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Effects of sediment disturbance by the heart urchin *Echinocardium cordatum* on the sediment–seawater solute exchange: an exclusion experiment

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Abstract

Spatangoid heart urchins are dominant bioturbators in marine soft-sediment ecosystems worldwide. Their repeated sediment reworking prevents biogeochemical sediment stratification and colonisation by other species, with implications for sedimentary reaction processes that affect the local sediment–seawater solute exchange. Here, we used a simple exclusion experiment to investigate how a subtidal *Echinocardium cordatum* population (18.2 ± 6.7 individuals m^{-2}), foraging at an individual speed of ~45 cm per day affects the sediment–seawater solute exchange. To do so, we removed all heart urchins from eight one-meter-diameter areas of the 10-m deep seafloor of Man O'War Bay, Hauraki Gulf, New Zealand, and prevented recolonisation and hence sediment reworking for 56 days. Subsequently, we measured the sediment–seawater exchange of O_2, NO_3^-, NO_2^-, NH_4^+, and N_2 both within and outside the exclusion areas, under light or dark conditions, and found no difference. We conclude that, although foraging *E. cordatum* may enhance the sediment–seawater solute exchange in their immediate surrounding when and where they displace sediment particles, this effect does not necessarily outlast the particle displacement event. This underlines the importance of evaluating the influence of bioturbators on the sediment–seawater solute exchange in the context of local environmental conditions, urchin behaviour, and population characteristics.

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Introduction

Macrofaunal bioturbation profoundly influences the mineralisation of carbon in seafloor sediment by displacing particles and solutes (Aller and Aller, 1998; Banta et al., 1999; Solan and Wingham, 2005; Kristensen et al., 2012). Persistent sediment disturbances by, for example, bottom trawling or deposition of organic fish farm waste, can alter the composition of the resident macrofaunal assemblage and therefore affect carbon remineralisation rates and the associated sediment–seawater exchange of dissolved carbon and nitrogen. Because this exchange links seafloor with pelagic ecosystem functions, changes in sediment bioturbation can have far-reaching consequences for coastal primary and secondary production (Forster et al., 1995; Lohrer et al., 2004; Volkenborn et al., 2007).

Heart urchins of the genus *Echinocardium* Gray, 1825 have a disproportionally large influence on sedimentary transport and reaction processes (Osinga et al., 1997; Lohrer et al., 2004, 2005, 2015). They are globally widespread through soft sediment environments, inhabiting intertidal flats to abyssal plains, and can form up to 60% of the macrobenthic biomass in some ecosystems (Nakamura, 2001; De Ridder & Saucède, 2020). Functioning as key bioturbators, they alter the physical and biological structure of their surrounding sediment both directly, by mixing sediment particles and porewater, and indirectly, by supporting or suppressing the presence and activity of other benthic organisms (Lohrer et al., 2004, 2005; Kristensen et al., 2012).

One well-studied species of the genus *Echinocardium*, *E. cordatum* (Pennant, 1777), forages by burying itself at depths of up to 20 cm in sandy sediment and up to 6 cm in muddy (silt and clay) cohesive sediment (Buchanan, 1966; Foster-Smith, 1978; De Ridder & Saucède, 2020). Once buried, *E. cordatum* ploughs the sediment horizontally at speeds ranging from 1–8 cm h^{-1} (Buchanan, 1966; Lohrer et al., 2005; Vopel et al., 2007), selectively consuming microalgae and organic detritus (Smith, 1980; Boon & Duineveld, 2012; De Ridder et al., 2020). When foraging, *E. cordatum* can displace and mix 60–150 times more sediment particles than the amount it ingests (Hollertz & Duchêne, 2001; Lohrer et al., 2005).

To meet its respiratory requirements while buried, *E. cordatum* maintains a current that irrigates the restructured sediment with oxygenated seawater, thereby enhancing the oxidation of reduced solutes and particulates, a process that would otherwise be constained

by molecular diffusion. Using dorsal spines and tube feet, the urchin constructs and sustains a vertical funnel, connecting the ambulacrum with the sediment surface (Buchanan, 1966; Smith, 1980). The cilia of the ambulacral groove move oxygenated seawater down this funnel, facilitating gas exchange over respiratory tube feet (Buchanan, 1966; De Ridder & Saucède, 2020). To prevent suffocation due to the collapse of the respiratory funnel, the funnel-building tube feet excrete and apply mucus to the wall of the funnel (Kanazawa, 1995; De Ridder & Saucède, 2020). Once the urchin has abandoned the funnel, microbial activity degrades the mucus, causing the funnel to eventually collapse (Foster-Smith, 1978). Individuals dwelling in shallow cohesive sediment often maintain a second, larger funnel that connects the sediment surface in front of the urchin with the urchin's mouth (Vopel et al. 2007). Furthermore, subanal spines and tube feet construct and sustain a sanitary drain, extending laterally behind the urchin to accommodate excrements (De Ridder & Saucède, 2020).

The displacement of particles and porewater by *E. cordatum* may create effects that last beyond the duration of the displacement event. For example, the tracks of *E. cordatum* contribute to the small-scale roughness of the sediment surface, potentially influencing the solute transport across the sediment–seawater interface (Buchanan, 1966. Vopel et al. 2007). Furthermore, particle mixing can stimulate sedimentary remineralisation and oxidation processes by, respectively, introducing fresh organic matter into subsurface sediment layers either in the form of excrements or by displacement from the surface, and displacing reduced particles at depth to the surface, where they are exposed to oxygenated seawater (Aller, 1982; Glud, 2008; Lohrer et al., 2004; Vopel et al., 2007). These effects can collectively enhance the remineralisation of labile and refractory organic carbon, potentially altering the rates of the sediment–seawater exchange of dissolved carbon and nitrogen.

If the influence of an *E. cordatum* population on sedimentary solute transport and reaction processes extends beyond the sediment in the immediate surrounding of an individual, then removing this species from the seafloor ecosystem should result in measurable changes in solute exchange across the sediment surface between individuals and outside their immediate surroundings. Here, we report the results of a study in which we experimentally tested this prediction. To do so, we removed urchins from eight plots of the 10-m deep seafloor of Man O'War Bay, Hauraki Gulf, New Zealand, and prevented recolonisation and

thus sediment reworking for about two months, and then measured the sediment–seawater exchange of O_2, NO_3^-, NO_2^-, NH_4^+, and N_2 within and outside the exclusion areas under conditions of light or darkness.

Methods and Materials

Study site

Man O'War Bay is situated on the east coast of Waiheke Island in the Hauraki Gulf, New Zealand (S 36° 47' 38", E 175° 10' 14", Fig. 1). The Hauraki Gulf covers nearly 4,000 km^2, with water depths up to 50 m and provides sheltered conditions that facilitate particle settling. The sediment in Man O'War Bay, which is a mix of terrigenous mud (silt and clay) and calcareous gravel and sand (Manighetti & Carter, 1999), is iron-rich, resulting in a dark grey-to-black subsurface layer due to an abundance of iron sulphides. Organic matter accounts for >6 % of the sediment dry weight, but the pore water of the top 20 cm of the sediment remains free of dissolved sulphides (Wilson & Vopel 2012).

The seafloor at our 10-m deep site in Man O'War Bay is devoid of macroalgae and sessile epifauna, with golden-brown diatom patches that accentuate the centimetre-scale surface topography shaped by two bioturbators: a burrowing mud shrimp of the genus *Upogebia*, and the ploughing heart urchin *E. cordatum*. Other macroinfauna consists of small polychaetes (*Prionospio*, *Sthenelasi,* and *Cossura*), an amphipod species (*Paraphoxus*), and a bivalve species (*Theora lubrica*) (Wong & O'Shea 2010).

To describe the resident population of *Echinocardium cordatum*, a seafloor survey was conducted two weeks before the exclusion experiment. SCUBA divers used a GoPro Hero 4 camera to capture a still images of a 0.5 × 0.5-meter quadrate placed on the surface of the seafloor at 40 locations randomly distributed within a 1260 m^2 area. At 10 locations, time-lapse photography was used to estimate the speed at which individuals ploughed the sediment.

Experimental procedures

On 3 May 2022, two SCUBA divers buried eight plastic rings (1 m diameter, 28 cm wide) within a ~700 m^2 circular area. The placement of each ring was carried out with a 30-m guide rope anchored in the sediment and eight pre-determined compass/distance

coordinates (i.e., 0–360 degrees, 1–30 m away from the anchor). The divers pushed each ring ~25 cm deep into the sediment, leaving about 3 cm exposed above the sediment surface. Subsequently, they carefully removed all urchins (10–20 individuals per ring) from the area within the rings. The rings remained free of *E. cordatum* and in place for 56 days, effectively isolating the enclosed sediment from further sediment restructuring by the urchins.

On 27 June 2022, the divers returned to collect one intact sediment core from within and outside each ring. To do so, they placed an acrylic tube (height: 300 mm, internal diameter: 90 mm) perpendicular to the seafloor and pushed it into the sediment until two-thirds were filled. They then inserted a lid with an open valve into the protruding end of the tube. This was done slowly, to avoid creating pressure inside the tube that would otherwise resuspend the silt sediment. Following this, the divers inserted a lid in the buried end of the tube pushing the sediment core inside the tube upwards by about one centimetre. They then closed the valve in the top lid and lifted the core out of the sediment. The sediment cores were stored upright in two large 50 L ice boxes and transported to the laboratory within two hours.

Laboratory setup

In the laboratory, we removed the top lids of the acrylic tubes, and then submerged the sediment cores in the recirculating seawater of two 450-L holding tanks for acclimatisation. A third and identical tank (measurement tank) was set up to which sets of 5 cores were transferred for sediment–seawater solute flux measurements (see below).

Each tank was fitted with a pump (3260, Eheim) that moved the seawater through a chiller unit (HC Chiller 300A, Hailea) and a UV steriliser (Pond One UV-C 9W, ClearTec) to a 200 L header tank from which the seawater returned to the tank by gravity. The chiller maintained the seawater temperature close to the in-situ seawater temperature (15 ± 0.5 °C). An additional pump pushed seawater through a UV particle filter (Aqua One Ocellaris 1400 UVC). A wave maker (SW, Jebao) attached to the inner wall of each tank, along with two jets of returning seawater from the UV particle filter and the header tank, ensured that advection was sufficient to prevent the seawater overlying the submerged sediment cores from becoming stagnant. Each tank had a Kessil A160WE Tuna Blue LED mounted above it,

gradually increasing the intensity of photosynthetically active radiation (PAR) from 06:00 h to a midday maximum of ~120 µmol quanta m^{-2} s^{-1} and then gradually decreased this intensity until 18:00 h, when the LED was turned off. To account for evaporation, we monitored and adjusted the salinity of tank water each morning using reverse osmosis water.

Solute flux measurements

We transferred four cores at a time from the holding tanks into the measurement tank to determine the sediment–seawater solute flux under conditions of light and darkness. The light and dark solute flux was derived from the difference in the solute concentration in seawater collected ~10 mm above the sediment surface before and after a 4-h incubation period. During this period, the acrylic tube holding the sediment core and its overlying seawater was closed with a valved O-ring sealed lid. A peristaltic pump recirculated the enclosed seawater through Teflon tubes to prevent stagnation. The seawater oxygen concentration was measured at the beginning and the end of each incubation with a dipping probe (DP-PSt3, Presens GmbH) connected to a portable fibre optic oxygen meter (Microx 4, Presens GmbH).

Sample analyses

For analyses of nitrate, nitrite, and ammonium, we collected, filtered (Sartorius CA 0.45 µm filter), and froze 10 mL of the seawater from each core, at the beginning and the end of each incubation. These samples were kept frozen until analyses. Seawater aliquots collected for N_2 analyses (2 x 12 ml exetainers) were poisoned with 0.01 mL of mercuric chloride. Following the seawater sampling, we decanted the seawater above the sediment cores, extruded the cores, and extracted the top 2 cm of sediment for granulometric analyses.

We determined the sediment granulometric indices by laser particle size analyses (Mastersizer 2000, Malvern Instruments Ltd.) of 10 homogenised samples, and the sediment water content as the loss of weight after 24 h drying at 90 °C. The seawater N_2 content was measured with a Pfeiffer Prismaplus QME mass spectrometer and a Bay Instruments S-25-75D membrane inlet X, and the seawater concentrations of nitrite, nitrate, and ammonium were determined with an Astoria Pacific 2 micro-segmented flow analyser following the Astoria protocols A177, A182, and A027 for operating their respective individual nutrient channels.

Solute flux estimates

We determined the sediment–seawater solute flux (µmol m^{-2} h^{-1}) considering the start–end difference in solute concentrations, the volume of enclosed seawater, the surface area of the sediment core, and the duration of the incubation. Because previous measurements revealed that the consumption/production of solutes in the seawater itself is negligible, this was not considered in our flux calculation. Note that a positive flux indicates sediment consumption whilst a negative flux is interpreted as solute release from the sediment.

Statistical Analysis

We performed all statistical data analyses with RStudio (R Core Team, 2022), used Shapiro-Wilk tests to check normality of our data, and a two-way analysis of variance (ANOVA) to further investigate the effects of light conditions, treatment, and their interaction, on the sediment–seawater exchange rate for each solute. When a significant result was found, we followed with post-hoc TukeyHSD analyses to further investigate significant individual effects.

Results

The sediment in the sheltered Man O'War Bay consisted of ~74% silt, 17% sand, and ~9% clay. The laser particle size analyses returned the following granulometric indices: Median = 30 µm (silt), Lower Quartile Q1 = 63 µm, Upper Quartile Q3 = 10 µm, Inclusive Sorting Coefficient QD1 = 1.95 (poorly sorted), and Inclusive Graphic Skewness Sk_1 = 0.07. The water content of the sediment decreased from 75% in the top 2 cm to 65% at 9 cm depth.

Analyses of 100 photographs of the sediment surface revealed ~18.2 $\pm$ 6.7 (mean $\pm$ SD, n = 100) *Echinocardium cordatum* individuals per square meter. Time-lapse videos showed that urchins moved at ~45 $\pm$ 12 cm per day (mean $\pm$ SD, n = 6).

The sediment between foraging *E. cordatum*, away from the immediate surrounding of the urchin (at the time of sampling), consumed O_2 at similar rates under conditions of darkness and light (Table 1). In light, this sediment took up on average ~39% more N_2 from the overlying seawater then under conditions of darkness, although this difference was not significant. The average sediment–seawater fluxes of nitrate and nitrite were an order of

magnitude lower than that of N_2; on average nitrate was released while nitrite was taken up by the sediment, at similar rates under conditions of light and darkness.

The flux of ammonium in light differed significantly from that measured in darkness (Table 2). In light, the sediment released ammonium into the overlying seawater, while the average of fluxes measured in darkness indicated a small uptake (Table 1).

Effect of sea urchin exclusion

The solute fluxes across the surface of the sediment collected within the exclusion rings did not significantly differ from that measured in the Control sediment, under conditions of both light and darkness.

Discussion

We expected that the exchange of dissolved oxygen and nitrogen across the surface of the sediment that lies beyond the immediate surrounding of foraging *E. cordatum* individuals would reflect a history of repeated reworking, so that after a 56-day cessation of this reworking a measurable change in this exchange could be observed. Our measurements, however, did not confirm such change. We considered the potential influence of *E. cordatum* on sedimentary solute reaction processes; repeated particle mixing and porewater oxygenation should have altered remineralisation rates and thus modified the associated sediment–seawater solute exchange. Apparently, the rate at which the sediment was mixed and oxygenated by the resident *E. cordatum* population did not cause the expected influence, so that the removal of urchins didn't make a difference.

Besides the potential direct effects of sediment mixing on microbial reaction processes, we expected indirect effects, which can result from the influence of *E. cordatum* on cohabiting biota, most importantly, benthic microphytes. Photosynthesis of microphytes can cause dark/light differences in the total sediment–seawater O_2 exchange as measured by core incubations, and an influence of *E. cordatum* on the abundance and activity of microphytes would then be evident from either an increase or decrease of these differences. Our sediment core incubations revealed, however, that the Control sediment removed as much O_2 from the bottom seawater in darkness than it did in light (Table 1). Assuming that the O_2 demand of the sediment in light did not differ from that in darkness, this suggests that benthic photosynthetic O_2 production must have been negligible. If this was the result of

heart urchin predation limiting the growth of microphytes, then we would expect algae growth and photosynthesis to increase following the exclusion of the heart urchins. However, there was no evidence of such increase; apparently, benthic primary production in the Control sediment was not limited by predation, so that removal of predation as a potential factor made no difference.

Other studies reported a positive correlation between the abundance *E. cordatum* (consuming microphytobenthos) and the chlorophyll *a* content of its surrounding sediment (Needham et al., 2011; Lohrer et al., 2004, 2005, 2015). In habitats where photosynthetically active radiation (PAR) is not limiting microphytobenthic production, this may follow from a stimulation of bacterial mineralisation processes, increasing the porewater concentrations of inorganic nitrogen, so that algal growth outweighs consumption. Such gardening effect will be subject to seasonal variations in environmental conditions and heart urchin abundance and activity. Lower PAR and temperature in winter, for example, can hamper benthic primary production and slow urchin movement, respectively (Seike et al., 2022). A repeat of our study in November/December may reveal if the influence of *E. cordatum* on the sediment–seawater solute exchange at our site in fact depends on seasonal changes in conditions for growth and production of microphytes or if what we have observed in May/June generally applies throughout the year.

Interestingly, both sediments, Control and Treatment, served as a sink for N_2, on average removing more nitrogen in light than in darkness. This light–dark difference, however, was short of being significant. Others have reported nitrogen fixation in ammonium-rich sediments, like those found in seagrass beds (Aoki & McGlathery, 2019) or subtidal coastal sediments (Fulweiler et al., 2007, Newell et al., 2016), and such fixation may be limited to microenvironments in which nitrogen becomes limiting (Whiting et al. 1986). As Bertics et al. (2013) pointed out, however, sediments rich in organic matter and reduced substrates provide an unusual conundrum for anaerobic organisms—the excess electrons can damage cells and there is a need to regenerate electron carriers. Nitrogen fixation may be a mechanism for dissipating reducing power and maintaining an ideal intracellular redox state (Joshi & Tabita, 1996, Bombar et al., 2016), so that nitrogen fixation is observed despite high ammonium concentrations.

The significant light–dark difference in the ammonium exchange of the Control sediment—a small uptake under conditions of darkness, but release in light—suggests an influence of photosynthesis on nitrogen cycling. This is contrast to the interpretation of our light/dark O_2 exchange data (negligible benthic photosynthesis, see above), and raises the question if our assumption of similar sediment O_2 demand in light and darkness was valid. If the sediment O_2 demand in light was greater than in darkness, then benthic photosynthesis may have played a role without leaving a measurable signature in the total sediment–seawater O_2 exchange. Assuming that the ammonium and N_2 concentrations in the sediment overlying seawater remained stable and independent of light, then the difference in the derived sediment–seawater flux must have resulted from changes in the sediment porewater solute concentrations. Phototrophs assimilating ammonium in darkness, but not in light, would then cause a light/darkness difference in the sediment–seawater ammonium exchange. Similarly, if more porewater N_2 was to be consumed by diazotrophs in light than in darkness (energy limited N_2 fixation; Stal, 2015), then this would explain why the sediment uptake was greater in light than in darkness. Alternatively, a production of N_2 via anammox in darkness would increase the porewater N_2 concentration and so lower the rate at which the sediment removes N_2 from the bottom seawater. Because this process also lowers the porewater ammonium concentration, it can explain both observations, a lower release or even uptake of ammonium, and lower uptake of N_2 under conditions of darkness.

In conclusion, although foraging *E. cordatum* enhance the sediment–seawater solute exchange where and when they displace sediment particles, this effect does not necessarily outlast the disturbance event. At our subtidal site, at least in May/June, removal of the heart urchins did not alter the solute exchange across the surface of the sediment area that is not actively disturbed. This underlines the importance of evaluating the influence of bioturbators on ecosystem processes in the context of local environmental conditions, seasonal changes in these conditions and biological activity, urchin behaviour, and population characteristics.

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M.S. measured the inorganic nitrogen content of seawater samples, and R.M. and K.V. analysed the data and wrote the manuscript.

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Figure captions

Figure 1. Map depicting the study site Man O'War Bay (yellow marker), at the East shore of Waiheke Island, Hauraki Gulf (S 36° 47' 38", E 175° 10' 14"). Insert: North Island, New Zealand.

Figure 2. (A) Sediment surface at Man O'War Bay, Hauraki Gulf, New Zealand, showing tracks (tr) made by the heart urchin *Echinocardium cordatum*. Orange arrows indicate the direction of the heart urchin's movement. Black arrows indicate the respiratory (rf) and feeding (ff) funnels. Larger holes are the openings of shrimp burrows. Darker areas lining the tracks are diatoms. (B) Schematic illustrating the direction and magnitude of the sediment–seawater solute flux under conditions of light (light grey arrows) and darkness (dark grey arrows). The horizontal line indicates the sediment surface.

Figure 3. Solute flux across the surface of sediment cores collected outside (Control) and inside (Treatment) urchin exclusion rings 56 days after ring deployment. The solute flux was measured under conditions of light (L) and darkness (D). Negative flux indicates sediment solute release. The asterisk indicates a significant difference.

Table 1. Sediment–seawater flux (µmol m^{-2} h^{-1}, Mean ± SD, n = 9) of ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), nitrogen gas (N_2), and oxygen (O_2) in darkness and light, derived from laboratory incubations of sediment collected in Man O' War Bay, Hauraki Gulf, New Zealand outside (Control) and inside (Treatment) sea urchin exclusion rings after 56 days. A positive flux indicates sediment solute uptake.

	Control		Treatment	
	Darkness	Light	Darkness	Light
N_2	121.4 ± 43.7	169.2 ± 53.7	93.7 ± 37.6	141.3 ± 43.9
O_2	149.6 ± 34.9	140.4 ± 34.3	148.2 ± 44.4	137.6 ± 69.3
NO_2^-	13.3 ± 29.0	8.1 ± 39.7	5.8 ± 11.9	7.6 ± 24.7
NO_3^-	-22.8 ± 31.9	-22.9 ± 40.5	-18.2 ± 13.9	-22.4 ± 29.5
NH_4^+	2.5 ± 44.4	-49.7 ± 21.0	-6.5 ± 17.4	-30.4 ± 18.0

Table 2. Two-way ANOVA and TukeyHSD (adjusted P Values, CI 95%) of the solute flux across the surface of sediment cores collected outside (Control, C) and inside (Treatment, T) urchin exclusion rings following a 56-day deployment. The solute flux was measured under conditions of light (L) and darkness (D).

	C : T	D : L	Interaction	TukeyHSD
N_2	0.055	0.179	0.456	
O_2	0.458	0.247	0.429	
NO_2^-	0.674	0.857	0.714	
NO_3^-	0.803	0.839	0.843	
NH_4^+	0.577	0.00023	0.133	CL:CD < 0.025; CL:TD < 0.019

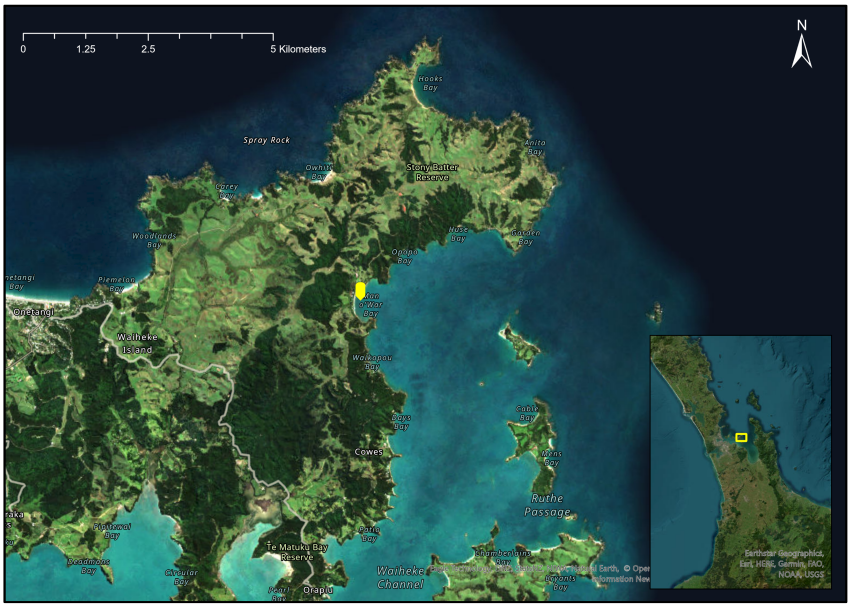
0
1.25
2.5
5 Kilometers
N
Hooks Bay
Spray Rock
Anita Bay
Stony Batter Reserve
Owhiti Bay
Corey Bay
Woodlands Bay
Hobbs Bay
Golden Bay
Opoid Bay
Piemiemi Bay
Oneraingi
Waiheke Island
Man O War Bay
Waikanoi Bay
Cable Bay
Bays Bay
Cowes
Wilds Bay
Ruthe Passage
Palm Beach
Te Matuku Bay Reserve
Waiheke Channel
Oneroa Bay
Orapiu
Earthstar Geographics, Esri, HERE, Garmin, FAO, NOAA, USGS

Figure 1.

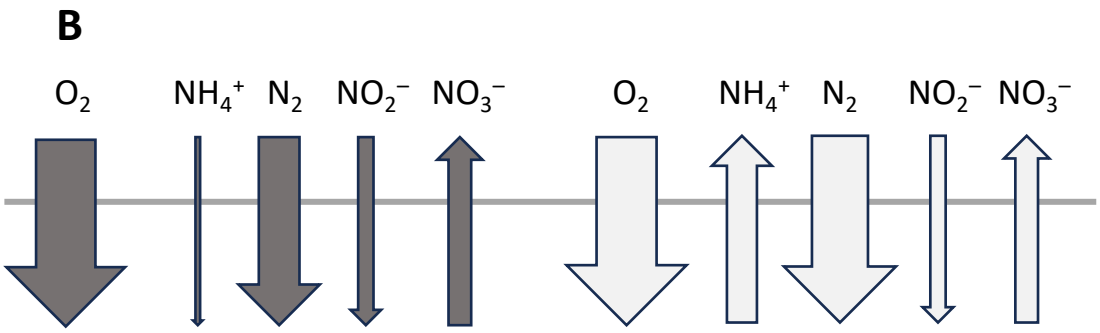

Figure 2.

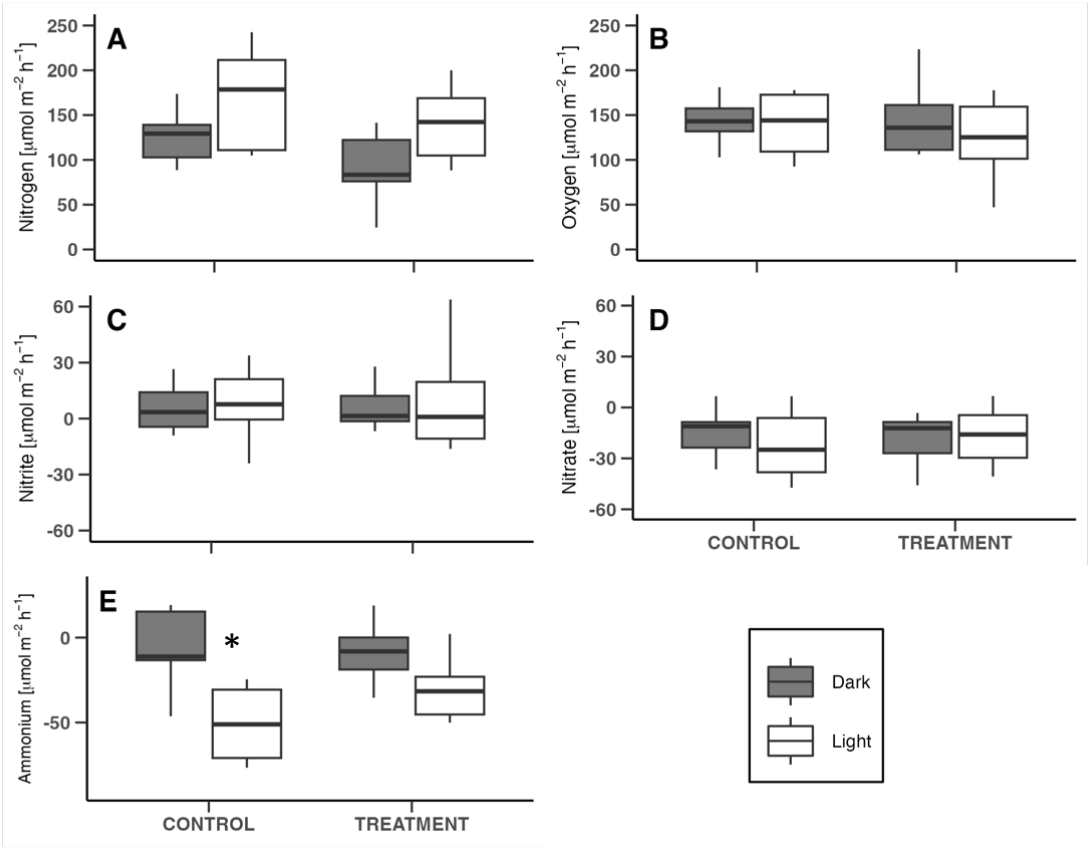
A
B
C
D
E
Nitrogen [µmol m^{-2} h^{-1}]
Oxygen [µmol m^{-2} h^{-1}]
Nitrite [µmol m^{-2} h^{-1}]
Nitrate [µmol m^{-2} h^{-1}]
Ammonium [µmol m^{-2} h^{-1}]
250
200
150
100
50
0
60
30
0
-30
-60
-50
*
CONTROL
TREATMENT
Dark
Light

Figure 3.