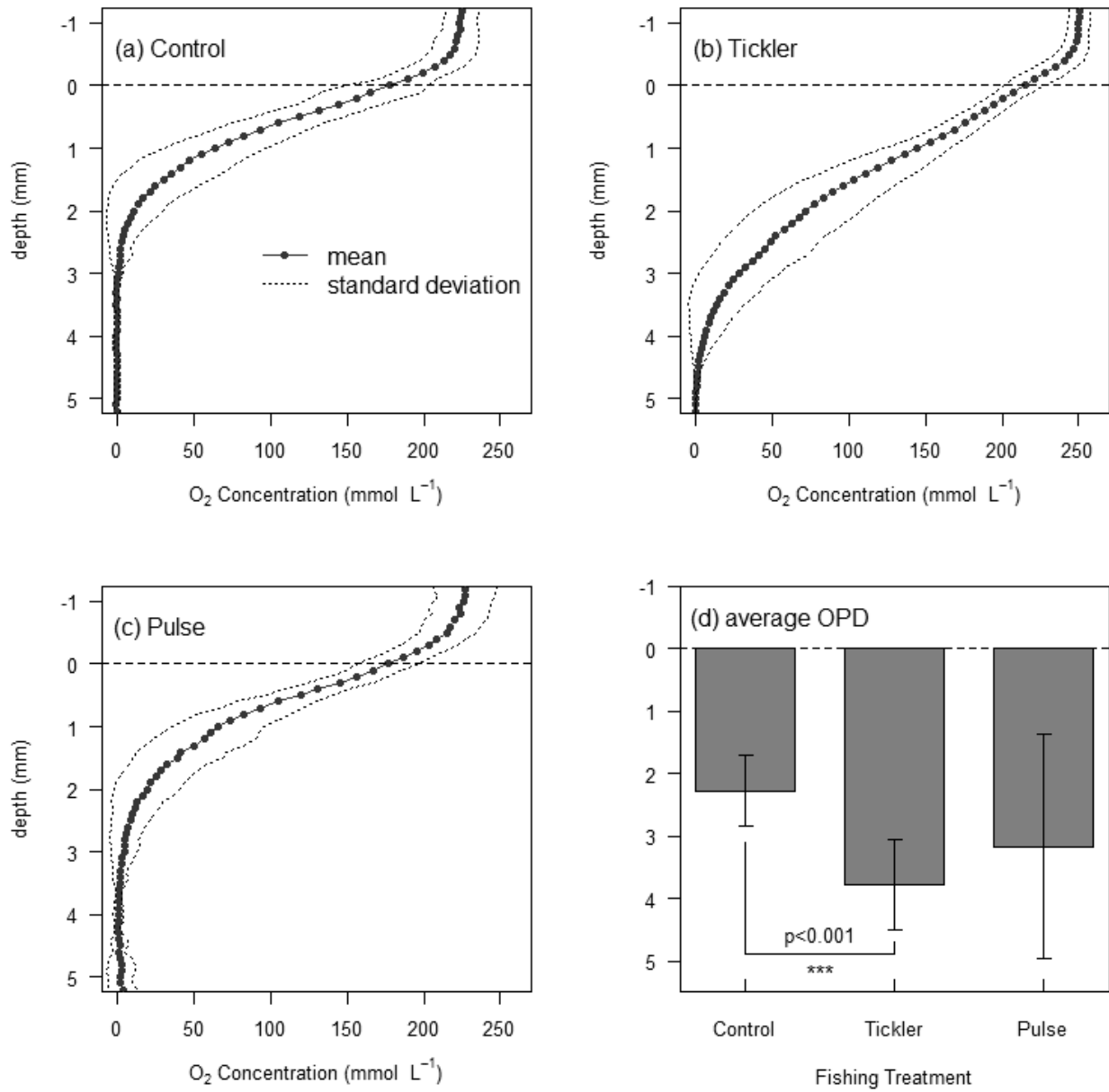
745 samples.



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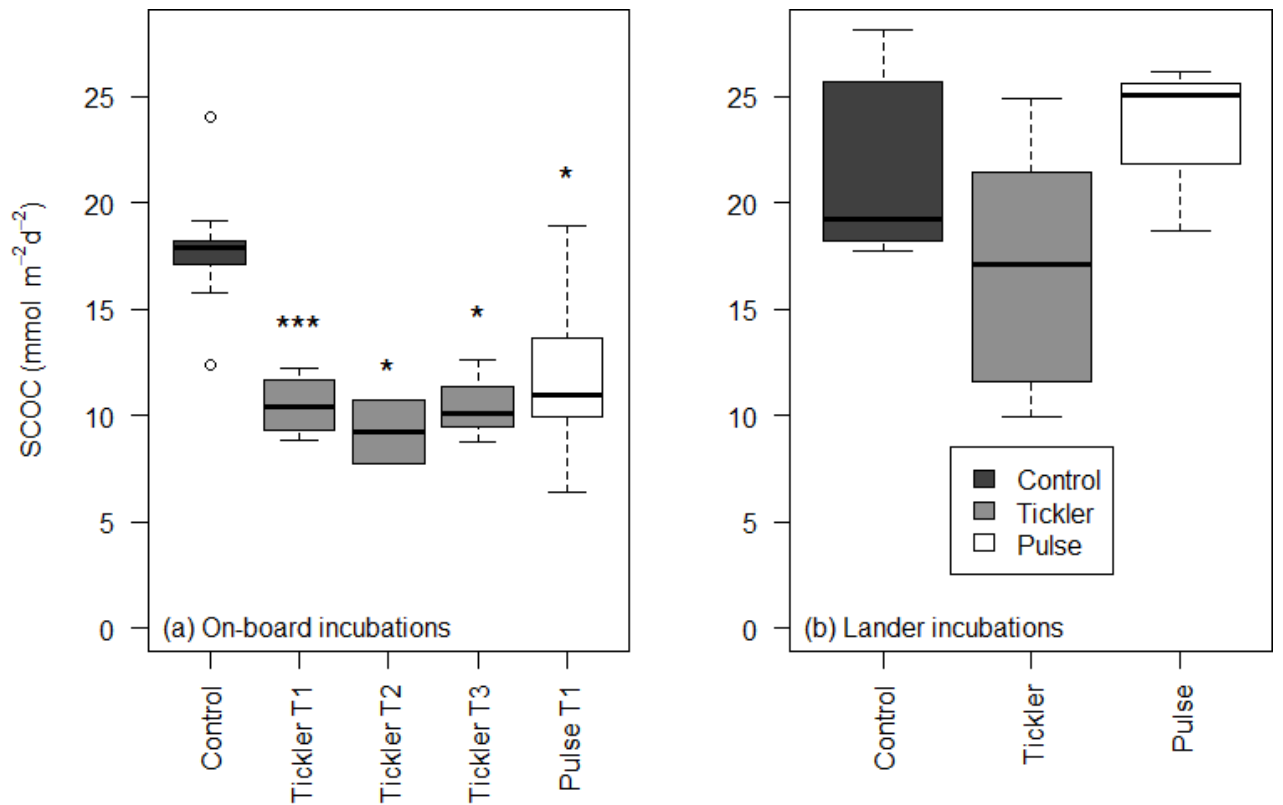
747 **Figure 6.** Porewater NH_4^+ concentrations comparing (a) tickler T1 and (b) pulse T1 with control

748 (untrawled) samples



749

750 **Figure 7.** Oxygen microprofiles for (a) control, (b) tickler T1, and (c) pulse T1 areas. (d) Average O₂
 751 penetration depth (mm) and standard deviation from each treatment.



752

753 **Figure 8.** Sediment community oxygen consumption (SCOC) in control, tickler chain trawled and
 754 PulseWing trawled sediments. **(a)** SCOC in on-board measurements taken from box core samples. **(b)**
 755 O_2 consumption measured from *in-situ* ALBEX landers. *p < 0.05; **p < 0.01; ***p < 0.001
 756 significant differences compared to control samples.

757

758

Tables

Table 1. Grain size parameters taken from the top 2.5 cm: % silt (<63 μm), % fine sand (63-125 μm), D50 = median grainsize (μm), D10 = diameter at which 10% of particles in the sample are smaller (μm).

	% Silt mean \pm sd	% Fine sand mean \pm sd	D50 mean \pm sd	D10 mean \pm sd	<i>n</i>
Control	33.06 \pm 7.33	36.37 \pm 3.96	91.81 \pm 11.95	6.78 \pm 1.26	9
Tickler T1	26.17 \pm 2.74	41.09 \pm 1.62	99.46 \pm 3.22	9.21\pm1.21*	4
Tickler T2	20.46\pm2.85***	44.59\pm2.48*	105.22 \pm 2.63	12.13\pm1.42***	2
Tickler T3	35.96 \pm 6.67	34.94 \pm 2.47	88.55 \pm 9.83	6.14 \pm 1.53	3
Pulse T1	37.21 \pm 4.48	33.53 \pm 2.26	87.74 \pm 6.29	5.58 \pm 1.03	7

759 **Bold** = significantly different than control samples. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

Table 2. Percentage organic carbon and nitrogen content from the top 2.5cm

	% OC mean \pm sd	% TN mean \pm sd	<i>n</i>
Control	0.35 \pm 0.09	0.041 \pm 0.009	9
Tickler T1	0.30 \pm 0.04	0.031 \pm 0.003	4
Tickler T2	0.24 \pm 0.04	0.026\pm0.002**	2
Tickler T3	0.37 \pm 0.15	0.041 \pm 0.015	3
Pulse T1	0.43 \pm 0.04	0.045 \pm 0.004	7

760 **Bold** = significantly different than control samples.

761 *p < 0.05; **p < 0.01; ***p < 0.001

762

Table 3. Porewater nutrient concentrations in the upper 3 cm ($\mu\text{mol/L}$)

	NH_4^+ mean \pm sd	NO_x mean \pm sd	PO_4^{3-} mean \pm sd	SiO_2 mean \pm sd	<i>n</i>
Control	13.85 \pm 7.64	2.94 \pm 5.64	0.46 \pm 0.31	85.48 \pm 19.16	15
Tickler T1	26.97\pm9.27**	2.52 \pm 1.85	0.53 \pm 0.34	80.00 \pm 23.46	6
Tickler T2	18.24 \pm 3.55	2.55 \pm 1.60	0.72 \pm 0.19	69.40 \pm 14.63	6
Pulse T1	21.96\pm8.10*	1.58 \pm 0.42	0.62 \pm 0.27	80.53 \pm 12.78	12

763 **Bold** = significantly different than control samples. * $p < 0.05$; ** $p < 0.01$

764

765

Table 4. Benthic oxygen and nutrient fluxes ($\text{mmol m}^2 \text{d}^{-1}$) from on-board incubations and in-situ lander deployments. n.d. = no data, O_2 “fluxes” are denoted as negative.

<i>On-board incubations</i>	O_2	NH_4^+	NO_x	PO_4^{3-}	Si(OH)_4	<i>n</i>
	mean \pm sd	mean \pm sd	mean \pm sd	mean \pm sd	mean \pm sd	
Control	-17.78 \pm 3.07	0.25 \pm 0.34	0.106 \pm 0.03	-0.003 \pm 0.02	1.43 \pm 0.37	9
Tickler T1	-10.46\pm1.50***	0.35 \pm 0.41	0.095 \pm 0.02	0.001 \pm 0.01	1.10 \pm 0.41	4
Tickler T2	-9.23\pm2.14*	0.10 \pm 0.13	0.097 \pm 0.02	0.001 \pm 0.01	0.70 \pm 0.36	2
Tickler T3	-10.51\pm1.96*	n.d.	n.d.	n.d.	n.d.	3
Pulse T1	-11.93\pm4.02*	0.28 \pm 0.25	0.108 \pm 0.02	0.002 \pm 0.01	1.30 \pm 0.52	7
<i>In-situ incubations</i>	O_2	NH_4^+	NO_x	PO_4^{3-}	Si(OH)_4	<i>n</i>
	mean \pm sd	mean \pm sd	mean \pm sd	mean \pm sd	mean \pm sd	
Control	-21.40 \pm 4.45	0.39 \pm 0.29	0.177 \pm 0.05	0.071 \pm 0.03	2.85 \pm 1.04	6
Tickler	-17.01 \pm 6.36	0.61 \pm 0.55	0.088\pm0.02*	0.076 \pm 0.04	2.22 \pm 0.84	6
Pulse	-23.30 \pm 4.05	0.17 \pm 0.12	0.089 \pm 0.06	0.047 \pm 0.02	3.78 \pm 0.98	3

766 **Bold** = significantly different than control samples. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

767