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# Marine Pollution Bulletin

## Benthic nutrients and oxygen fluxes at the water sediment interface in a pearl farming atoll (Ahe, Tuamotu, French Polynesia)

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<b>Abstract:</b>	<p>Benthic exchanges of oxygen and nutrient at the sediment-water interface were investigated under light and dark conditions at 5 sites in a sub-tropical atoll. Mean oxygen fluxes were <math>-1316.5 \pm 242.0 \mu\text{mol m}^{-2} \text{h}^{-1}</math> and mean effluxes of oxygen under light conditions were <math>2231.7 \pm 626.4 \mu\text{mol m}^{-2} \text{h}^{-1}</math>, presumably due to microphytobenthos present at the sediment-water interface. The consequences of this high related productivity was a systematic consumption of nutrients (<math>\text{DIN}</math>, <math>\text{PO}_4</math> and <math>\text{Si(OH)}_4</math>) during almost all light incubations, contrasting with the effluxes of nutrients during dark incubations. Our results suggest that sediments were net autotrophic and the oxygen balance in favor of microbenthic production versus community demand. Diurnal rates of gross benthic primary productivity were high (<math>3423 \pm 1192 \mu\text{mol m}^{-2} \text{h}^{-1}</math>) which emphasize the role of microphytobenthos in maintaining the oxygen reservoir in tropical lagoons.</p>

## Benthic Nutrients and oxygen fluxes at the water sediment interface in a pearl farming atoll (Ahe, Tuamotu, French Polynesia)

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**Keywords:** Benthic nutrient fluxes, sediment respiration, phytobenthic production, Atoll lagoon, Pearl farming, French Polynesia

### ABSTRACT

Benthic exchanges of oxygen and nutrient at the sediment-water interface were investigated under light and dark conditions at 5 selected sites in a sub-tropical atoll. Mean oxygen fluxes were  $-1316.5 \pm 242.0 \mu\text{mol m}^{-2} \text{h}^{-1}$  and mean effluxes of oxygen under light conditions were  $2231.7 \pm 626.4 \mu\text{mol m}^{-2} \text{h}^{-1}$ , presumably due to microphytobenthos present at the sediment-water interface. The consequences of this high related productivity was a systematic consumption of nutrients (DIN,  $\text{PO}_4$  and  $\text{Si}(\text{OH})_4$ ) during almost all light incubations, contrasting with the effluxes of nutrients during dark incubations. Our results suggest that the sediments were net autotrophic and the oxygen balance in favor of microbenthic production when compared to community demand. Diurnal rates of gross benthic primary productivity were high ( $3423 \pm 1192 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) which emphasize the role of microphytobenthos in maintaining the oxygen reservoir in tropical lagoons.

### 1. Introduction

Sediment compartment contributes intensely to the biogeochemical cycling of organic matter through mineralization of settled particles driven by living benthic macro and microorganisms (Aller & Cochran, 2019; Middelburg et al., 1993; Middelburg, 2018). These processes have a profound effect on the local and global cycling of many elements (Burdige, 2006) especially in coastal areas due the shallowness of the water column and the high primary production compared to open ocean (Kopp et al., 2015). Benthic pelagic coupling processes play a major role in the balance between carbon preservation and

40 remineralization (Ehrnsten et al., 2019). Moreover, most of the microbial degradation and nutrient  
41 recycling occurs at the sediment-water interface where benthic microbes are confined and gather  
42 most valuable electron acceptors for organic matter degradation (Canfield et al., 2005). As a  
43 consequence, recycled nutrients can return to surface waters via mixing processes (Caffrey et al., 2002)  
44 and supply potentially the pelagic N and P demand for phytoplankton production (Grenz et al., 2003;  
45 Boynton et al., 2018).

46 As the pelagic plankton represents the main portion of the black pearl oyster (*Pinctada margaritifera*)  
47 diet for juveniles and adults, productivity of oyster farming depends on pelagic phytoplankton biomass.  
48 Pelagic primary production was shown to be nitrogen limited in Ahe atoll (Charpy et al., 2012; Pagano  
49 et al., 2017). Gaertner-Mazouni et al. (2012) estimated that benthic nitrogen fluxes could contribute  
50 up to 28% of the pelagic nitrogen demand.

51 Due to the shallowness of coastal environments, benthic primary production may be significant at  
52 some sites, even where only small amounts of light reach the sediment surface (Jahnke et al. 2000).  
53 Microphytobenthos (MPB), a mixture of benthic unicellular algae and cyanobacteria (MacIntyre et al,  
54 1996) significantly contributes to primary production, and it is responsible for more than 50% of the  
55 total primary production in some shallow waters (Underwood & Kromkamp, 1999; Underwood, 2002).  
56 Indeed, benthic primary production can considerably moderate the sediment–water fluxes of nutrients  
57 (Sundbäck *et al.*, 1991) and compete with the macroalgal mats for the sediment nutrient pool  
58 (Sundbäck and Miles, 2002). In some sub-tropical lagoons, photosynthetic oxygen production by MPB  
59 enhance oxygen availability and increase oxygen penetration into the sediment favouring coupled  
60 nitrification-denitrification within the sediments (An and Joye 2001).

61 Sub-tropical atoll lagoons are generally highly productive ecosystem compared to the surrounding  
62 oligotrophic ocean (Harcher 1997). Their shallowness and the very high amount of light at sediment  
63 surface may facilitate the microphytobenthic primary production and nutrient regeneration and  
64 accentuate the asymmetric light-nutrient competition between benthic and pelagic primary producers  
65 in freshwater (Jäger and Diehl, 2014) and marine (Chatterjee et al., 2013) systems.

66 The aim of this study was to quantify spatial patterns in oxygen and nutrient exchanges at the sediment  
67 water interface and the role of MPB in nutrient cycling in a sub-tropical lagoon submitted to intense  
68 black pearl oyster cultivation in French Polynesia.

## 69 **2. Materials and Methods**

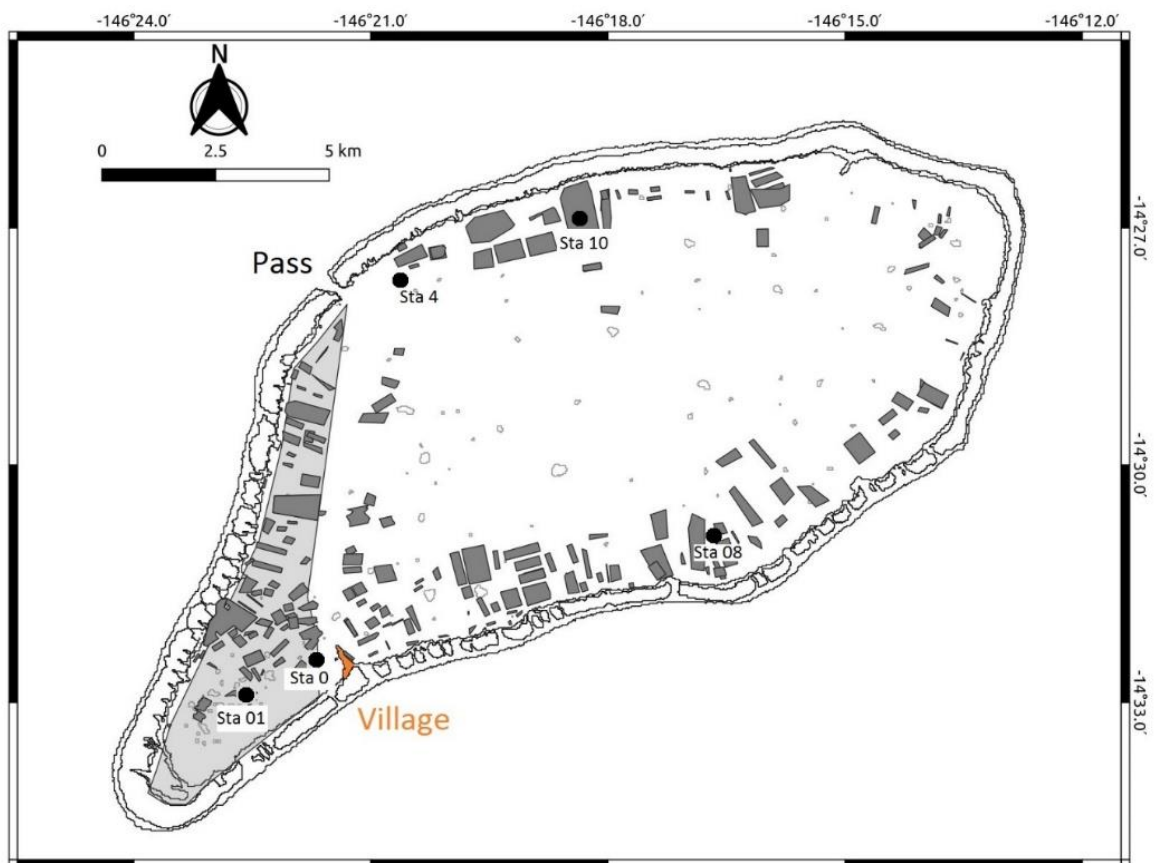
### 70 *2.1. Context, site description and water column sampling*

71 This work is a contribution of the MANA project which aim is to produce new knowledge and develop  
72 numerical tools designed to support management decisions in the context of exploited atoll lagoons  
73 affected by the impact of climate change. Ahe atoll like other lagoons of the Central Pacific Ocean is  
74 dedicated to aquaculture and specifically the culture of the black lip oyster *Pinctada margaritifera* that  
75 produces the prized black pearls.

76 Ahe atoll located 456 km North-East from Tahiti, is one of the 76 coral atolls of the Tuamotu  
77 Archipelago (French Polynesia) and, like most of these, is characterized by an internal lagoon.  
78 Measuring around 20 km in length and up to 12 km across, the lagoon covers an area of 138 km<sup>2</sup>  
79 bordered by a land area of around 12 km<sup>2</sup>. Like all the atolls of the region, Ahe atoll rises sharply from  
80 the seabed (2700 m depth) and is connected to the open ocean by a 200 m wide pass (Tiareroa pass)  
81 located on the north-western side of the atoll rim. The mean depth is around 40 m and water renewal  
82 time was estimated at 252 days (Dumas et al., 2012). Ahe atoll is exposed year round to easterly trade  
83 winds and tidal amplitudes are small (Andréfouët et al, 2012a) but exhibits some seasonal variations  
84 (Bouvy et al., 2012; Charpy et al., 2012; Lefèbvre et al., 2012; Thomas et al., 2010). The general climate

85 is characterized by a wet and a dry season and dominant trade winds (Dutheil et al., 2020). Our  
1 86 experiments took place at the beginning of the hot season during a period of moderate trade winds.

2  
3 87 Five study sites (Fig. 1) were studied during a field campaign in Ahe lagoon between 27 November and  
4 88 7 December 2017, chosen to reflect a range of different bathymetric (lesser than 20 m depth) and  
5 89 environmental conditions related to pearl culture. At each station a CTD profiler (SBE 19+, SeaBird)  
6 90 was used to record a vertical profile from surface to the bottom of temperature, salinity and PAR  
7 91 (Photosynthetic Available Radiation). Bottom water samples for nutrient analyses were sampled with  
8 92 a 5L Niskin bottle operated by the divers at the beginning of each incubation.



109  
110 **Fig. 1.** Location of the sampling stations (black dots) in Ahe atoll (Tuamotu Archipelago) during the  
111 field trip in Nov – Dec 2017. Concessions for oyster breeding (dark grey) and spat collection (light  
112 grey) were redrawn from Direction des Ressources Marines (Pu Fa' Ahuta Moana). Tiareroa pass  
113 (North) and the village (South) are shown along the atoll rim.

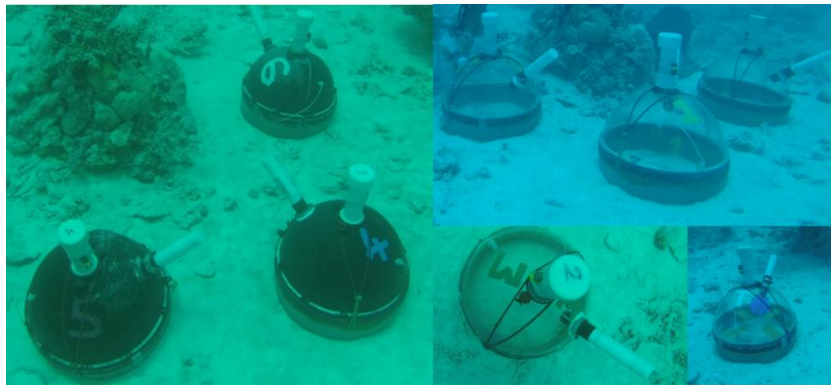
## 114 115 2.2 Sediment core sampling and analyses

116 Sediments were sampled in each station by scuba divers using 3 cores (20 cm high, diameter 3 cm) and  
117 the upper cm of the core was analysed for water content, porosity and pigments. A first surface level  
118 of samples was wet and dry weighted for water content. Porosity was calculated using the classical  
119 formulation of Berner (1980):

$$POR = \frac{\frac{WW - DW}{1.035}}{\left(\frac{WW - DW}{1.036}\right) + \left(\frac{DW - FW}{2.56}\right)}$$

Where WW is the sample wet weight, DW dry weight, FW empty flask weight, and considering a water density of 1.036 (mean salinity 36.3) and a bulk density of 2.56 g cm<sup>-3</sup>.

Pigments were determined on a second 1 cm thick sediment sample, measured fluorometrically before and after acidification (methanol extraction) and using a Turner Design fluorometer equipped with the module No 7200-040 (Le Bouteiller et al., 1992). A third surface level (3 cm thick) was used to extract under pressure the interstitial water. Water samples were immediately poisoned by HgCl<sub>2</sub> (at 6g/l) and stored in an icebox and analysed while back at lab. Concentrations of nitrate and nitrite (NO<sub>x</sub>), phosphate and silicates were determined by colorimetric methods using a segmented-flow Auto-Analyzer (AA3, SEAL corporation, Mequon, WI, USA), as described in Raimbault et al. (1990) and Aminot and K erouel (2007). The detection limits for NO<sub>x</sub>, PO<sub>4</sub> and NH<sub>4</sub> were 0.05, 0.02, and 0.01 µmol L<sup>-1</sup> respectively.



**Fig. 2.** Clear and opaque benthic chambers placed on the sediment. Control chamber (bottom right).

### 2.3 Fluxes at the sediment water interface

Benthic primary production and respiration as well as fluxes of dissolved nutrients were measured using opaque and transparent benthic chambers. We used similar devices as Barranguet et al (1996) slightly adapted to host new equipment. Briefly, the 37 cm diameter chambers (Fig. 2) are hemispherical domes made of polymethyl methacrylate isolating a water volume of 13.3 L over a sediment area of 0.108 m<sup>2</sup>. The chambers are clipped on cylindrical PVC frames equipped with an O-ring to avoid any leaking. The 10 cm high frames are inserted into the sediment depending on the toughness of the bottom. On top of the chamber, watertight housing hosts a battery powered motor and is coupled to a magnetic stir bar to homogenize the enclosed volume, preventing the formation of a gradients within the chamber (Tengberg et al., 2004). During deployment, divers control visually that no resuspension is artificially created. A diffusive oxygen probe (SDOT – NKE equipped with an Aanderaa 3835 Optode) is inserted in a lateral sampling port for dissolved Oxygen (DO) and temperature measurements. A second sampling port at the opposite position is used by divers to withdraw water sub-samples (120 ml syringe equipped with a 10 cm silicone tube) during the in situ incubations. When a sample is withdrawn, it fills up with external water that remains isolated from the incubated water, so that it avoids a pressure change inside the chamber. The port holes are sealed with stoppers between the samplings. Control chambers equipped with a round plate isolating the chamber space from the bottom are used in parallel as a “blank” correction and to separate water-

column processes from benthic fluxes. As suggested by Foster et al. (2016), between 2 and 3 observational chambers and a control chamber (clear and opaque respectively) were used during every sampling occurrence as well as recordings of ambient conditions (outside the chambers).

DO content and temperature were continuously recorded at a 1 min frequency during 4 h cycles. The oxygen concentrations in the chambers never fell below 85% (respiration) or above 125% (production) of the initial O<sub>2</sub> content. Nutrient sampling was performed by divers every 1 h, during the first experiment to test the linear uptake or release of nutrient from the sediments. During the following experiments, enclosed water was sampled at the beginning and the end of each 4 h-incubation period. This start-end strategy was favored in order to reduce the number of samples (Dalsgaard et al., 2000).

Fluxes at the sediment water interface were calculated by regressing the change of oxygen concentrations in the chambers against time (μmol O<sub>2</sub> m<sup>-2</sup> h<sup>-1</sup>). A correction for pelagic processes was applied by subtracting the changes calculated for the control chambers. The equation used was as follows:

$$\frac{(\frac{\Delta C_1}{\Delta t} Vol_1) - (\frac{\Delta C_2}{\Delta t} Vol_2)}{Surf}$$

Where ΔC/Δt represent the uptake or release of O<sub>2</sub> and nutrients in the chambers (μmol L<sup>-1</sup> h<sup>-1</sup>), Vol the total volume of the chambers (L<sup>1</sup>) and Surf the area of the sediment enclosed (m<sup>2</sup>). Subscript 1 and 2 correspond to observational chambers and control chambers, respectively. The volume of the PVC base frames was added to the volume of the dome for Vol<sub>1</sub>. The volumes were corrected to take account of the space occupied by the equipment (mixing device and oxygen probes). Once the syringe retrieved on board, water samples were filtrated on GFF filters and immediately poisoned by HgCl<sub>2</sub> (at 6g/l) and stored in an icebox for later analysis of nutrients using an autoanalyser (same methods as for incubation samples - see above 2.2).

### 3. Results

#### 3.1 Environmental settings

Our study period was characterized by a hot season during the austral winter in 2017, with only few rain events observed. Table 2 shows the main environmental conditions during the sampling period. The temperature of the water column was vertically homogenous between 28.4 and 28.9 °C (mean 28.6 ± 0.2°C) and showed a slight increase at the south-western part of the lagoon. Bottom water nutrient concentrations were low and typical of oligotrophic conditions. Oxygenation of the water masses was efficient with O<sub>2</sub> saturation reaching between 83 and 97 %. Light conditions at the bottom were optimal, between 17 and 42 % of the surface irradiance depending on depth and cloud cover.

**Table 1**

Physical and chemical features of the bottom waters measured at the five sampling sites in the Ahe lagoon. DO and PAR correspond to values measured outside the chambers and averaged over the incubation period.

Stations	T (°C)	Depth (m)	Nutrients (μmol L <sup>-1</sup> )				DO (μmol L <sup>-1</sup> )	DO % sat	PAR (%)
			NH <sub>4</sub>	NO <sub>x</sub>	PO <sub>4</sub>	Si(OH) <sub>4</sub>			
L0	28.7	9	0.07	0.29	0.29	1.41	233.5	96.7	42
L1	28.9	13	0.05	0.13	0.24	1.36	206.2	85.8	17
L8	28.4	15	0.05	0.22	0.35	1.29	210.5	86.7	30
L4	28.5	18	0.03	0.33	0.35	1.68	213.9	88.1	30
L10	28.4	15	0.08	0.59	0.51	1.53	202.9	83.0	34

Sediments were characterized by fine grained white sands with a mean water content of 15.8 % and a porosity of 0.32. Nutrients in interstitial waters were high for  $\text{NH}_4$  (between 30.6 and 85.1  $\mu\text{mol L}^{-1}$ ) and  $\text{PO}_4$  (8.1 to 30.5  $\mu\text{mol L}^{-1}$ ) and low for  $\text{NO}_x$  (0.7 to 1.4  $\mu\text{mol L}^{-1}$ ). Silicates showed intermediate values (from 1.6 to 10.0  $\mu\text{mol L}^{-1}$ ). Sediment pigments (chlorophyll a and phaeopigments) were comparable between stations L1, L8 and L10 and higher for station L4 (Table 2).

**Table 2**

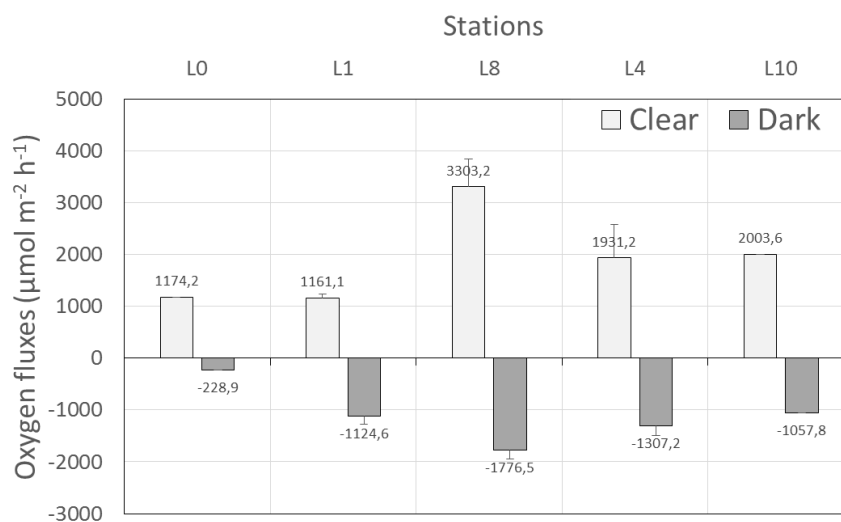
Sediment characteristics in the first sediment layer at sampling sites L1 to L10. Water Content (WC) in %, porosity (Porosity) dimensionless, interstitial nutrients in  $\mu\text{mol L}^{-1}$ , sediment chlorophyll a (SCH) and phaeopigments (SPH) in  $\text{mg m}^{-2}$  and %CH is the percentage of Chla over total pigments. Interstitial nutrient were extracted from a 0-3 cm sediment layer and 0-1 cm for the other variables.

Stations	WC	Porosity	Interstitial nutrients ( $\mu\text{mol.L}^{-1}$ )				SCH	SPH	%CH
			$\text{NH}_4$	$\text{NO}_x$	$\text{PO}_4$	$\text{Si(OH)}_4$			
L1	16.7	0.33	68.2	1.2	30.5	7.2	2.99	2.87	51
L8	16.5	0.33	65.1	1.4	8.1	10.0	2.79	2.66	51
L4	14.8	0.30	85.1	ND	ND	ND	11.30	5.42	67
L10	15.1	0.30	30.6	0.7	13.3	1.6	2.21	3.83	37

Station L0 samples were lost. ND: not determined.

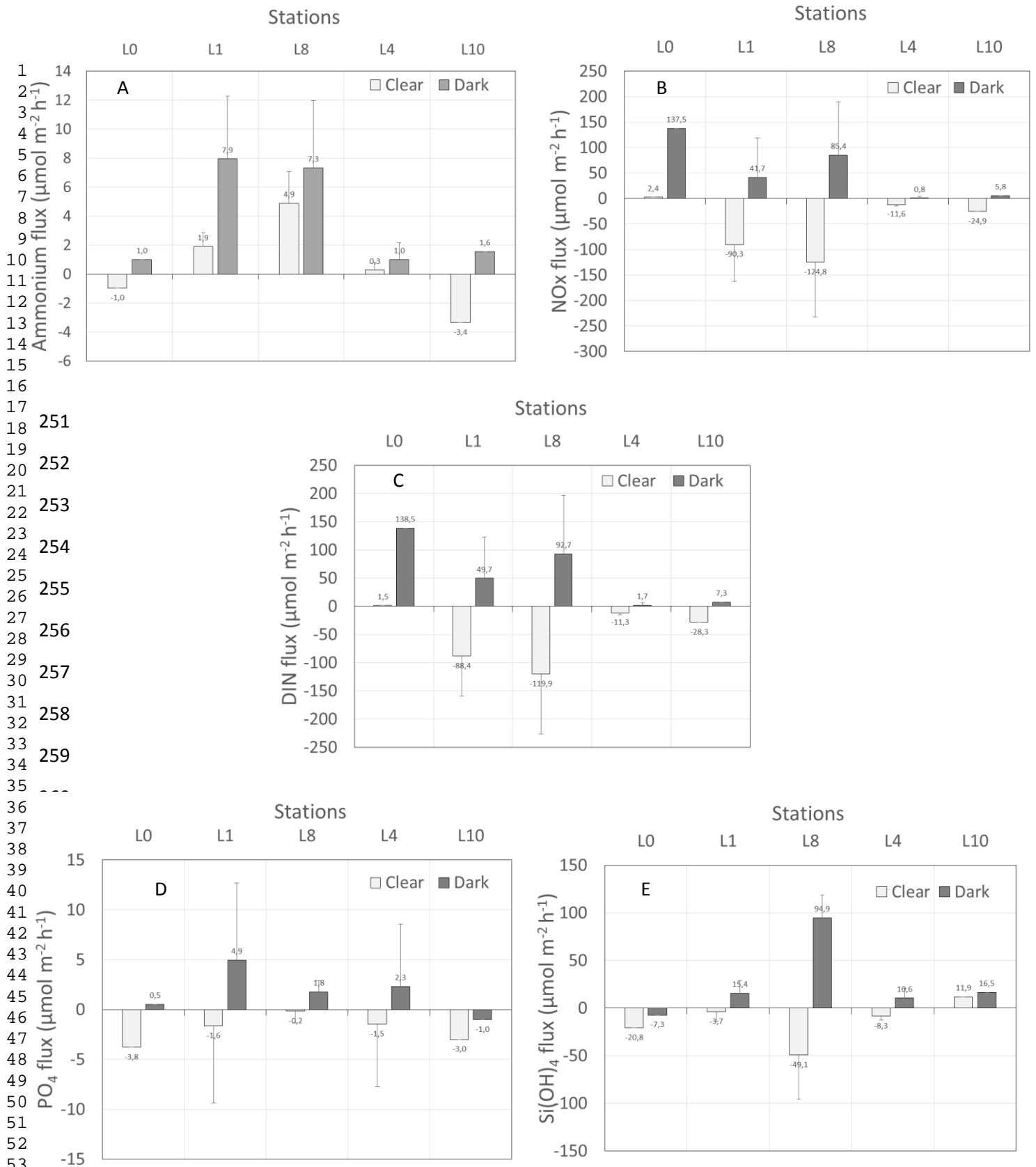
### 3.2 Sediment oxygen exchanges and nutrient fluxes at the sediment-water interface

The use of dark and transparent benthic chambers allows to infer both sediment oxygen demand (SOD) and light  $\text{O}_2$  fluxes (LOF). Results (Fig. 3) showed the variability observed between the different stations. Station 8 showed the highest rates in SOD and LOF, -1776.5 (sd 169.9) and 3303.2 (sd 534.0)  $\mu\text{mol m}^{-2} \text{h}^{-1}$  respectively. Stations L4 and L10 showed similar values around -1307.2 and 1057.8  $\mu\text{mol m}^{-2} \text{h}^{-1}$  for SOD respectively, and 1934.2 and 2003.6  $\mu\text{mol m}^{-2} \text{h}^{-1}$  for LOF respectively. Stations L0 and L1 showed the lowest values of 1167.7  $\mu\text{mol m}^{-2} \text{h}^{-1}$  for mean LOF, but different values for SOD (228.9 and 1124.6  $\mu\text{mol m}^{-2} \text{h}^{-1}$ ). Unfortunately we got only one replicat for both clear and dark chambers at station L0. Excluding this station we calculated a mean SOD of  $-1316.5 \pm 242.0 \mu\text{mol m}^{-2} \text{h}^{-1}$  and a mean LOF of  $2231.7 \pm 626.4 \mu\text{mol m}^{-2} \text{h}^{-1}$ .



**Fig. 3.** Sediment oxygen fluxes measured during light (light grey) and dark (dark grey) incubations at the different stations (vertical bars indicate sd for triplicates).





**Fig. 4.** Nutrient fluxes at the sediment water interface measured at 5 different stations in Ahe atoll: A)  $\text{NH}_4$ , B)  $\text{NO}_x$ , C)  $\text{DIN} = \text{NO}_x + \text{NH}_4$ . D)  $\text{PO}_4$ , E)  $\text{Si(OH)}_4$ . Vertical bars indicate sd for triplicates

273 Nutrient fluxes showed also a large variability between replicate chambers and stations (Fig. 4).  
1 274 Concerning nitrogen, dark chambers showed generally an efflux directed towards the water column.  
2 275 Conversely, clear chambers showed an influx at all stations. DIN fluxes representing the sum of  $\text{NH}_4$   
3 276 and  $\text{NO}_x$  fluxes were largely driven by  $\text{NO}_x$  fluxes because these fluxes were an order of magnitude  
4 277 higher than  $\text{NH}_4$  fluxes. Highest DIN effluxes in dark chambers were recorded at stations L0, L1 and L8  
5 278 ( $138.5$ ,  $49.7$  and  $92.8 \mu\text{mol m}^{-2} \text{h}^{-1}$  respectively) whereas stations L4 and L10 showed fluxes close to  
6 279 zero. Highest DIN influxes in clear chambers were recorded at L1 and L8 ( $-88.4$  and  $119.9 \mu\text{mol m}^{-2} \text{h}^{-1}$   
7 280 respectively) whereas these were close to zero at L0 and slightly negative for L4 and L10 ( $-11.3$  and  $-$   
8 281  $28.3 \mu\text{mol m}^{-2} \text{h}^{-1}$  respectively). It is noteworthy that the variability between replicate chambers is  
9 282 elevated enabling any statistical significant comparison test.

13 283 For  $\text{PO}_4$  fluxes (Fig. 5A), the same observations were made with a general efflux in the dark chambers  
14 284 and an influx in the clear chambers. As for N-nutrients, the huge variability enables to test  
15 285 statistically the difference between the stations. The range of values we found is between  $0.5$  and  $4.9$   
16 286  $\mu\text{mol m}^{-2} \text{h}^{-1}$  in the dark chambers and between  $-0.2$  and  $-3.8 \mu\text{mol m}^{-2} \text{h}^{-1}$  in the clear chambers.

19 287 Finally, silicate fluxes (Fig. 5B) were positive most of the time in the dark chambers (efflux) and negative  
20 288 (influx) in clear chambers. Again the inter-chamber variability was high but the general trend observed  
21 289 for the dark chambers was a higher efflux of silicates at station 8 ( $94.9 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) and a lower Si flux  
22 290 for all other stations ( $-7.3$ ,  $15.4$ ,  $10.6$  and  $16.5 \mu\text{mol m}^{-2} \text{h}^{-1}$  respectively for stations L0, L1, L4 and L10).  
23 291 In the clear chambers the Si influxes were also highly variable, and showed the same trend with a  
24 292 highest influx observed for station L8 ( $-49.1 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) and the lowest at the other stations ( $-20.8$ ,  
25 293  $3.7$ ,  $-8.3$  and  $11.9 \mu\text{mol m}^{-2} \text{h}^{-1}$  respectively for stations L0, L1, L4 and L10).

#### 31 295 4. Discussion

32 296 Ahe atoll is one of the most thoroughly studied lagoon of the Tuamotu Archipelago (Andréfouët et al.,  
33 297 2012b). Nevertheless, nutrient fluxes and SOD measurements at the sediment water interface are  
34 298 poorly documented in Ahe atoll. Gaertner-Mazouni et al. (2012) measured nutrient fluxes at 4 stations  
35 299 in October 2010. Lacoste & Gaertner-Mazouni (2016) supplemented the data of 2010 by new ones  
36 300 obtained at 3 similar stations in May 2013. To our knowledge no published data are available regarding  
37 301 SOD or microphytobenthic production in this system.

41 302 Nutrient fluxes we measured in the dark chambers were in the same range of variation than those  
42 303 published previously by Lacoste & Gaertner-Mazouni (2016) in the case of ammonia and slightly higher  
43 304 for  $\text{NO}_x$ . In New Caledonia lagoon, Boucher and Clavier (1990) and Grenz et al. (2010) observed a  
44 305 similar range of nutrient fluxes, with a prevalence of fluxes oriented towards the water column  
45 306 indicating a net source of nutrients for the pelagic compartment. Through mineralization processes of  
46 307 organic matter at the sediment interface, the release of dissolved nitrogen concurrently to nitrification  
47 308 processes should lower the accumulation of  $\text{NH}_4$  and raise  $\text{NO}_x$  which in turn diffused to the overlying  
48 309 waters. Dunn et al. (2012) measured SOD and DIN effluxes during light and dark incubations in a  
49 310 subtropical coastal lagoon (Coomababah Lake, Australia). They concluded that rates of total nitrate  
50 311 reduction were relatively low, ranging from  $3$  to  $26 \mu\text{mol N m}^{-2} \text{h}^{-1}$  and exhibited only minor seasonal  
51 312 variations. Finally, they stated that dissimilatory nitrate reduction to ammonium (DNRA) was the  
52 313 dominant pathway for nitrate reduction and denitrification processes seemed a less effective process  
53 314 probably because of the high amount of oxygen available (Sørensen, 1978). Same conclusions were  
54 315 made by Sundbäck et al. (1991) who performed a laboratory continuous-flow study with sediments  
55 316 from SE Kattegat maintained at  $15^\circ\text{C}$ . In our case we measured lower concentrations of  $\text{NO}_x$  compared  
56 317 to ammonium in the interstitial water in the sub-surface sediment layer.

Silicate and phosphate fluxes in dark were in the same order of magnitude than those found by Gaertner-Mazouni et al. (2012) for the same lagoon and as for Terminos lagoon in Mexico during the dry season (Grenz et al., 2019). Silicate release by sediments is a fast reaction possibly resulting from dissolution of biogeochemical Si from freshly deposited diatom frustules (Willey, 1978, Kamatani, 1982).

During light incubations DIN, PO<sub>4</sub> and silicate fluxes were oriented towards the sediment. This could be related to the photosynthetic processes of the microphytobenthos at the sediment water interface. The mean DIN/PO<sub>4</sub> flux ratio was estimated around 16.6 during day light which is close to the Redfield ratio(16/1) underlying a potential sink of nutrients driven by microphytobenthic production. During the dark incubation this ratio increased to 45.6 showing that the proportion of nitrogen produced by remineralization is higher than the phosphate produced. The loss of phosphate can be due to other processes like phosphorous adsorption by iron or manganese oxides (Sarrazin et al., 1988, Jensen and Thamdrup, 1993, Van Cappellen and Wang 1996) and/or reduced dissimilatory sulfate reduction (Pan et al., 2020). Conversely, an increase in the nitrogen pool, due to a reduced assimilation of N by microphytobenthos in the dark, can enhance the available N in the interstitial waters and subsequently modify the solute exchange rates between the sediment and the overlaying water column. Nevertheless firm conclusions cannot be drawn as the calculated ratios were highly variable between the individual flux measurements (Ratio confidence intervals of ± 144.8 and ± 57.0, respectively for light and dark incubations).

**Table 3 Example of benthic oxygen consumptions (min max) measured in subtropical shallow aquatic systems.**

Site	Latitude	O <sub>2</sub> (μmol m <sup>-2</sup> h <sup>-1</sup> )		Author
Shing-Mun River, Hong Kong	22°23N	1188	18988	Chen et al., 2000
Tolo Habor	22°25N	607	1653	Chau, 2002
New Caledonia lagoon	22°22N	550	1570	Grenz et al., 2003
Nichupte, Mexico	21°70N	250	12875	Valdes-Lozano et al., 2006
Goa, W Coast India	15°27N	1460	4120	Pratihary et al., 2009
Pompey Reef, Australia	21°00S	821	3400	Alongi et al., 2011
Cochin Backwater System	9°49N	995	2267	Abhilash et al., 2012
Semariang Batu River, Malaysia	1°37N	982	14803	Ling et al., 2009
<b>Ahe lagoon</b>	<b>15°00N</b>	<b>1150</b>	<b>3300</b>	<b>This study</b>

The sediment oxygen demand (SOD) is a good measure for total system mineralization as oxygen in sediments is utilized both directly for organic matter respiration (aerobic mineralization) and for reoxidation of reduced substances formed by anoxic mineralization (Rasmussen and Jorgensen, 1992). Our SOD values recorded in Ahe lagoon were in the range of observations made in New Caledonia lagoon (Clavier et al., 2005, Grenz et al., 2010) and other subtropical systems (Table 3). Temperature combined with organic matter influx to the sediments control benthic mineralization logically driving coastal tropical lagoons in the upper range of SOD values, as demonstrated by the maximum values reported from shallow rivers in Hong Kong and Malaysia (Chen et al. 2000, Ling et al. 2009), and from coastal lagoons near Cancun (Valdes-Lozano et al. 2006). Gaertner-Mazouni et al. (2012) measured low organic matter content in Ahe lagoon sediment, underneath oyster cultures and at a control station (around 3 %). This low values indicated that organic matter deposition produced by oyster biodeposition or natural sedimentation from the pelagic compartment is not stored in the sediment they sampled but either transported and deposited elsewhere, or metabolized by the local benthic community. The low organic content can also be related to the dilution by terrigenous particles but in

363 the case of atoll lagoons with low terrestrial inputs, this process should be restricted in space as in  
1 364 Tahiti lagoon (Frouin 2000). The low range in temperature variation encountered during our  
2 365 measurements precludes any temperature dependency related to our SOD estimates but the elevated  
3 366 temperature of the bottom waters suggests optimal conditions for microbial-mediated benthic  
4 367 degradation processes (Hicks et al., 2018).

6  
7 368 Chlorophyll pigments indicated densities of live microphytobenthos while phaeopigments, the amount  
8 369 of decaying microalgal material present in the sediments. We found pigment concentrations in the  
9 370 upper sediment layers close to the lowest values reported for Nouméa lagoon (Garrigue, 1993) and for  
10 371 Tikehau atoll, French Polynesia (Charpy and Charpy-Roubaud, 1990) but equivalent to the  
11 372 concentrations measured in Terminos lagoon at stations distant from river discharge and urbanized  
12 373 areas (Grenz et al., 2019). A mean ratio of 1:1 was calculated between Chla versus phaeopigments  
13 374 indicating a microphytobenthos in relative healthy conditions.

16 375 Heil et al.(2004) showed for coral reef sediments that benthic microalgal biomass was strongly  
17 376 correlated with oxygen production by sediments. Moreover they showed that microphytobenthos  
18 377 dominated over pelagic biomass by a factor of around 100, when integrated through the water depth.  
19 378 Taking the pelagic Chla measurements reported for the same cruise by Rodier et al. (2021), i.e.  
20 379 between 2.3 and 5.0 mg m<sup>-2</sup>, we found about the same biomasses in the surficial sediments, underlying  
21 380 the importance of this compartment for the ecosystem.

24  
25 381 Incubations in clear chambers enable to quantify the exchanges of nutrients under light conditions but  
26 382 also the microphytobenthos production during the diurnal period. The net oxygen production (NOP)  
27 383 was always higher than SOD suggesting that the sediments were net autotrophic and the oxygen  
28 384 balance in favor of microbenthic production when compared to community demand. This has been  
29 385 observed in New Caledonia lagoon by Clavier et al. (2005), but not by Dunn et al. (2012). These later  
30 386 authors observed that oxygen fluxes under light or dark conditions were consistently directed towards  
31 387 the sediment. In our case, light O<sub>2</sub> fluxes were positive and diurnal rates of gross benthic primary  
32 388 productivity ( $\Delta O_2$  = difference between the light and dark O<sub>2</sub> fluxes) were high ( $3423 \pm 1192 \mu\text{mol m}^{-2}$   
33 389 h<sup>-1</sup>). Our values are close to the gross productivities observed by Dunn et al. (2012) at 2 stations in  
34 390 summer and autumn, but lower than the gross productivity measured by Eyre et al. (2011) in southern  
35 391 Moreton Bay, Australia, especially in summer. To our knowledge, there is no data available on benthic  
36 392 microalgal composition for Ahe lagoon. This lack of data should be addressed in future studies as  
37 393 benthic microalgae are key components of coral reef ecosystems (Heil et al., 2004) and probably also  
38 394 in atoll lagoons.

43 395 As already stated by Gaertner-Mazouni et al. (2012), the impact of oyster culture on the sediments of  
44 396 Ahe lagoon is limited, due to a low sedimentation rate of organic matter underneath the spat collectors  
45 397 and breeding lines. Our data on nutrient fluxes confirm the order of magnitude already published but  
46 398 at a larger scale. The impact of oyster culture on sediment metabolism seems to be reduced compared  
47 399 to other areas where intense shellfish aquaculture at high stocking density disturb ecological systems  
50 400 (see review of Dumbauld et al., 2009), moreover in poorly flushed bays. This has some direct  
51 401 implications in the management of pearl oyster farming, especially in the context of the assimilative  
52 402 capacity for organic loading to the sediment and the subsequent benthic metabolism (Ferreira et al.,  
53 403 2018).

55  
56 404 Finally, benthic gross productivity/respiration (p/r), a measure of the balance between autotrophic  
57 405 production and heterotrophic respiration in the benthic communities, were almost > 1 (between 1.2  
58 406 and 1.7) underlying the net autotrophic character at the sediment-water interface and the prominent  
59 407 role of the sediment compartment in the lagoon wide oxygen balance, in the tropics.

## 5. Conclusion

This study investigated the nutrient and oxygen fluxes at the sediment water of Ahe atoll in the Tuamotu Archipelago (French Polynesia). The use of clear and dark chambers incubated in situ allowed to quantify simultaneously sediment oxygen demand (SOD) and microphytobenthic (MPB) production as net oxygen production (NOP). Baring in mind the high variability encountered and the lack of spatial replicates, our results showed some interesting points.

NOP were consistently directed towards the water column at all sampling stations whereas SOD logically pointed to the opposite direction, with a lower rate. Gross oxygen production (GOP) may contribute to the reported high oxygen saturation rates. The ratio between GOP and SOD over 1 underlined the autotrophic state of the sediment water interface where light conditions are optimal. We observed nutrient effluxes during almost all dark incubations and a sink during light conditions due to the influence of the photosynthetic activity of MPB, reducing the availability of recycled nutrients for the pelagic demand. The relatively stable environmental conditions over the year, compared to temperate regions, enable our results to be broadened on other temporal scales and extended to similar systems. These new data on mineralization and production rates at the sediment-water interface will be used in the frame of numerical modeling as foreseen in the MANA project (MANagement of Atolls - Seceh et al., 2021).

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## Credit author statement

**Grenz Christian** Conceptualization, Investigation, Supervision, Writing-Original Draft

**Rodier Martine** : Conceptualization, Investigation, Writing-Review & Editing

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**Declaration of interests**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: