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Trawling effects on biogeochemical processes are mediated by fauna in high-energy biogenic-reef-inhabited coastal sediments

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S.1. Supplementary figures

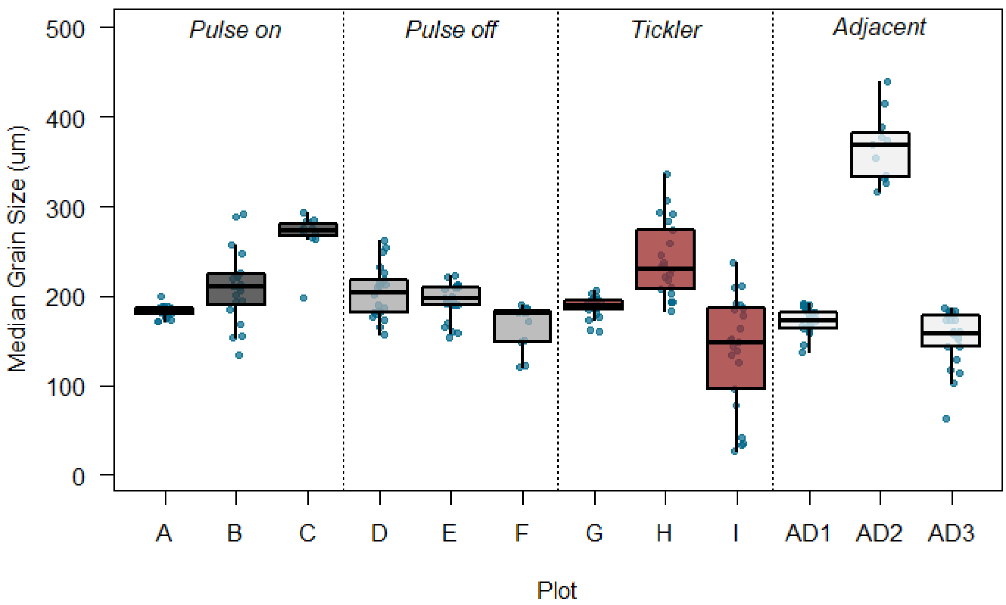


Figure S1: Median grain sizes found in T0 experimental (pulse on, pulse off, tickler) plots and untrawled adjacent locations.

a b c d

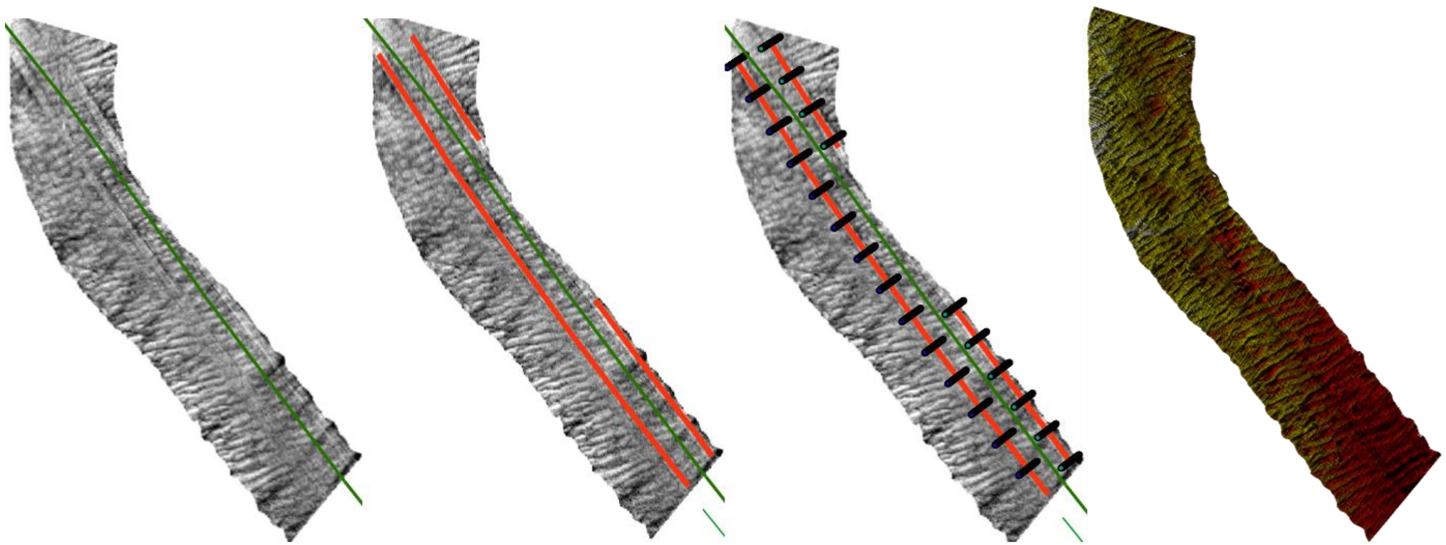


Figure S2: Identification of trawl tracks using backscatter (a-c) and bathymetry (d) imagery.

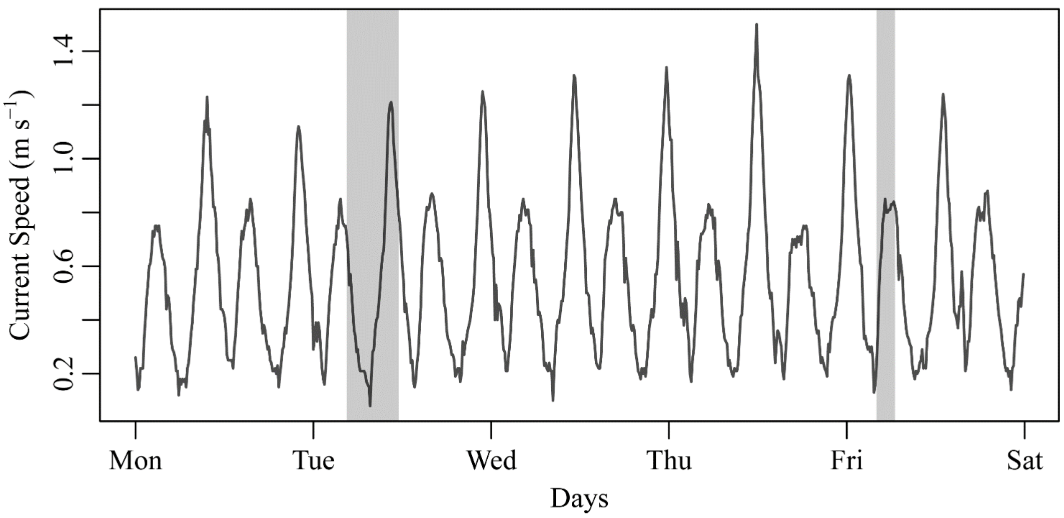


Figure S3: Water current speeds during the week of bottom trawl measurements. The shaded region on the left indicates the time of pulse trawling while the shaded region on the right indicates the time of beam trawling. This data was obtained from the "Scheur Wielingen" measuring station located in the Vlakte van de Raan.

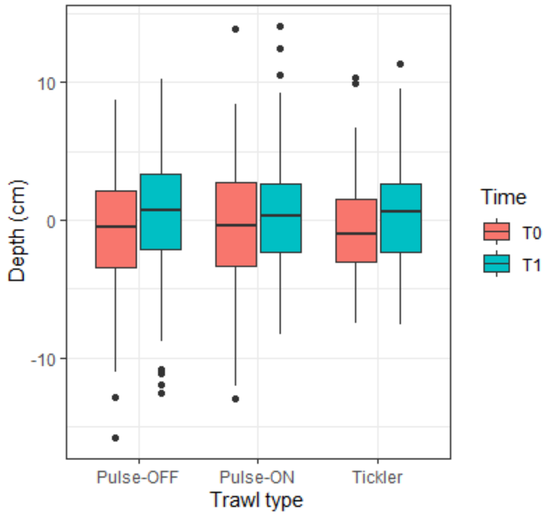


Figure S4: Box plots of bathymetrical differences in water depth (cm) from outside and inside the location of the trawl track before (T0) and after (T1) experimental trawling.

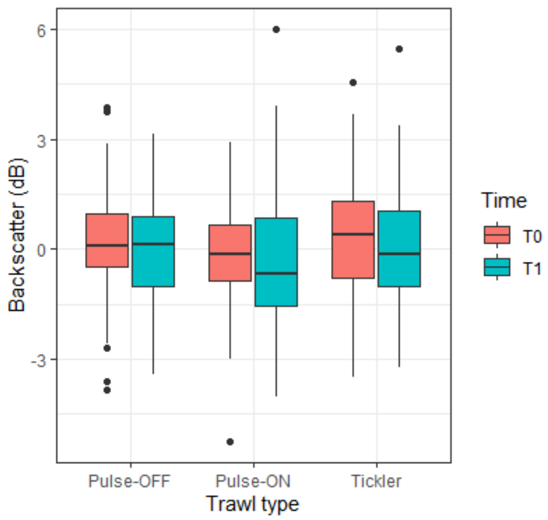


Fig S5: Box plots of backscatter differences (dB) from outside and inside the location of the track before (T0) and after (T1) experimental trawling.

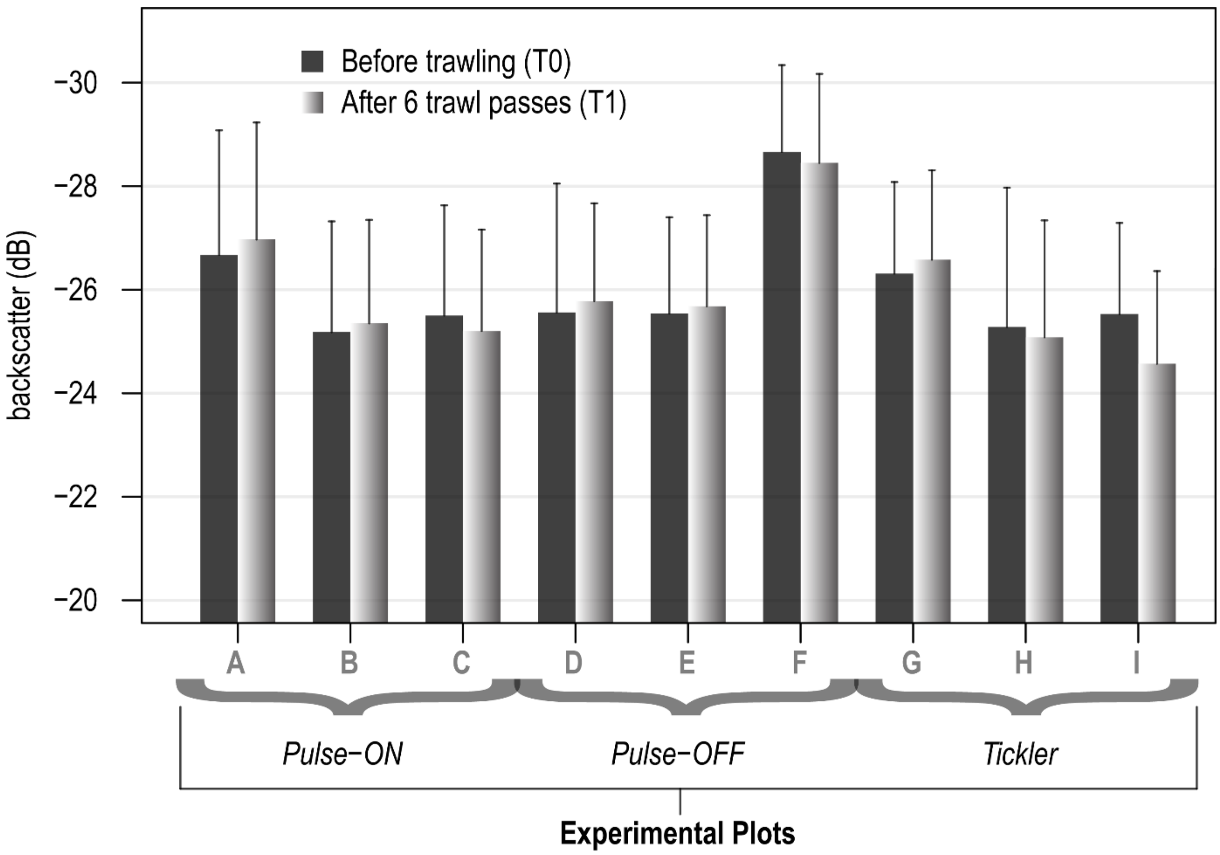


Figure S6: Mean backscatter values (dB) per experimental plot (before and after trawling) with the standard deviations.

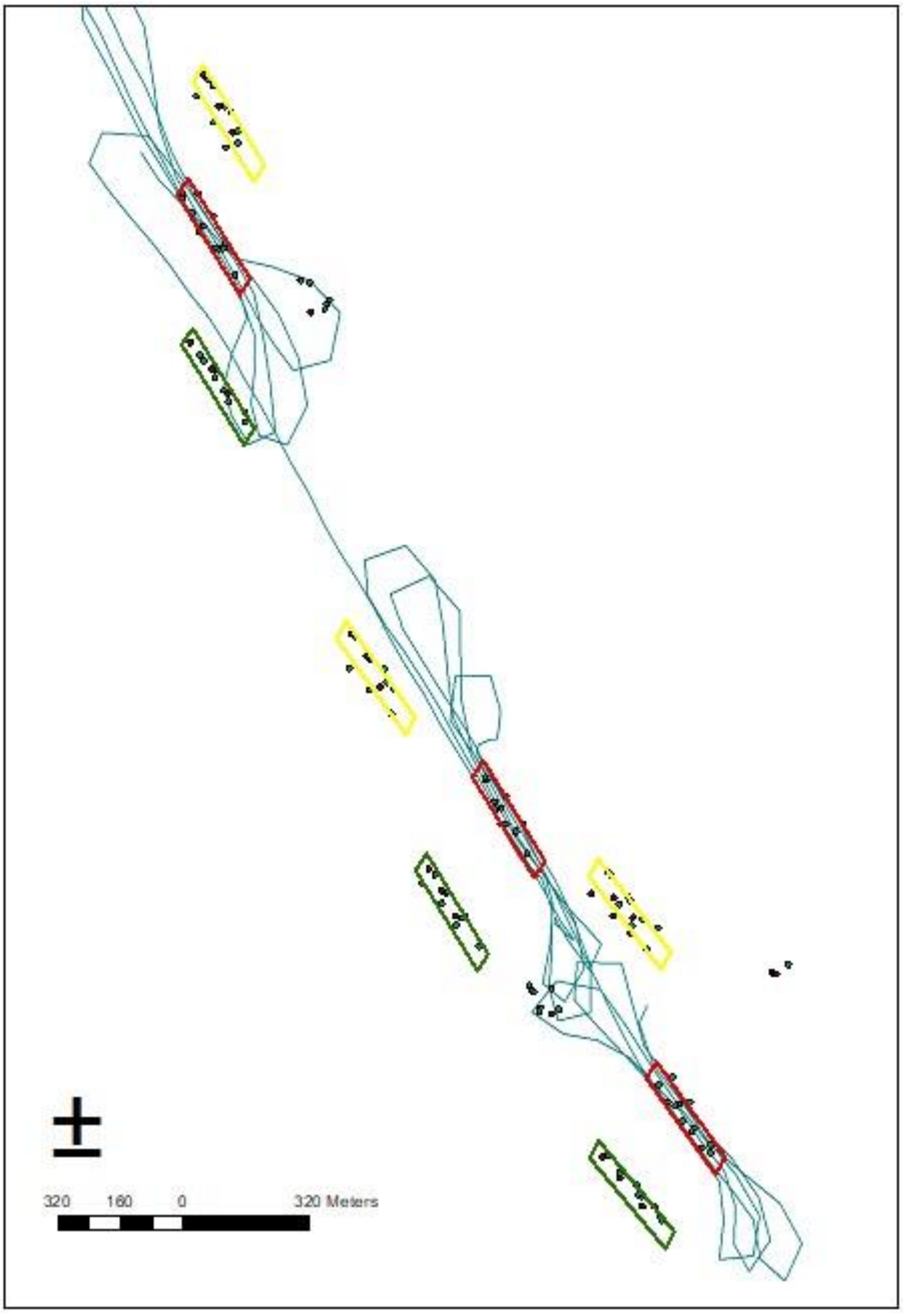


Figure S7: Beam trawl fishing paths through "tickler" treatment plots. Dots are SPI and box core sample locations.

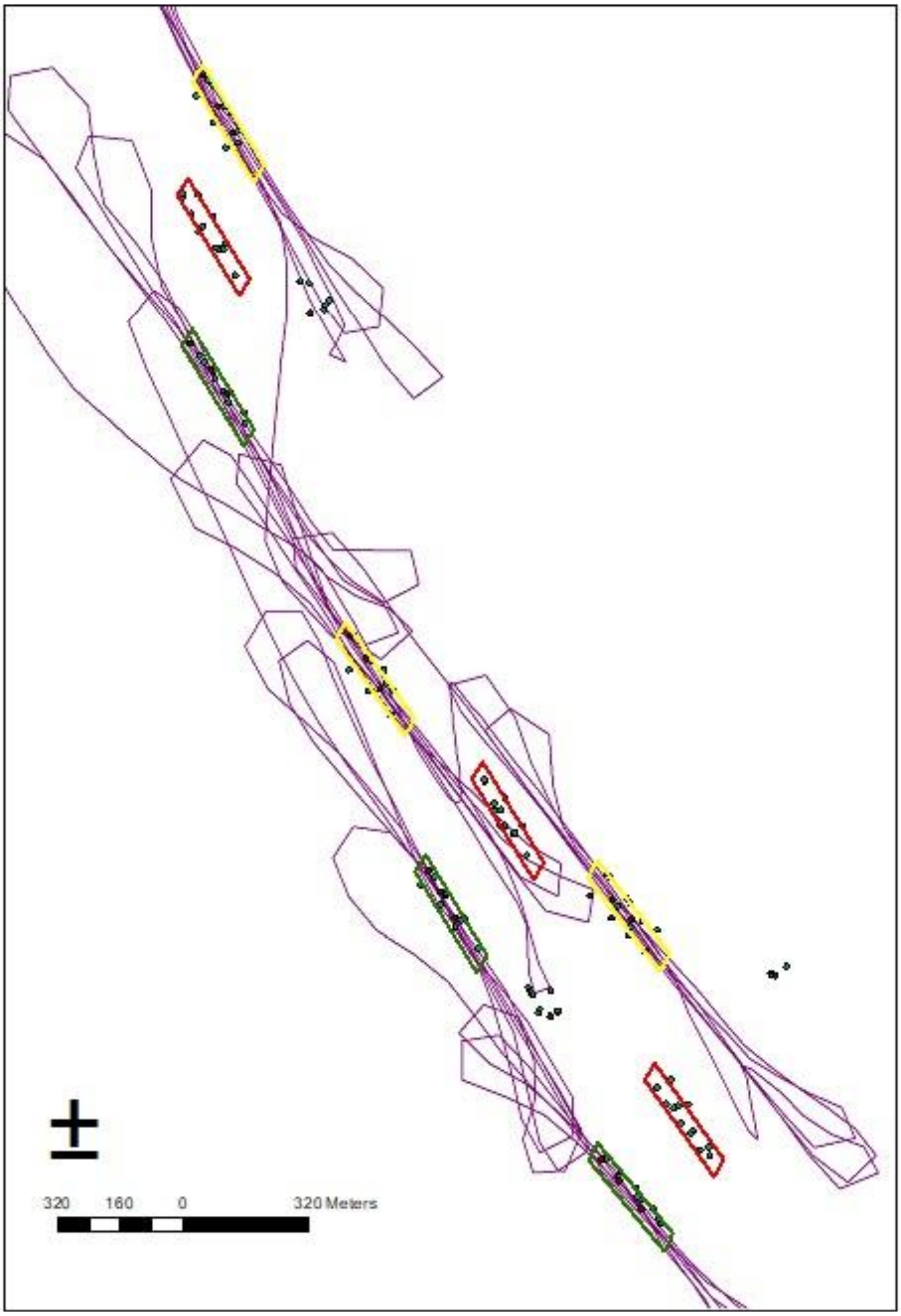


Figure S8: Pulse trawl fishing paths through "pulse on" and "pulse off" treatment plots. Dots are SPI and box core sample locations.

S.2 Supplementary Tables

Table S1: Sampling information. Activities include experimental trawling, sediment profile imagery (SPI), sediment and macrofauna sampling (Box Core), bathymetry and backscatter (Sonar) and water column turbidity and organic matter measurements (Water Column). Benthic samples from box cores (taken in triplicates) were also used to obtain porewater nutrients and biogeochemical flux data. Figure 1 displays the sampling locations specified in the "Areas" column.

Date	Activity	Treatment & Timestep	Areas
07 June 2018	SPI	Pulse-On T0	Plots: A, B, C
08-Jun-18	SPI	Pulse-OFF T0	Plots: D, E, F
		Adjacent T0	AD1, AD2, AD3
11 June 2018	Box Core	Pulse-On T0	Plots: A, B, C
		Pulse-OFF T0	Plots: D, E, F
		Pulse-On T0	Plots: A, B, C
		Pulse-OFF T0	Plots: D, E, F
		Adjacent T0	AD1, AD2
12 June 2018	Experimental Trawling	Pulse-On T1	Plots: A, B, C
		Pulse-OFF T1	Plots: D, E, F
	Sonar	Pulse-On T1	Plots: A, B, C
		Pulse-OFF T1	Plots: D, E, F
	Water Column	Pulse-On T1	Plots: A, B, C
		Pulse-OFF T1	Plots: D, E,
	Box Core	Pulse-On T0	Plots: A, B, C
		Pulse-OFF T0	Plots: D, E, F
	SPI	Pulse-OFF T1	Plots: D, F
13 June 2018	SPI	Pulse-OFF T1	Plots: E
		Pulse-ON T1	Plots: A, B, C
		Tickler T0	Plots: G, H, I
	Box Core	Tickler T0	Plots: G, H, I
	Box Core	Tickler T0	Plots: G, H, I
15 June 2018	Experimental Trawling	Tickler T1	Plots: G, H, I
	Box Core	Tickler T1	Plots: G, H, I
		Adjacent T1	AD1, AD2, AD3
	Sonar	Tickler T1	Plots: G, H, I
	Water Column	Tickler T1	Plots: G, H, I
	SPI	Tickler T1	Plots: G, H, I
	SPI	Adjacent T1	AD1, AD2, AD3

Backscatter comparison between treatments after one trawl pass

The backscatter values of the track locations were consistently reduced, but the magnitude of the changes was on average too low to be considered as a substantial change in backscatter value due to trawling. There was no statistical difference between the three trawl types ($\chi^2(2)=0.16$, $p = 0.92$).

Table S2.
Backscatter changes following the one trawl pass (dB).

Treatment	Time	mean	sd	Q25	median	Q75	Q025	Q975	CI95	n
Pulse-OFF	T1-T0	-0.23	1.87	-0.30	-1.39	0.92	-3.49	3.31	6.81	88
Pulse-ON	T1-T0	-0.20	2.25	-0.47	-1.62	0.98	-4.00	4.58	8.58	74
Tickler	T1-T0	-0.30	2.09	-0.38	-1.70	1.31	-4.54	3.24	7.78	89

Comparison of backscatter of the entire plot for each treatment (6 trawl passes)

Mean backscatter strength (dB values) was between -26.64 dB and -25.40. The mean backscatter strength did not differ more than 2 dB between any of the treatments at any of the time steps T0 and T1 and was not significantly different between any of the time-treatment interactions ($\chi^2(5) = 4.23$, $p = 0.52$).

Backscatter values were not statistically different by experimental sites ($\chi^2(9) = 15.47$, $p = 0.051$), as confirmed by a post-hoc Dunn test with Benjamin-Hochberg correction on the p-values. Uncorrected p-values suggested that sites A and F were different, as indicated by significant pairwise differences ($p < 0.05$) between A and B, H and I, as well as pairwise differences between F and B, C, H and I.

Table S3
Summary statistics of backscatter data (dB) for each of the combination of time and trawl type.

Treatment	Time	mean	sd	Q25	median	Q75	Q025	Q975	CI95	n
Pulse-OFF	T0	-26.57	2.51	-28.43	-26.54	-24.65	-31.26	-21.50	9.76	156016
Pulse-OFF	T1	-26.64	2.20	-28.12	-26.54	-24.97	-30.95	-22.45	8.50	162561
Pulse-ON	T0	-25.74	2.30	-27.17	-25.60	-24.34	-30.32	-21.19	9.13	129962
Pulse-ON	T1	-25.83	2.22	-27.17	-25.91	-24.34	-30.32	-21.50	8.82	162605
Tickler	T0	-25.66	2.18	-27.17	-25.60	-24.34	-30.00	-21.19	8.81	147976
Tickler	T1	-25.40	2.12	-26.86	-25.44	-24.02	-29.53	-21.19	8.34	162578

Note. The lack of backscatter difference may be due to the averaging across 4 m wide transects.

Table S4: Measured oxygen (O_2), dissolved inorganic nitrogen (ammonium [NH_4^+], nitrite [NO_2^-], nitrate [NO_3^-]), phosphate (PO_4^{3-}), and silica ($Si(OH)_4$) fluxes in mmol m^{-2} d^{-1}.

Date	Treatment	Timestep	Station	O_2	NH_4^+	NO_2^-	NO_3^-	PO_4^{3-}	$Si(OH)_4$
11/06/2018	Pulse-On	T0	A1	-54.4	1.322	-0.002	-0.041	0.003	1.502
11/06/2018	Pulse-On	T0	A2	-92.7	0.139	0.001	-0.003	0.015	0.658
11/06/2018	Pulse-On	T0	A3	-108.2	0.554	0.004	0.012	-0.004	1.125
11/06/2018	Pulse-On	T0	B1	-56.5	0.651	0.016	0.009	0.027	1.143
11/06/2018	Pulse-On	T0	B2	-19.6	-0.040	-0.001	-0.011	-0.007	0.066
11/06/2018	Pulse-On	T0	B3	-663	6.595	0.001	-0.016	0.083	1.679
11/06/2018	Pulse-On	T0	C1	-36.2	0.075	0.001	0.007	-0.002	0.059
11/06/2018	Pulse-On	T0	C2	-109.7	0.661	0.010	0.045	0.008	0.394
11/06/2018	Pulse-On	T0	C3	-158.5	0.207	-0.002	0.007	0.014	0.135
11/06/2018	Pulse-Off	T0	D1	-53.6	0.146	0.007	0.012	0.012	0.428
11/06/2018	Pulse-Off	T0	D2	-26.1	0.039	0.004	0.007	-0.011	0.240
11/06/2018	Pulse-Off	T0	D3	-121.6	1.974	0.007	0.003	0.152	2.990
11/06/2018	Pulse-Off	T0	E1	-52.5	0.117	0.007	0.043	0.003	0.646
11/06/2018	Pulse-Off	T0	E2	-82.9	1.413	0.015	0.009	0.153	2.672
11/06/2018	Pulse-Off	T0	E3	-36.3	0.000	0.000	0.000	0.000	0.000
11/06/2018	Pulse-Off	T0	F1	-89.5	0.555	0.005	0.015	0.039	1.767
11/06/2018	Pulse-Off	T0	F2	-61.7	1.483	0.010	-0.019	0.155	2.881
11/06/2018	Pulse-Off	T0	F3	-123.5	0.027	-0.006	-0.021	-0.012	0.635
11/06/2018	Adjacent	T0	AD1	-227.9	1.357	-0.002	-0.041	0.092	2.031
11/06/2018	Adjacent	T0	AD1	-242.4	0.199	0.003	0.017	0.003	0.074
11/06/2018	Adjacent	T0	AD1	-158.7	1.353	0.005	0.001	0.021	0.910
11/06/2018	Adjacent	T0	AD2	-29.4	0.019	0.000	-0.001	0.000	0.059
11/06/2018	Adjacent	T0	AD2	-21.8	0.409	0.020	0.046	0.016	0.383
11/06/2018	Adjacent	T0	AD2	-20.1	2.709	0.005	-0.005	0.074	1.903
12/06/2018	Pulse-On	T1	A1	-83.4	0.401	0.008	0.061	0.003	0.267
12/06/2018	Pulse-On	T1	A2	-24.5	0.368	0.009	0.029	0.004	0.412
12/06/2018	Pulse-On	T1	A3	-83.1	0.319	0.008	0.023	-0.001	0.111
12/06/2018	Pulse-On	T1	B1	-24.4	0.434	0.005	0.009	0.020	0.591
12/06/2018	Pulse-On	T1	B2	-25.6	1.165	0.022	0.020	0.052	1.762
12/06/2018	Pulse-On	T1	B3	-307	1.031	0.009	0.001	0.061	1.403
12/06/2018	Pulse-On	T1	C1	-44.1	0.536	0.003	-0.001	0.039	1.390
12/06/2018	Pulse-On	T1	C2	-38.3	0.364	0.005	0.002	0.029	1.417
12/06/2018	Pulse-On	T1	C3	-67.8	0.990	0.007	0.005	0.100	2.948
12/06/2018	Pulse-Off	T1	D1	-76.7	0.347	0.005	0.028	0.017	0.820
12/06/2018	Pulse-Off	T1	D2	-177.8	0.342	0.004	0.017	0.027	0.852
12/06/2018	Pulse-Off	T1	D3	-84.3	0.814	0.003	0.002	0.089	2.162
12/06/2018	Pulse-Off	T1	E1	-47.4	0.043	0.001	0.006	-0.001	0.291
12/06/2018	Pulse-Off	T1	E2	-32	0.412	0.003	0.005	0.012	1.136
12/06/2018	Pulse-Off	T1	E3	-93.1	0.657	0.006	0.009	0.032	1.544
12/06/2018	Pulse-Off	T1	F1	-52.6	1.046	0.005	0.001	0.049	1.891
12/06/2018	Pulse-Off	T1	F2	-43	0.721	0.007	0.007	0.049	1.579
12/06/2018	Pulse-Off	T1	F3	-52.5	0.061	0.002	0.010	0.002	0.125
13/06/2018	Tickler	T0	G1	-68.1	3.102	0.001	-0.004	0.076	2.762
13/06/2018	Tickler	T0	G2	-130.3	1.227	0.009	0.009	0.073	2.600
13/06/2018	Tickler	T0	G3	-177.9	0.347	0.007	0.018	0.042	0.630
13/06/2018	Tickler	T0	H1	-163.2	0.599	0.010	0.019	0.015	0.455
13/06/2018	Tickler	T0	H2	-140.9	1.257	0.013	0.010	0.028	1.116
13/06/2018	Tickler	T0	H3	-37.3	3.969	0.002	-0.010	0.045	1.296
13/06/2018	Tickler	T0	I1	-401.6	0.421	0.006	0.018	0.018	0.487
13/06/2018	Tickler	T0	I2	-276.5	0.880	0.011	0.026	0.023	0.779
13/06/2018	Tickler	T0	I3	-156	0.043	0.004	0.031	0.000	0.088
15/06/2018	Adjacent	T1	AD1	-277.5	1.059	0.003	-0.001	0.101	3.101
15/06/2018	Adjacent	T1	AD1	-78.2	1.026	0.004	-0.002	0.035	1.319
15/06/2018	Adjacent	T1	AD1	-446.6	1.429	0.004	-0.010	0.062	2.860
15/06/2018	Adjacent	T1	AD2	-509.8	3.895	0.000	-0.087	0.079	2.223
15/06/2018	Adjacent	T1	AD2	-170.2	2.755	0.013	-0.024	0.065	2.928
15/06/2018	Adjacent	T1	AD2	-33.6	1.289	0.002	-0.025	0.093	2.025

Table S4: continued

Date	Treatment	Timestep	Station	O_2	NH_4^+	NO_2^-	NO_3^-	PO_4^{3-}	$Si(OH)_4$
15/06/2018	Adjacent	T1	AD3	-293.5	0.077	-0.013	-0.030	0.005	0.278
15/06/2018	Adjacent	T1	AD3	-223	0.523	-0.001	-0.071	0.034	1.627
15/06/2018	Adjacent	T1	AD3	-231	-0.011	-0.003	-0.041	0.000	0.170
15/06/2018	Tickler	T1	G1	-25.9	1.004	0.012	0.013	0.039	1.583
15/06/2018	Tickler	T1	G2	-39.4	0.454	0.008	0.008	0.030	1.891
15/06/2018	Tickler	T1	G3	-79.8	5.116	0.000	0.000	0.038	2.710
15/06/2018	Tickler	T1	H1	-57.3	3.421	-0.004	-0.014	0.041	1.666
15/06/2018	Tickler	T1	H2	-103	0.852	0.008	0.013	0.041	1.083
15/06/2018	Tickler	T1	H3	-21.8	0.126	0.005	0.023	0.004	0.354
15/06/2018	Tickler	T1	I1	-94.9	1.173	0.011	0.011	0.086	1.956
15/06/2018	Tickler	T1	I2	-128.8	1.007	0.009	0.005	0.036	1.756
15/06/2018	Tickler	T1	I3	-120	1.351	0.009	0.005	0.068	2.844

Table S5: Results for sediment and biogeochemical parameters between T0-T1 for untrawled adjacent sampling areas (mean ± SD). Nitrogen (N) and phosphorus (P) removal are presented as the percentage of inorganic N or P removed from the sediments after being formed from organic matter mineralization. Most Adjacent 3 samples were only obtained at the end of the experimental period (T1).

	Adjacent 1				Adjacent 2				Adjacent 3			
	T0	n	T1	n	T0	n	T1	n	T0	n	T1	n
Sediment: very fine sand (%), chlorophyl a (μg g^{-1}), silt (%), median grain size (D50: μm)												
Very fine sand	14±3.1	21	-	-	1.7±1.9	11	-	-	-	-	15±3.3	22
Chl *a*	12±11	21	-	-	2.0±2.7	11	-	-	-	-	22±23	22
Silt	8.4±7.8	21	-	-	1.2±1.7	11	-	-	-	-	17±14	22
D50	172±15	21	-	-	366±38	11	-	-	-	-	153±31	22
Sediment profile imagery (SPI): prism penetration (mm), anoxic surface area (%)												
Penetration	37±3.9	3	36±4.7	3	49±11	3	41±7.5	3	135±5.2	3	60±47	3
Anoxic surface	0.98±23	3	**20±15****	3	0.21±0.36	3	3.4±1.7	3	0.47±50	3	1.9±3.4	3
Porewater nutrients (mmol m^{-3})												
NH_4^+	40±27	6	30±23	6	23±11	6	15±4.3	6	-	-	80±61	12
NO_3^-	5.7±4.2	6	5.2±2.9	6	7.4±4.5	6	6.9±1.8	6	-	-	7.2±8.1	12
PO_4^{3-}	3.3±0.83	6	2.5±1.4	6	3.9±2.3	6	2.0±1.5	6	-	-	6.4±5.6	12
$Si(OH)_4$	82±37	6	40±23	6	20±4.8	6	21±8.7	6	-	-	90±49	12
Nutrient Fluxes (mmol $m^{-2}d^{-1}$)												
O_2	-209±45	3	-267±184	3	-23±5.0	3	-237±245	3	-	-	-249±39	3
NH_4^+	0.97±0.67	3	1.2±0.22	3	1.0±1.4	3	2.6±1.3	3	-	-	0.20±0.30	3
NO_3^-	-7.9e-3±0.03	3	-4.5e-3±5.0e-3	3	0.01±0.03	3	-0.04±0.04	3	-	-	-0.05±0.02	3
PO_4^{3-}	pda0.04±0.04	3	0.06±0.03	3	0.03±0.04	3	0.08±0.01	3	-	-	0.01±0.02	3
$Si(OH)_4$	1.0±1.0	3	**2.4±1.0*****	3	0.8±1.0	3	**2.4±0.47*****	3	-	-	0.78±0.70	3
Mass Budgets: total mineralization and denitrification (mmol C $m^{-2}d^{-1}$), nitrification (mmol N $m^{-2}d^{-1}$), nitrogen (N) and phosphorus (P) removal (%)												
Mineralization	189±40	3	241±166	3	22±3.8	3	215±221	3	-	-	224±34	3
Denitrification	34±8.1	3	44±31	3	2.8±2.3	3	37±40	3	-	-	42±6.7	3
Nitrification	27±6.5	3	35±25	3	2.3±1.2	3	30±32	3	-	-	34±5.3	3
% N removal	96±2.9	3	95±4.1	3	64±48	3	85±11	3	-	-	99±0.90	3
% P removal	98±2.4	3	96±1.2	3	84±21	3	87±17	3	-	-	99±0.96	3
Macrofauna (individuals m^{-2})												
Species Densities	33723 ±11051	3	27359 ±20164	3	4626 ±2814	3	18628 ±18474	3	-	-	28961 ±6755	3

Bold signifies that T1 is significantly different compared to T0. *$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

S.4. Sediment Profile Images

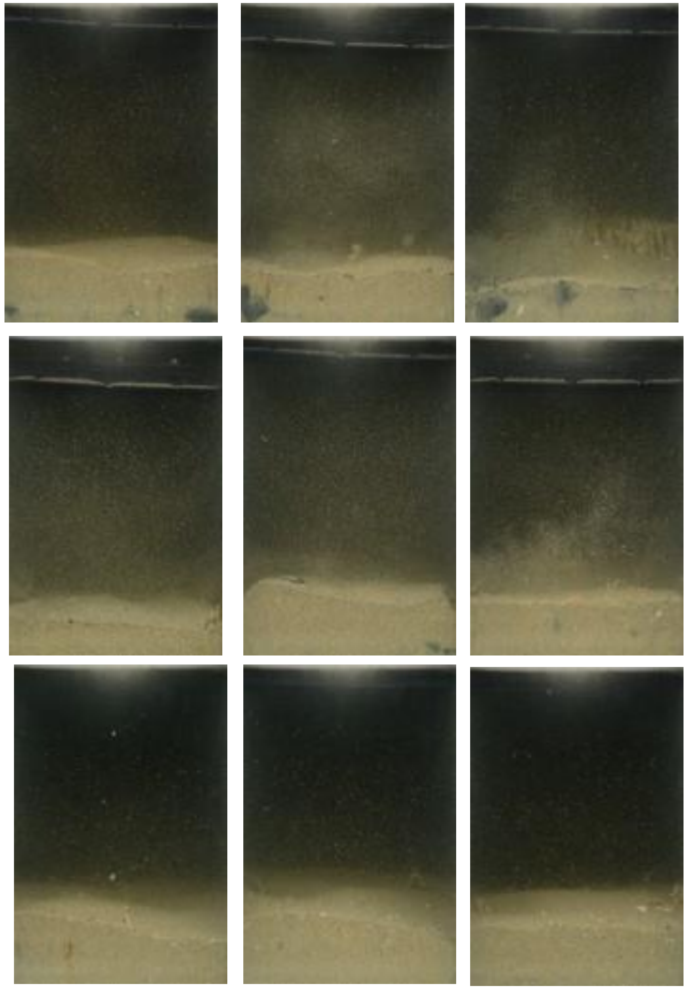
T0- Pulse on (Zone A)

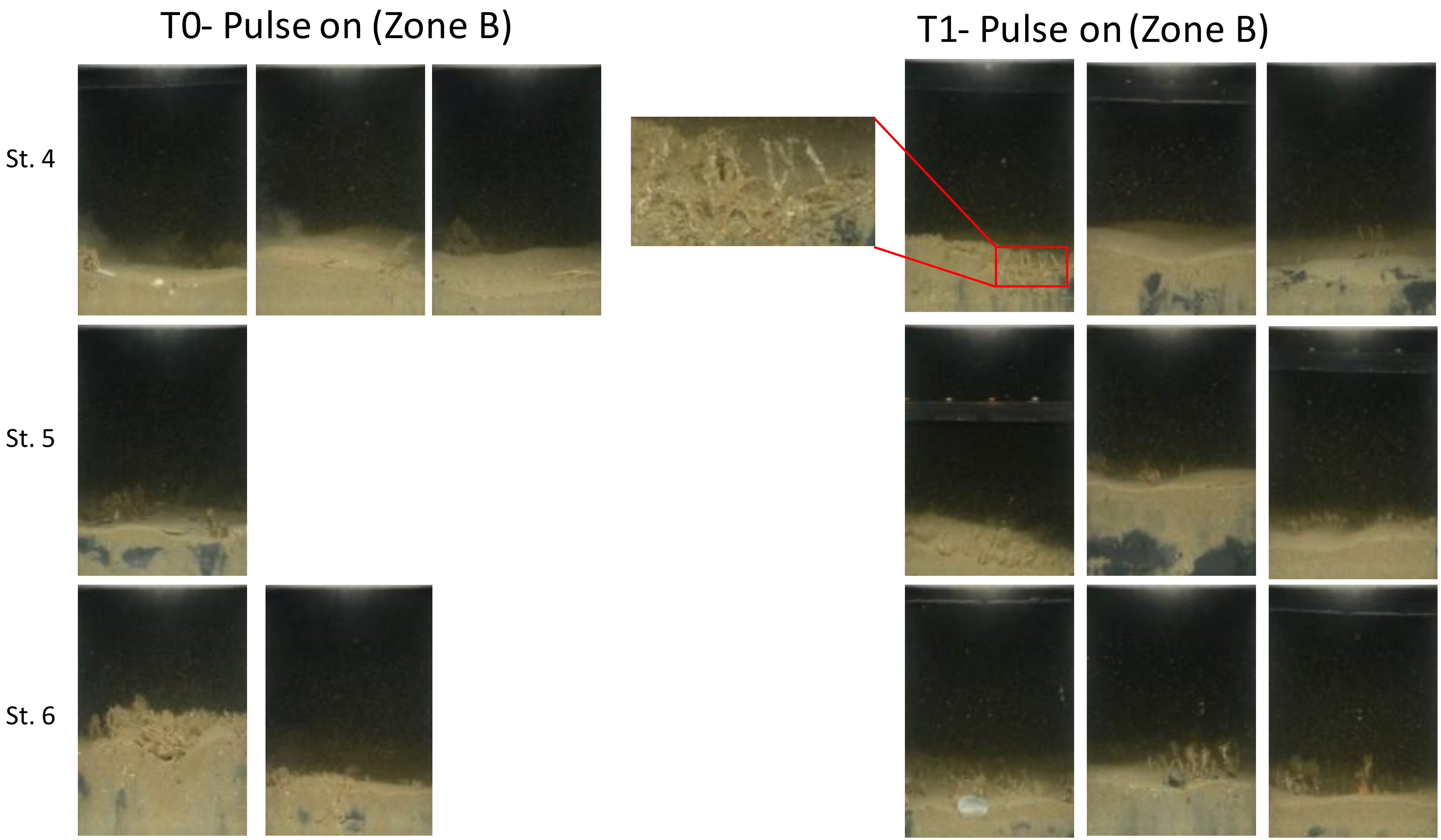
Station 4

Station 5

Station 6

T1- Pulse on (Zone A)




T0- Pulse on (Zone B)
T1- Pulse on (Zone B)
St. 4
St. 5
St. 6

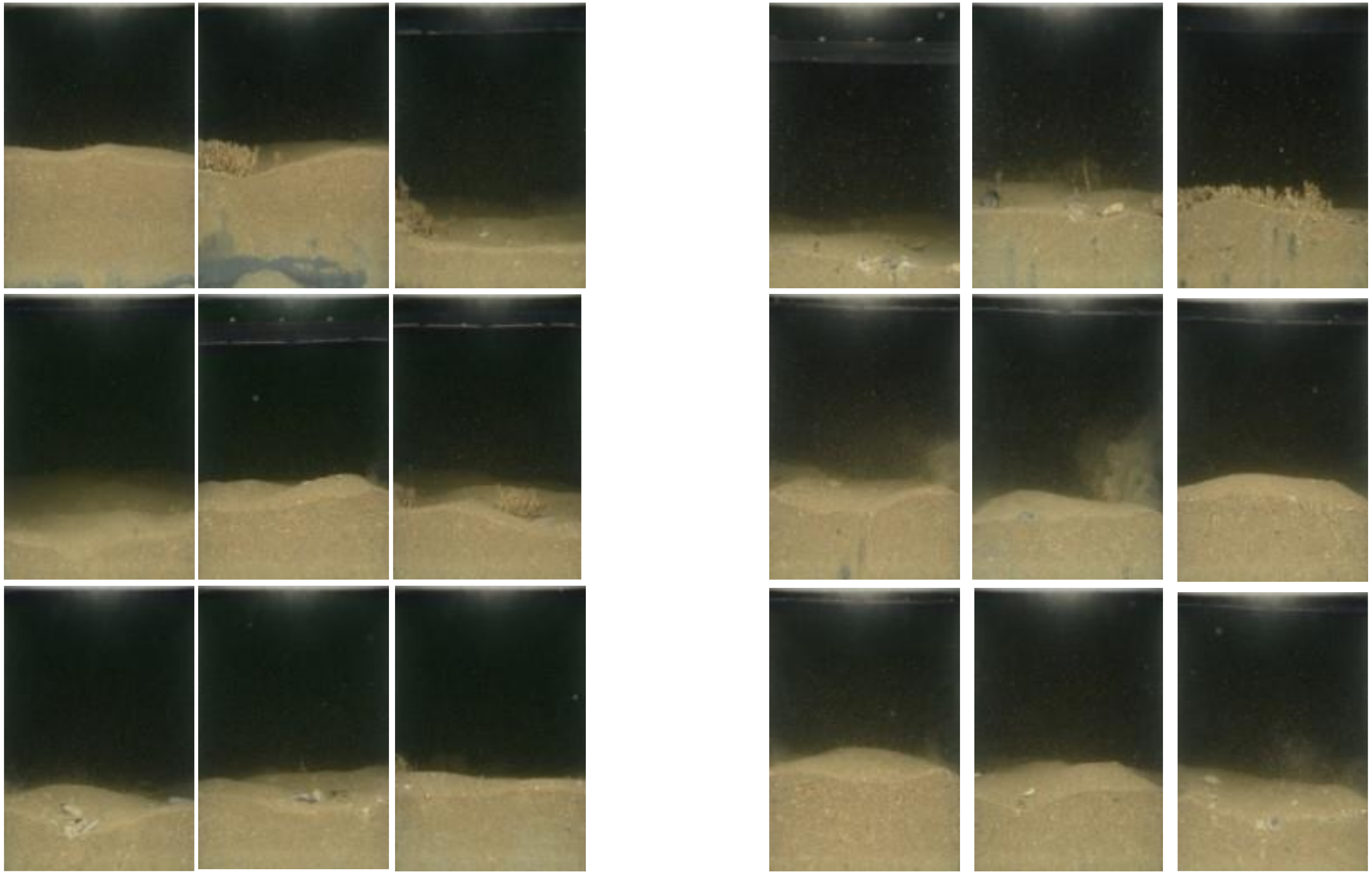
T0- Pulse on (Zone C)

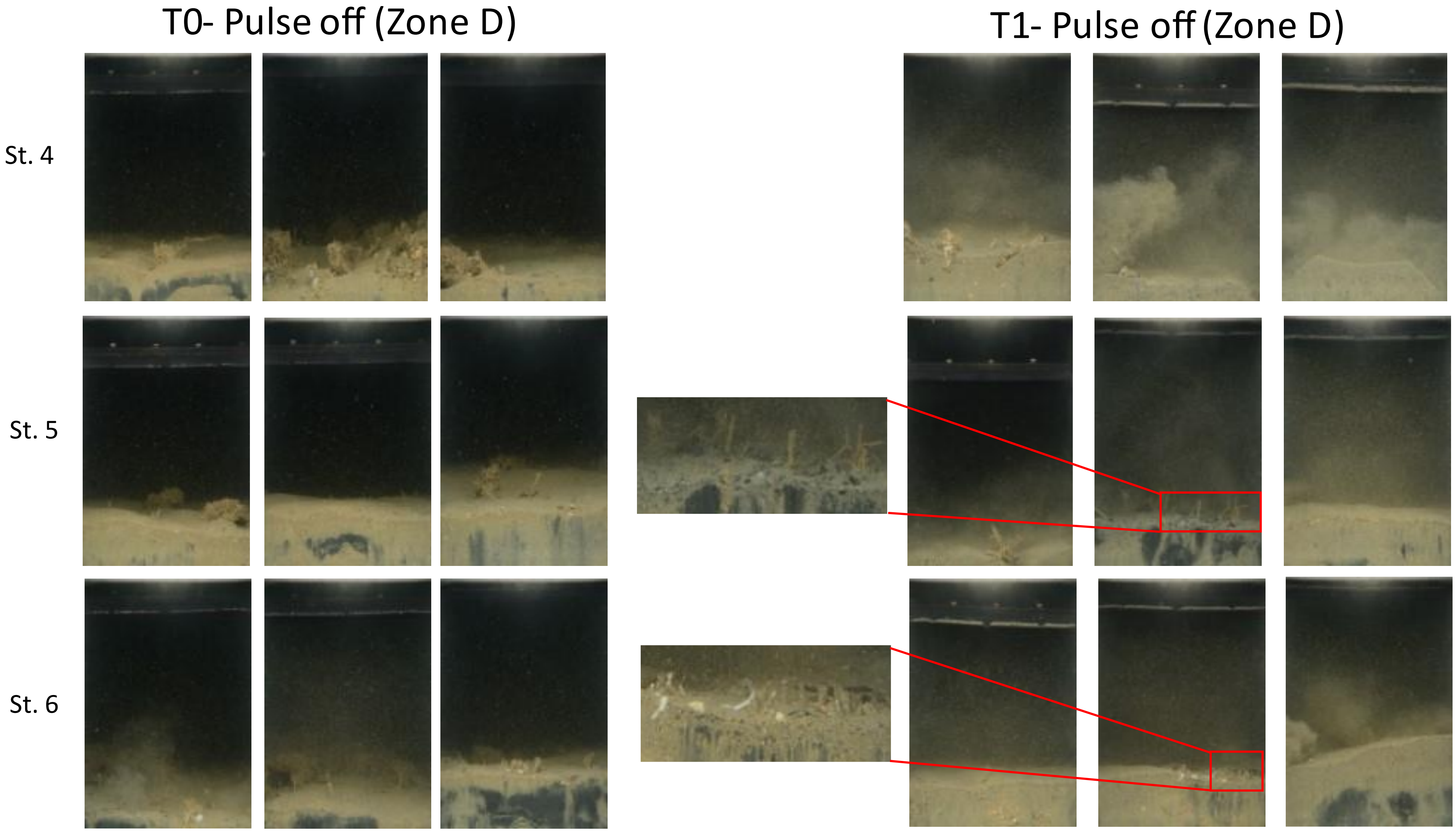
T1- Pulse on (Zone C)

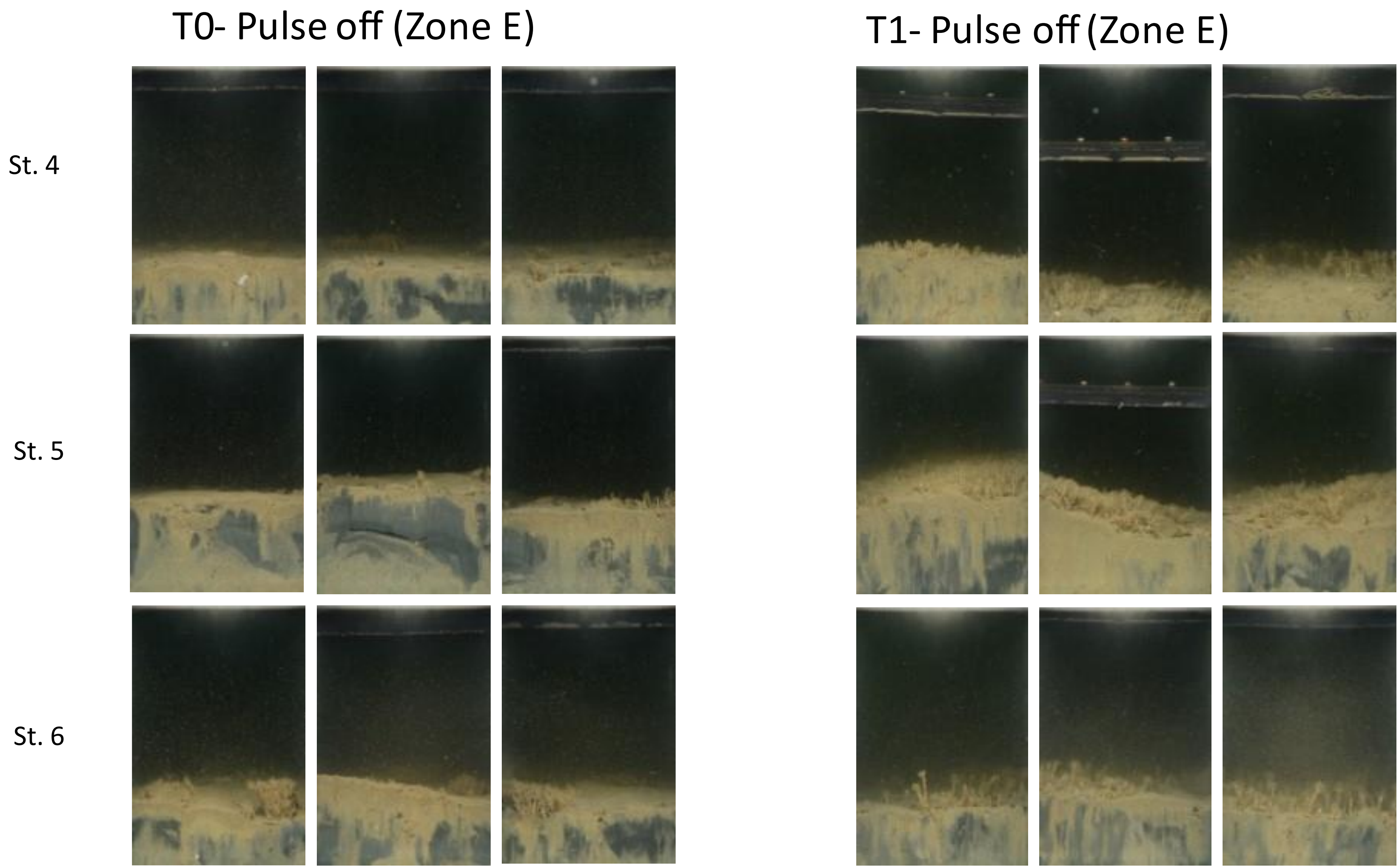
St.4

St. 5

St. 6




T0- Pulse off (Zone D)
T1- Pulse off (Zone D)
St. 4
St. 5
St. 6


T0- Pulse off (Zone E)
T1- Pulse off (Zone E)
St. 4
St. 5
St. 6

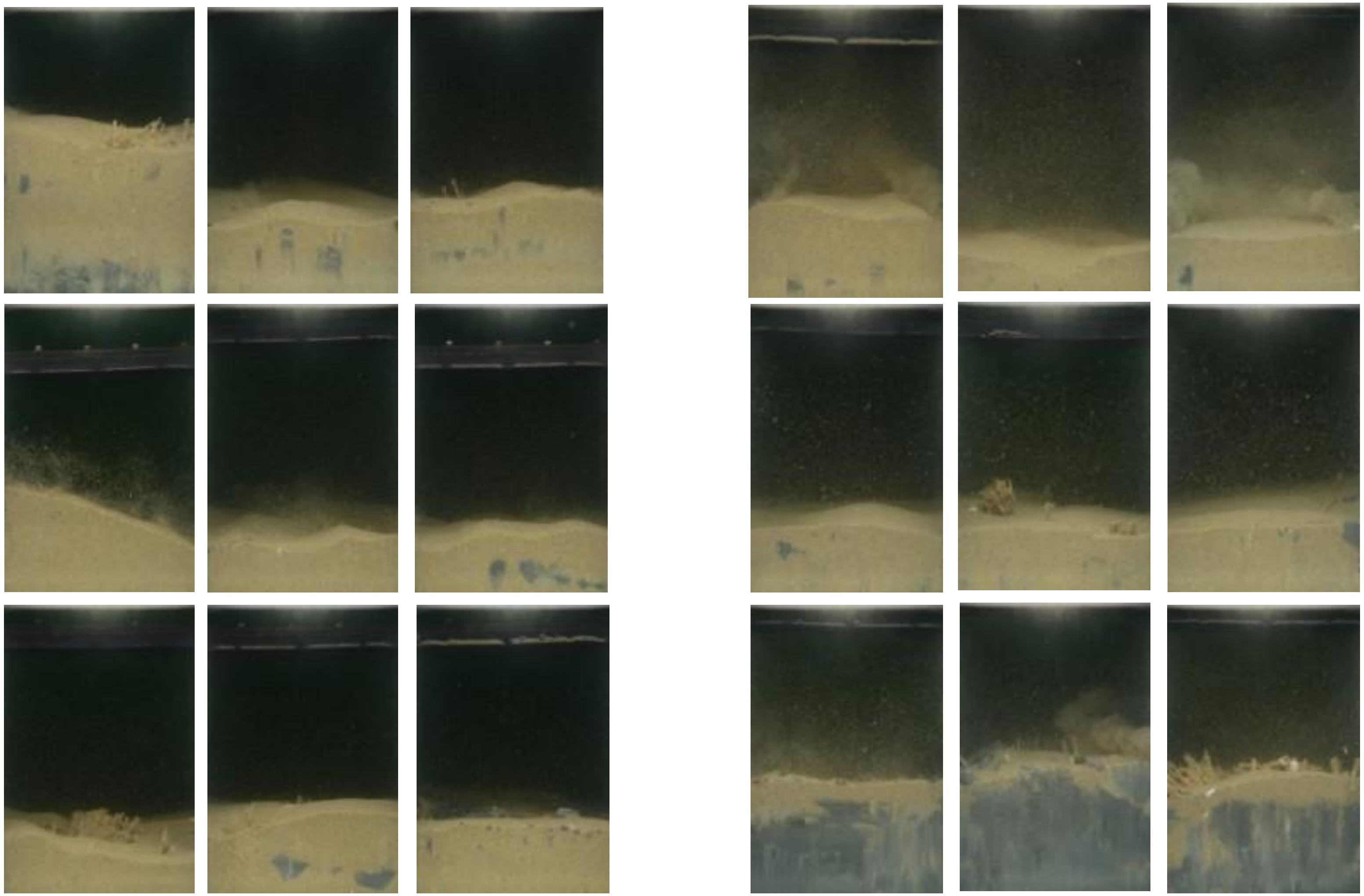
T0- Pulse off (Zone F)

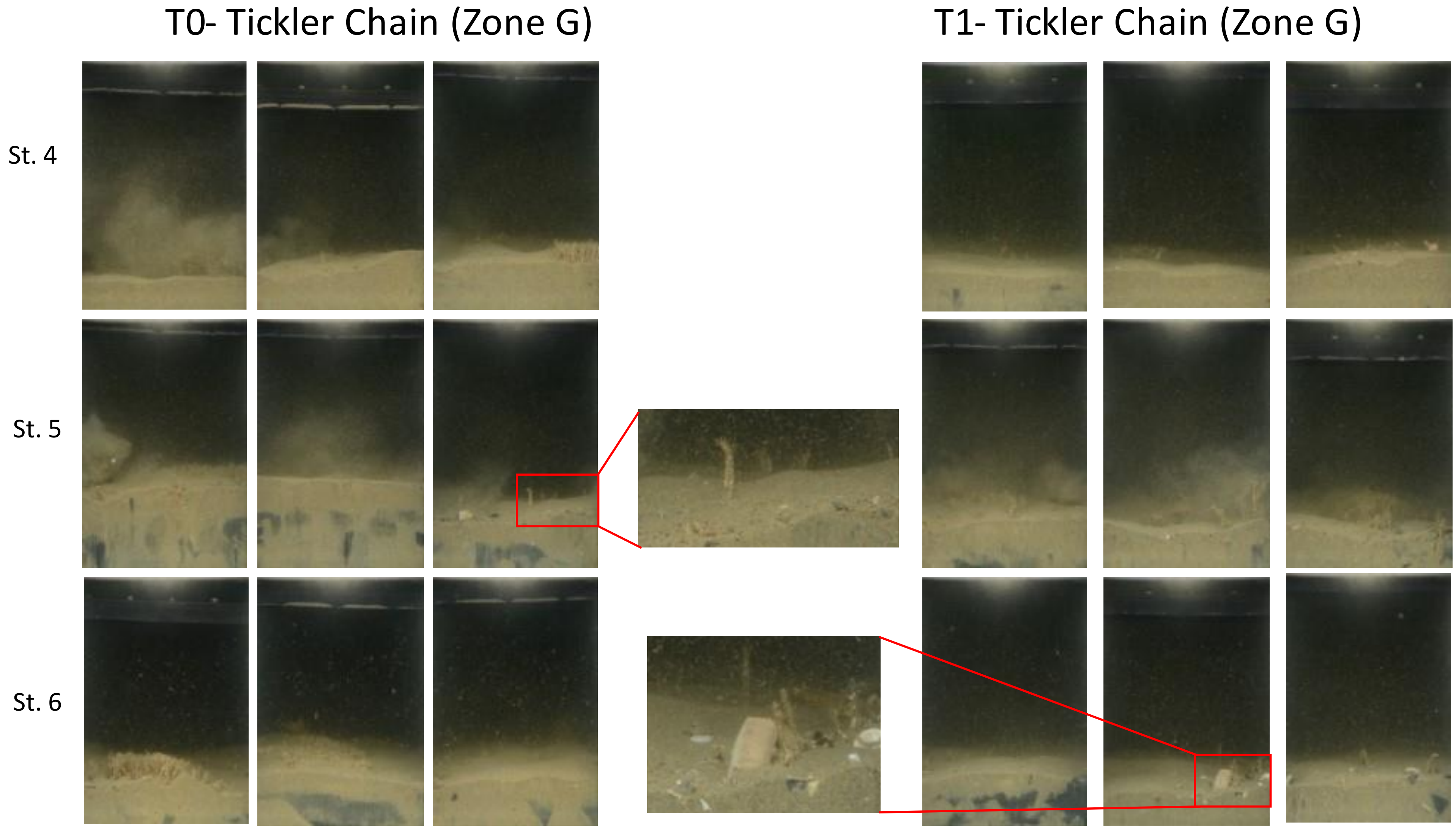
T1- Pulse off (Zone F)

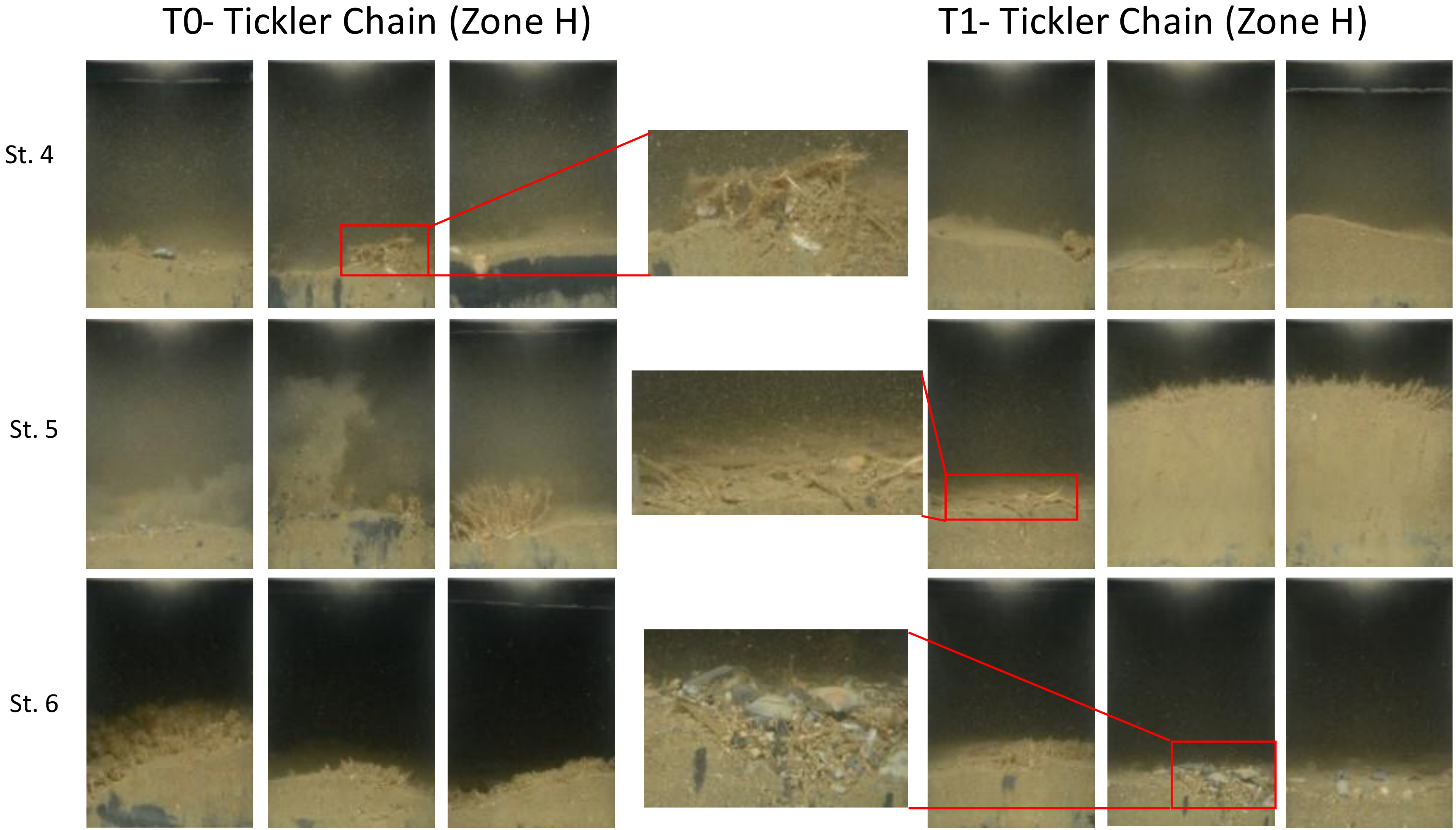
St. 4

St. 5

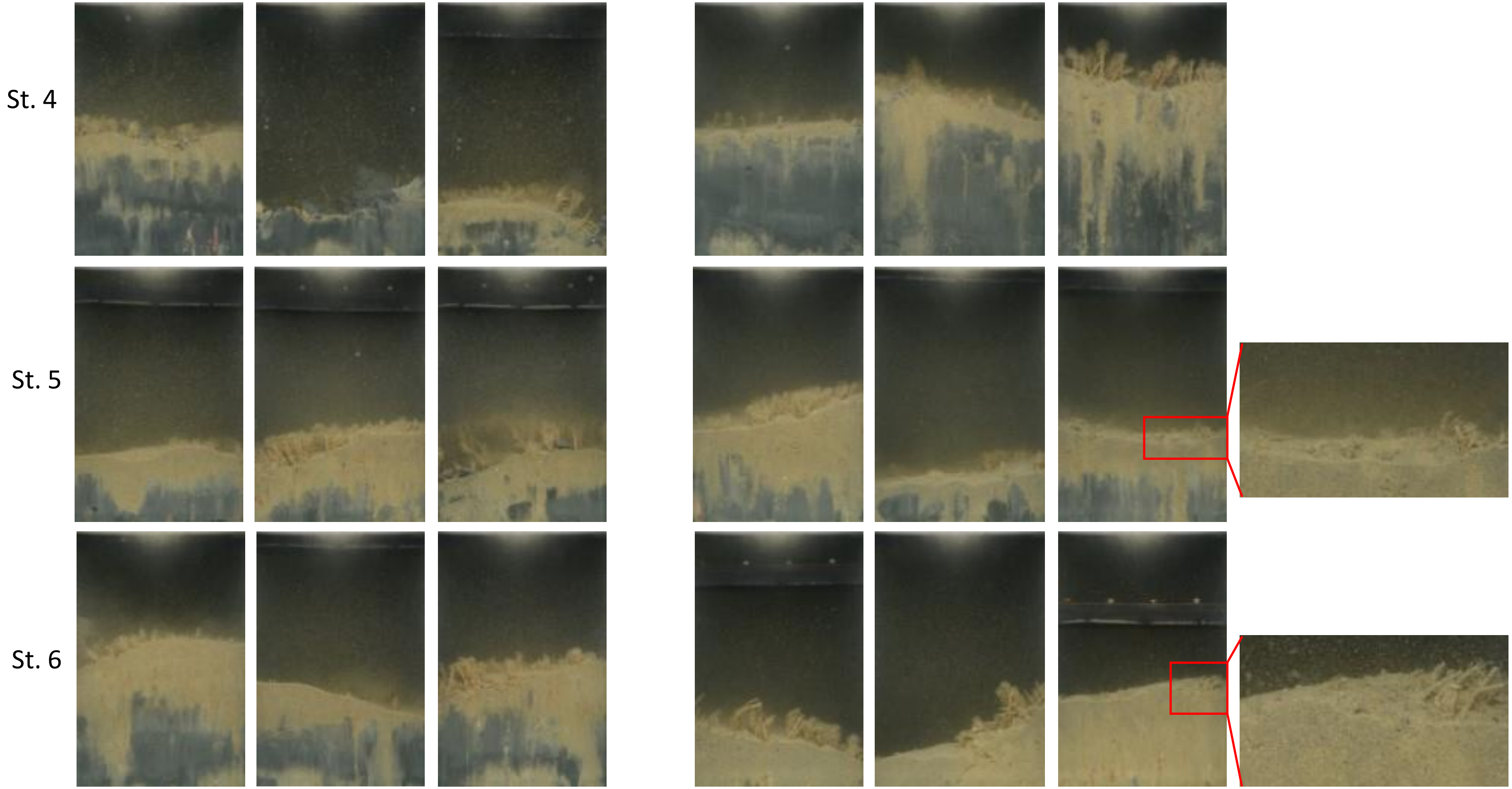
St. 6




T0- Tickler Chain (Zone G)
T1- Tickler Chain (Zone G)
St. 4
St. 5
St. 6

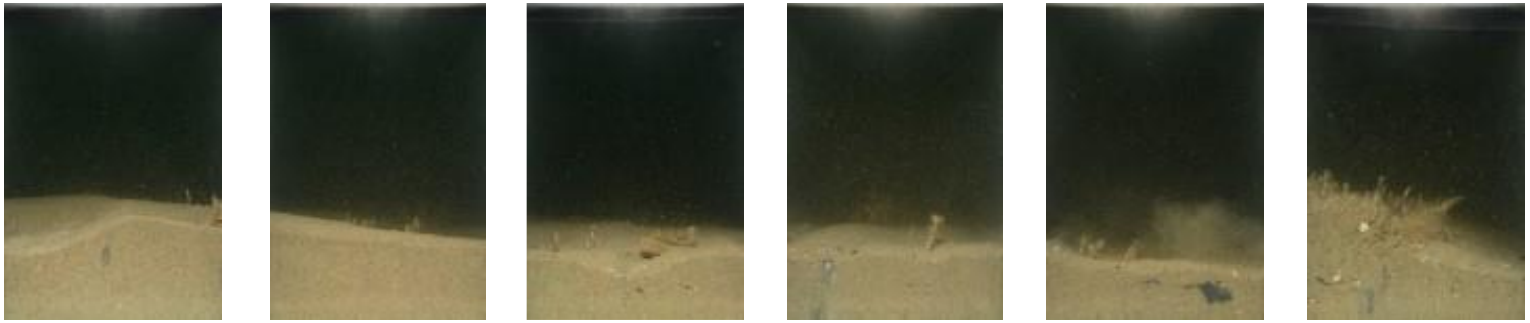

T0- Tickler Chain (Zone H)
T1- Tickler Chain (Zone H)
St. 4
St. 5
St. 6

T0- Tickler Chain (Zone I)   T1- Tickler Chain (Zone I)

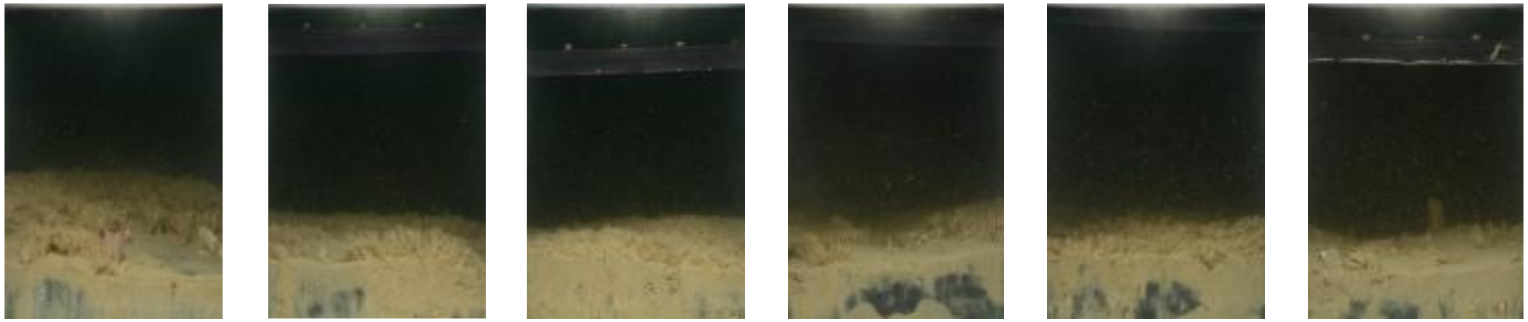


Reference

Reference T0



Reference T1



S.5. Mass budget modeling methodology

Sediment-water exchange fluxes of O_2, NH_4^+, NO_2^-, NO_3^-, and PO_4^{3-} calculated from the core incubations were used to estimate rates for total mineralization of organic matter, denitrification, nitrification and the specific mineralization and sequestration of nitrogen and phosphorous from the sediment. These fluxes were used to obtain integrated mass budget of these solutes within the sediment column following the methods in (Braeckman et al., 2010; Soetaert et al., 2001; Toussaint et al., 2021). Oxygen is consumed (Eq. 1) directly through oxic mineralization (*OxicMin*) and nitrification (2 moles O_2 consumed per 1 mole NO_3^- produced), and indirectly through anoxic mineralization (*AnoxicMin*), which produces reduced substances that are re-oxidized (*Reoxidation*) as they diffuse towards the sediment-water interface (Soetaert et al., 1996). Ammonium is produced through the mineralization of organic nitrogen (*Nmineralization*), which is derived from the total mineralization (*OxicMin* + *AnoxicMin* + *Denitrification*) multiplied by the Redfield N:C ratio (16:106), and removed through nitrification (Eq. 2). The mass balance of nitrate receives its input from nitrification and is removed through denitrification (0.8 moles NO_3^- removed per mole of carbon mineralized; Eq. 3). Inorganic phosphorus enters the system through the degradation of organic phosphorus (*Pmineralization*), which is calculated by multiplying the Redfield P:C ratio (1:106) with the total mineralization, and is removed through adsorption to solid particles (*Premoval*; Eq. 4). The mass balance equations describing these processes are summarized below:

$$\frac{dO_2}{dt} = O_2flux - OxicMin - Reoxidation - 2 * Nitrification \qquad \text{(Eq. 1)}$$
$$\frac{dNH_x}{dt} = NH_xflux + Nmineralization - Nitrification \qquad \text{(Eq. 2)}$$
$$\frac{dNO_x}{dt} = NO_xflux + Nitrification - 0.8 * Denitrification \qquad \text{(Eq. 3)}$$
$$\frac{dPO_4^{3-}}{dt} = PO_4^{3-}flux - Pmineralization - Premoval \qquad \text{(Eq. 4)}$$

The rates of sediment water exchange fluxes (O_2flux, NH_xflux, NO_xflux, PO_4^{3-}flux) were obtained from the sediment incubations. The assumption of a geochemical steady-state causes the rate of change for the selected solutes (left side of equations 1 – 4) to be set to zero. Quantities for total OM mineralization, denitrification, nitrification, and *Premoval* were determined using the R package 'limSolve' for linear inverse models using the function 'lsei' (Least Squares with Equality and Inequality Constraints; (Soetaert et al., 2009)). *Nremoval* was estimated as the 0.8 proportion of denitrification while the percent of total nitrogen and phosphorous removed after mineralization was calculated as 100 * Nremoval/Nmineralization (%N sequestered) and 100 * Premoval/Pmineralization (%P sequestered).