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Sponge organic matter recycling: Reduced detritus production under extreme environmental conditions

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ABSTRACT

Sponges are a key component of coral reef ecosystems and play an important role in carbon and nutrient cycles. Many sponges are known to consume dissolved organic carbon and transform this into detritus, which moves through detrital food chains and eventually to higher trophic levels via what is known as the sponge loop. Despite the importance of this loop, little is known about how these cycles will be impacted by future environmental conditions. During two years (2018 and 2020), we measured the organic carbon, nutrient recycling, and photosynthetic activity of the massive HMA, photosymbiotic sponge *Rhabdastrella globostellata* at the natural laboratory of Bouraké in New Caledonia, where the physical and chemical composition of seawater regularly change according to the tide. We found that while sponges experienced acidification and low dissolved oxygen at low tide in both sampling years, a change in organic carbon recycling whereby sponges stopped producing detritus (i.e., the sponge loop) was only found when sponges also experienced higher temperature in 2020. Our findings provide new insights into how important trophic pathways may be affected by changing ocean conditions.

1. Introduction

Exponentially increasing carbon dioxide emissions are causing major changes in the Earth's climate (IPCC, 2021). Ocean Acidification (OA), Ocean Warming (OW) and Ocean Deoxygenation (OD) will have wide-ranging biological effects on marine organisms (IPCC, 2013). Coral reef survival is predicted to be compromised by climate change (Hughes et al., 2017), with impacts on reef structure and associated communities including biodiversity loss, ecosystem shifts, reduced habitat complexity, and declines in overall reef productivity (i.e., IPCC, 2013; Hoey et al., 2016).

Sponges are an important component of coral reefs across the world, and while corals are predicted to be generally negatively impacted by climate change (i.e., Hughes et al., 2003; Hoegh-Guldberg and Bruno, 2010), some sponges may increase in abundance and in some cases, become functionally dominant on coral reefs (Bell et al., 2013; Bennett et al., 2017; Bell et al., 2018). For example, the combined effects of OA and OW have been shown to have no impact on growth, survival, or secondary metabolite biosynthesis in many sponge species (e.g., Pansini et al., 2000; Vicente et al., 2016; Lesser et al., 2016; Bennett et al., 2017). However, some studies have shown that sponges are negatively affected under future climate change scenarios with greater impacts on mortality rates and symbionts (e.g., López-Legentil et al., 2008; Massaro et al., 2012; Fan et al., 2013). Although these earlier studies mainly focused on stress responses and tolerance of sponges to climate change impacts, no studies have investigated to what extent future environmental changes will affect sponge nutrient and organic matter cycling.

The complex association of sponges with microbes, which includes photosynthetic symbionts, have resulted in one of the most diverse and complex holobionts (i.e., the host plus its associated microbes) in the marine environment (Pita et al., 2018). Based on the abundance and diversity of microbes in tissues, sponges can be classified into high microbial abundance (HMA) or low microbial abundance (LMA) (10^5–10^6 bacteria per g of sponge wet weight; Hentschel et al., 2006). While

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sponges are mainly heterotrophic organisms, many species form relationships with photosynthetic symbionts, where their energy budget depends on associated cyanobacteria or dinoflagellates (Taylor et al., 2008). Sponges play a key role in both carbon recycling and nutrient fluxes (e.g., sink and/or source of nitrogen, phosphate and silicate) in reef ecosystems, and in the carbon transfer between the benthos and higher trophic levels (e.g., Wulff, 2006; Bell, 2008; De Goeij et al., 2008; McMurray et al., 2016). By both converting dissolved organic carbon (DOC) into particulate organic carbon (POC) and cellular detritus (i.e., the sponge loop pathway; De Goeij et al., 2013), and by assimilating DOC into biomass (Pawlik et al., 2016; McMurray et al., 2016, 2018), sponges support coral reef functioning, and contribute to the high productivity and biodiversity in otherwise oligotrophic environments (De Goeij et al., 2013; Rix et al., 2016; Pawlik and McMurray, 2020). Although the importance of these two different organic matter-recycling pathways has been identified, it is unknown how they will be impacted by predicted future changes in environmental conditions or whether sponges can switch between the sponge loop pathway and the production of biomass.

The largest organic resource in the oceans is dissolved organic matter (DOM) (Benner et al., 1992), which is released by primary producers. However, DOM is deemed biologically unavailable to most heterotrophic organisms directly (Carlson et al., 2002), and needs to be recycled in order to be available to higher trophic levels. In the water column, DOM is efficiently recycled by bacterioplankton through the microbial loop (Azam et al., 1983). In the same way, in shallow-water coral reefs, benthic species, particularly corals, release a large amount of DOM in the form of mucus, which can be recycled by sponges (Yahel et al., 2003; De Goeij et al., 2013; Mueller et al., 2014; Rix et al., 2016, 2018; Achlatis et al., 2018; Hoer et al., 2018). The sponge loop was first demonstrated for cryptic encrusting sponges, which transform DOM into a source of energy that is more readily available to other benthic reef fauna, particulate organic matter (POM) in the form of detritus (e.g., De Goeij et al., 2013; Alexander et al., 2014; Rix et al., 2017; Archer et al., 2017). This detritus subsequently feeds the detrital food chain. Therefore, sponges not only generate food for their associated detritivores through the production of detritus, but also provide a critical trophic link between corals and sponge-associated detritivores, allowing them access to the energy- and nutrient-rich DOC produced by corals (e.g., Rix et al., 2018). However, not all sponges participate in the sponge loop, nor produce detritus. While the sponge loop pathway is now well reported for some cryptic encrusting species (e.g., De Goeij et al., 2013, 2017), and in both encrusting and massive sponges living in deep-sea habitats (e.g., Rix et al., 2016; Bart et al., 2021), no studies have reported this pathway in massive Caribbean sponges inhabiting shallow reefs, for which only minor detritus production (i.e., no sponge loop pathway) has been reported in both LMA and HMA sponges (e.g., McMurray et al., 2018; Wooster et al., 2019). For such emergent sponges, it seems that DOM is preferentially stored as biomass and eventually transferred to higher trophic levels only via direct predation on sponge tissue (McMurray et al., 2018; Pawlik and McMurray, 2020). This apparent discrepancy in the detritus production may be due to the different methodologies used to assess the sponge loop. The two most commonly used methods are either: 1) incubations with isotopically enriched DOC, and following its release into the detritus (e.g., De Goeij et al., 2013; Rix et al., 2016, 2017, 2018); and 2) the In/Ex method where sponge recycling is measured by tracking the change in the composition of seawater as it is filtered by the sponges (e.g., McMurray et al., 2018; Wooster et al., 2019). Elements of both methodologies have been criticized (De Goeij et al., 2017), and further comparisons are needed for different sponge morphologies.

Natural laboratories, where seawater physical and chemical values deviate from the normal coastal conditions, are increasingly being used to study the responses of marine organisms to future climate change (e.g., Hall-Spencer et al., 2008; Camp et al., 2016, 2018; Burt et al., 2020; Maggioni et al., 2021). In this study, we used the semi-enclosed lagoon of Bouraké, New Caledonia (21°56′58.43″S; 165°59′29.46″E; Fig. 1) that is a natural laboratory, characterized by regular tidal fluctuations of pH (8.10–7.23 pH_T units), dissolved oxygen (DO, 7.34–1.87 mg L^{-1}), and temperature (from +1 °C to +3 °C). These parameters regularly change from close-to-normal conditions (high tide, HT) to extreme conditions (low tide, LT) (Camp et al., 2017; Maggioni et al., 2021). When averaged ($pH_T = -0.3$ units, T = +2 °C, DO = −26 %, compared to nearby control sites), environmental values are close to future climate predictions (RCP 8.5, IPCC, 2014). These fluctuating environmental conditions occur with chronically high concentrations of nutrients, and both dissolved and particulate organic matter, especially during low tide (Maggioni et al., 2021). At Bouraké, despite these extreme environmental conditions, a diverse and abundant benthic community was found, with coral species composition and richness similar to the local control reefs where environmental conditions are at ambient levels (Maggioni et al., 2021). Among sponges, the massive *Rhabdastrella globostellata* (Carter, 1883) is the most abundant species at Bouraké, reaching up to 40 % cover (Maggioni et al., 2021). This Indo-Pacific high microbial abundance (HMA) species (Moitinho-Silva et al., 2017a) has been demonstrated to efficiently filter bacteria cells and remove DOM from surrounding seawater (Hildebrand et al., 2022), fundamentally altering its composition.

The main aim of this study was to assess how the metabolism of *R. globostellata* (i.e., nutrient and organic carbon cycles) is affected by extreme environmental conditions, specifically, the three main drivers of future climate change: acidification, deoxygenation and warming. We also assessed how the extreme conditions affected the autotrophic and heterotrophic processes of the sponge holobiont. We hypothesize that the extreme conditions will negatively affect both sponge metabolism and its autotrophic and heterotrophic rates.

2. Materials and methods

2.1. Experimental design

During both April 2018 and March 2020, we performed in situ dark incubations (lasting 1 h) of *R. globostellata* to assess the effects of environmental conditions on its dark respiration, nutrient and organic matter recycling. In March 2020, these measurements were repeated in addition to light incubations to assess the effect on sponge photosynthetic symbionts (i.e., symbiont photosynthesis and sponge respiration, and photosynthetic efficiency of the symbionts in the sponge pinacoderm). In April 2018, seven incubations, using a set of four dark-shaded chambers, were performed during five consecutive days at different tidal phases, close to both low tide (LT; $n = 12$) and high tide (HT; $n = 16$). In March 2020, 15 incubations using a set of six chambers were performed over 14 days. This time we performed incubations exactly at high tide (HT; $n = 42$) and low tide (LT; $n = 48$). During the first week of fieldwork, seven out of 15 incubations were done in the dark only (HT = 18, and LT = 24), while the remaining eight incubations measured both photosynthesis and dark respiration during both high tide ($n = 24$) and low tide (n = 24). In these experiments, first we measured respiration rates in the dark in the morning at high tide, and subsequently using the same individuals, measured their photosynthesis in the light. In the afternoon, at low tide we first measured the photosynthesis and then dark respiration. This inverse procedure was adopted because during the afternoon the light availability was already lower (337.7 ± 257.7 μmol m^{-2} s^{-1}) than during the morning (1176.6 ± 88.4 μmol m^{-2} s^{-1}), likely affecting any comparison of the photosynthesis measured during HT in the morning (See Table S1 for summary of in situ incubations).

In addition to the in situ incubations, in 2020, sponges fragments (HT; $n = 9$, LT; n = 9) were also incubated ex situ on board the R/V Alis, to assess their photosynthetic responses by pulse-amplitude modulated fluorometry (PAM) (Genty et al., 1989) under both high tide and low tide conditions.

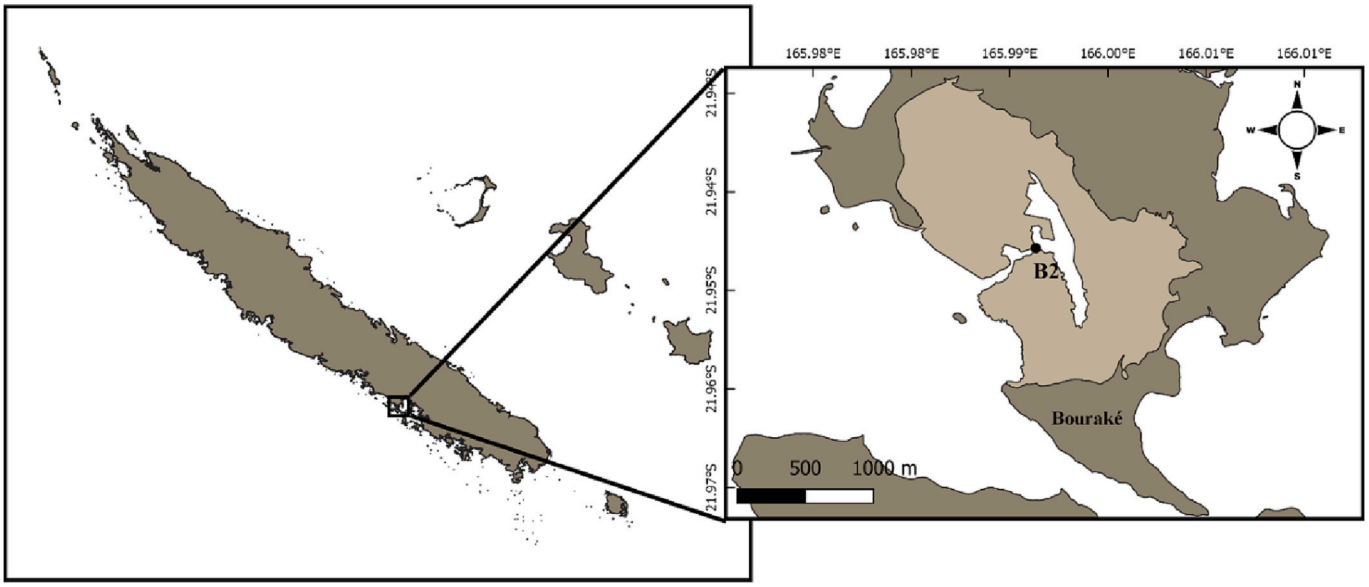

Fig. 1. Map of New Caledonia (South Pacific) and a magnified image (right panel) of Bouraké lagoon (study site B2) where the in situ experiment was performed. Georep New Caledonia database (https://georep.nc/) and QGis software were used to build the figure.

2.2. Incubation set up

For each in situ dark incubation or each pair of incubations (light and dark), a fresh independent (i.e., no sponge fragmentation) *R. globostellata* was used, each of similar volume ($n = 96$, 232 ± 73 cm^3). Sponges were collected attached to substrate by scuba diving at 2–4 m depth at the station B2 (Fig. 1). Sediment and epibionts on the surface of the sponges were gently removed underwater to ensure that only the sponge respiration was measured (i.e., the holobiont). Each sponge was placed in a transparent Plexiglas benthic chamber (total volume of 6.4 L; Fig. S1), which was hermetically closed and connected to a pump and an YSI 600 multiparameter probe (Biscéré et al., 2015). In the chamber system, the pump allows seawater to recirculate at a water flow of 2 L min^{-1} (Fig. S1), while the probe recorded the temperature and oxygen concentration every minute, therefore regularly monitoring sponge oxygen consumption (i.e., respiration R_{dark}) and production (i.e., net photosynthesis P_n, only in 2020). The chambers were dark shaded when measuring the holobiont respiration. During each incubation, which lasted ca. 1 h, one chamber with no sponge was used as a blank (i.e., control) to account for the contribution of photosynthetic organisms and microbial metabolism in the water. All the chambers, connecting tubes, and syringes were cleaned at the end of each day using a solution of 10 % HCl for 4 h and further rinsed in deionized water. This incubation protocol was tested in a preliminary experiment to verify that the duration of each incubation was long enough to detect oxygen depletion and avoid low oxygen concentrations in the chamber.

For the ex situ incubations on 14th March 2020, nine small fragments (3–4 cm in diameter) of *R. globostellata* were collected during low tide, and another set during high tide, from individual, spatially separated donor sponges. Seawater was collected from Bouraké using 2 × 25 L tanks. Samples were transported on board the R/V in individual hermetic plastic bags containing seawater and immersed in a cooler. Both sponge fragments and water were maintained in a temperature controlled room settled at the in situ temperature until data collection.

2.3. Data collection

At the beginning (i.e., 5 min after the chambers were closed) and at the end of each dark incubation in 2018 and 2020, 450 mL of seawater was collected from each chamber with a syringe to assess changes in nutrient and organic matter, and physical seawater parameters.

During light incubations, photosynthetically active radiation (PAR, 400–700 nm) was measured using a LI-1500 light sensor logger connected to a 30 m long cable and a spherical quantum sensor, which was positioned close to the chambers. The photosynthesis to respiration ratio (P: R_{dark}) was calculated as:

$$\mathrm{P : Rdark} = \frac{P_g \times hours\ of\ daylight}{Rdark \times 24}$$

with P_g and R_{dark} expressed in μmol O_2 cm^{-2} h^{-1}. The gross photosynthesis to respiration ratio was calculated based on daily budget of 12 h sunlight (photosynthesis) and 24 h respiration (Wilkinson, 1983).

Consumption (i.e., reduction, negative values) and/or production (i.e., increase, positive values) of nutrients, oxygen and organic matter (i.e., all the parameters measured during the incubations) were calculated as the difference between their concentrations at the beginning and end of the incubations, corrected by the change in concentration occurring in the control chamber, and normalized by the duration of incubation (h), the chamber volume (L), and sponge volume (cm^3). Sponge volume was calculated using a three-dimensional reconstruction technique. Between 80 and 200 photos of each sponge were taken underwater using a waterproof camera (Nikon AW 130) to cover the sponge whole surface. A reference square (3 cm × 3 cm) was placed close to each sponge to scale the model to its real size. The 3D Zephyr Pro software was then used to calculate the volume of each sponge.

In the ex situ incubations, sponge fragments were dark adapted for 30 min (Ralph et al., 1999; Biggerstaff et al., 2015), and the effective quantum yield (F_v/F_m) and the relative electron transport rate (rETR) were measured using a Diving-PAM, with the RLC curves function.

2.4. Seawater analyses

In 2018 and 2020 during the dark incubations, seawater samples were collected at the beginning (Table 1) and end of each in situ incubation to calculate the change in seawater physical and chemical parameters (nutrient and carbon) during the incubations (Table S3). In 2018, we measured pH_T (in total scale), dissolved oxygen (DO), temperature, nutrient concentrations (orthosilicic acid $[Si(OH)_4]$, nitrite + nitrate [NOx], ammonium $[NH_4]^+$, and phosphate $[PO_4]^{3-}$), bacterial abundance (BA), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC), particulate organic carbon (POC), and particulate organic nitrogen (PON). In 2020, in addition to the above measurements, we

Table 1
Summary of the environmental parameters measured at the beginning of the incubations in 2018 and in 2020, both at HT (high tide) and LT (low tide). Data are expressed as mean ± SD; number of replicates is in brackets; nd means not determined.

	2018		2020	
	HT (n = 16)	LT (n = 12)	HT (n = 18)	LT (n = 24)
Physical parameters				
T (°C)	26.28 ± 1.35	26.43 ± 0.74	29.38 ± 0.13	31.73 ± 0.71
pH_T	7.92 ± 0.18	7.57 ± 0.09	8.03 ± 0.01	7.56 ± 0.03
Chemical parameters				
DIC (μmol C L^{-1})	2158.7 ± 83.6	2376.5 ± 116.1	2103.5 ± 22.00	2647.1 ± 33.5
DO (mg O_2 L^{-1})	5.54 ± 1.36	4.26 ± 0.58	5.66 ± 0.24	3.94 ± 0.23
$Si(OH)_4$ (μmol L^{-1})	11.81 ± 3.95	19.37 ± 5.01	9.15 ± 0.21	21.03 ± 1.07
No_x (μmol L^{-1})	1.58 ± 1.77	1.35 ± 0.47	0.46 ± 0.07	0.64 ± 0.15
PO_4^{3-} (μmol L^{-1})	0.35 ± 0.11	0.35 ± 0.10	0.33 ± 0.02	0.35 ± 0.10
NH_4^+ (μmol L^{-1})	0.38 ± 0.10	0.37 ± 0.10	0.84 ± 0.46	0.86 ± 0.56
DOC (μmol C L^{-1})	93.09 ± 6.55	129.10 ± 12.77	130.43 ± 1.69	219.83 ± 22.68
POC (μmol C L^{-1})	29.93 ± 8.44	35.66 ± 16.13	16.29 ± 1.42	37.62 ± 11.80
PON (μmol N L^{-1})	1.94 ± 0.46	2.27 ± 1.14	1.59 ± 0.14	2.62 ± 0.69
BA (x10^8 cells L^{-1})	2.52 ± 4.44	3.91 ± 1.04	12.3 ± 1.09	13.6 ± 5.17
LPOC (μmol C L^{-1})	nd	nd	3.92 ± 1.90	1.01 ± 1.39
Phyto (x10^6 cells L^{-1})	nd	nd	55.5 ± 6.34	10.3 ± 4.22
Detritus (μmol C L^{-1})	nd	nd	14.03 ± 1.64	37.16 ± 11.75

also measured the live particulate organic carbon (LPOC), which is the total amount of bacteria and phytoplankton converted into carbon content and used to calculate the consumption/production of carbon discharged by the sponge as detritus (i.e., Detritus = POC - LPOC). In 2020, during the light incubations, we only measured pH_T, oxygen, and temperature. Further details of the methods used are in the Supplementary Information.

2.5. Data analysis

Each chamber was considered as a replicate. Because we performed all incubations at the peak of the tides, and the seawater parameters were fully monitored, we separated all measurements into two tide categories (HT and LT), and for both 2018 and 2020. In order to test for significant differences in: *i)* the environmental conditions at the beginning of the incubations (Table 1); and *ii)* the change in the chemical parameters during the incubations (Table S3), due to the sponge metabolism, two-way ANOVA, followed by post hoc Tukey tests (HSD), were performed between high and low tide (HT and LT, respectively), years (2018 and 2020) and their interactions (Table S2, Table S4). Significant ANOVA interactions were also graphically visualized and confirmed with interaction plots (Fig. S2). ANOVAs were performed after verification of normality and homogeneity of the data or residuals. In order to test for significant differences between tidal phases on LPOC, phytoplankton and detritus concentrations collected in 2020, unpaired *t*-tests were performed on: *i)* the environmental conditions at the beginning of the incubations (Table 1, Table S2); and *ii)* the change in the chemical parameters during the incubations (Table S3, Table S4). To better summarize and visualize the different responses in sponge metabolism between the two years and tidal phases, a principal Component Analyses (PCA) were performed separately for data collected in 2018 and 2020, and for both HT and LT using the absolute values of the data after normalization. Furthermore, to investigate the effect of the seawater composition on metabolic activities, a PCA using Spearman correlation matrix was performed on data collected in 2020 between the seawater chemical parameters measured at the beginning of the incubations (Table 1) and the absolute values of their changes (i.e., consumption and production) during the incubations (Table S3). In order to assess differences in photosynthesis (P_g), respiration rates (R_{dark}) and their ratios (P:R), as well as differences in photosynthetic efficiency of the photosymbionts using the maximum electron transport rate (rETR) and the effective quantum yield (Fv/Fm) during the dark/light incubations, unpaired *t*-tests were performed between tides (HT and LT) on data collected in 2020 (Table S7). Data were graphically presented using the generalized additive models (GAM). All analyses were conducted in RV4.1, using stats, factorminer, and vegan packages (R Core Team, 2019).

3. Results

3.1. Environmental conditions at the start of the dark incubations

Seawater temperature measured at the beginning of the incubations (chambers with sponges + blanks) was significantly different between years, tides and their interactions ($p < 0.001$; Table S2), while dissolved oxygen and pH were significantly lower at LT ($p < 0.001$; Table S2), and not significantly different between years (Table 1; pH $p = 0.55$, DO $p = 0.076$; Table S2). For these parameters, the highest average temperature (31.73 ± 0.71 °C) and lowest pH and DO (7.56 ± 0.03 pH_T units and 3.94 ± 0.23 mg O_2 L^{-1} respectively) were found at LT in 2020 (Table 1). HSD post hoc comparisons confirmed that seawater temperature did not differ between tides in 2018; but did differ between tides in 2020; and that temperature in 2020 was higher than in 2018 (Table S2).

Chemical parameters, with the exception of PO_4^{3-}, significantly differed between years and tides, showing some significant interactions (Table 1; Table S2). Some parameters differed between years, with bacterial abundance (BA), and NH_4^+ having lower concentrations in 2018 ($p < 0.001$; Table S2), and NO_x higher in 2018 ($p < 0.001$; Table S2). Most of the parameters including DIC, $Si(OH)_4$, DOC, PON and POC showed significant interactions between tides and years ($p < 0.05$; Table S2). HSD post hoc comparisons showed that all these parameters had higher concentrations during LT, and for both years, reaching the highest concentrations during LT in 2020 (Table 1). Both phytoplankton and LPOC showed significant differences between tides ($p < 0.001$; Table S2), with consistently higher concentrations at HT, while detritus, which mostly depends on the POC concentration, was higher at LT ($p < 0.001$; Table S2).

3.2. Metabolic activities of the sponge holobiont in the dark

In the dark, all sponges depleted dissolved oxygen in both 2018 and 2020 (Fig. 2; Table S3). ANOVA showed that oxygen consumption significantly differed between years ($p < 0.001$; Table S4), but not between tides ($p = 0.293$; Table S4). Mean oxygen consumption was highest during the LT in 2020, and was the lowest during the LT in 2018.

During the incubations there was a decrease in BA, $Si(OH)_4$, NH_4^+, DOC, LPOC and phytoplankton cells, and an increase in PO_4^{3-} and NO_x (Fig. 3; Table S3). Both reductions and increases were found for DIC, POC, and PON (Table S3). Metabolic parameters were significantly different between years, tide and had significant interactions, without any general common response (Table S4). DIC and DO only differed significantly between years ($p < 0.001$; Table S4), NH_4^+ and DOC only between tides ($p < 0.001$; Table S4). BA, POC and PON differed significantly between years and tides ($p < 0.01$; Table S4), while only $Si(OH)_4$ and NO_x showed significant interaction between year and tide ($p < 0.05$; Table S4). Orthosilicic acid $Si(OH)_4$ decreased during LT, reaching the highest average consumption in 2018, while NO_x increased more in 2020 reaching the highest value during HT (Fig. 3A, B; Table S3). The highest uptake of DOC was found during LT, while POC was always

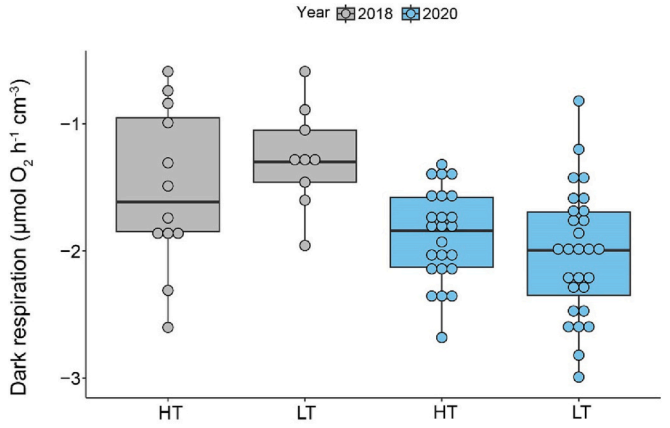

Fig. 2. Dissolved oxygen consumption per sponge volume measured during the incubations in the dark in 2018 (in gray) at both low tide (LT; $n = 9$) and high tide (HT; $n = 12$), and 2020 (in blue) at both high tide (HT; $n = 24$) and low tide (LT; $n = 28$). Boxes are the interquartile range of data (25th and 75th percentiles); the horizontal line is the median, and the whiskers represent the data range (i.e., minimum and maximum). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

produced except during LT in 2020 (Fig. 3E, F). Bacteria decreased more during LT in 2020 (Fig. 3H). Detritus, LPOC and phytoplankton were measured only in 2020, where they significantly differed between tides ($p < 0.05$; Table S4). Detritus increased at HT and decreased at LT, while the LPOC and phytoplankton always decreased (i.e., were consumed by the sponge) ($p < 0.05$; Table S4; Fig. 4).

Phytoplankton was consumed significantly more during HT than LT ($p < 0.001$; Table S4; Fig. 4B). Between phytoplankton and bacteria, *Synechococcus* (Syn) was the largest source of carbon at both HT and LT (Fig. S4). Phytoplankton composition showed that at both HT and LT, Syn was the most consumed phytoplankton group (Table S5). The first two principal components (Dim1 and Dim2) of the PCAs accounted for >52 % and 55 % of the changes in the seawater medium chemistry during the incubations made in 2018 and 2020, respectively (Fig. 5A, B). Samples clustered into two major groups according to the tide for both years. In both years, a clear difference was found for the two tidal phases and most of the parameters we measured contributed to the LT incubation clusters. In 2018, all parameters except DO, showed positive correlations with Dim1 scores, and were densely plotted on the right-hand side of the plot, where samples were clustered into the LT group. In 2020, only phytoplankton and LPOC showed strong negative correlations with the Dim1 scores and were plotted on the left-hand side of the plot, where samples were clustered into the HT group. All the remaining parameters were positively correlated with Dim1 scores and plotted on the right-hand side of the plot where samples were clustered to the LT group. Among them, detritus, PON, DOC and POC showed the strongest positive correlations and appeared to contribute the most to the variation in sponge metabolism during incubations at LT. Detritus, PON, DOC and POC were all more highly concentrated at the beginning of the LT incubations (Table 1).

PCA on a Spearman correlation matrix between seawater parameters measured at both the beginning of the incubations in 2020, and absolute value changes during the incubations (i.e., consumption and production) showed clear relationships for some parameters (Fig. 6). The first two principal components (Dim1 and Dim2) accounted for >90 % of the variation. Most of seawater parameters were positively correlated with Dim1, including DOC, BA, NH_4^+, and $Si(OH)_4$, which were correlated with the sponge nutrient utilization of DOC, $Si(OH)_4$, BA and NH_4^+, suggesting that their initial concentrations in the seawater affected their uptake. Furthermore, significant positive correlations were also found for these parameters (Fig. S3), showing higher consumption at LT when higher concentrations in seawater were observed. In the same way, LPOC and phytoplankton showed higher consumption at HT when they were more abundant in the seawater (Fig. 6; Fig. S3). The only exception was NH_4^+ which showed a positive relationship between the initial concentrations and its consumption, but it was not related to a specific tide.

3.3. Sponge holobiont photosynthetic activity

The photosynthetic rates and photosynthetic efficiency were only measured in 2020, the former in situ and the latter ex situ, and at both HT and LT conditions. During the in situ experiment, HT differed from LT conditions in the seawater pH (7.9 vs 7.4 pH_T units, respectively), DO (6.0 vs 3.4 mg O_2 L^{-1}, respectively) and temperature (29.9 vs 31.6 °C, respectively). However, light irradiance differed considerably between HT and LT, and were 1176.6 ± 88.4, and 337.7 ± 257.7 µmol m^{-2} s^{-1}, respectively. During the ex situ incubations, pH was comparable to the in situ incubations, and temperature was lower than the in situ incubations at 28.9–29.5 °C (Table S6).

Photosynthesis and P:R ratios were significantly higher at HT than LT, but dark respiration did not differ between tides ($p = 0.3381$; Table S7; Fig. S5). Gross photosynthesis (P_g) was always positive (due to oxygen production), and higher at HT than at LT (Table 2; Fig. S5; $p < 0.001$; Table S7). P:R ratios at both tide conditions revealed that the oxygen consumption was always higher than its production. The maximum rETR, as well as the initial F_v/F_m measured during the ex situ incubations in 2020 were significantly different between HT and LT. Both rETR and F_v/F_m versus irradiance (PAR) showed lower values during LT ($p < 0.05$; Table S7; Fig. 7; Table 2).

4. Discussion

In this study, we investigated how the extreme conditions experienced by the massive sponge *R. globostellata* in Bouraké during low tide affect sponge holobiont organic matter and nutrient recycling, and sponge photosynthetic activity. Our findings showed different responses between the two years of measurement. In 2018, both at normal (high tide, HT) and extreme (low tide, LT) seawater pH and dissolved oxygen values, our sponge always consumed DOC, and produced POC (i.e., the sponge loop pathway). In contrast, in 2020 we found that the organic matter recycling was altered, because although sponges always consumed DOC, they produced less POC and detritus at high tide, and stopped (i.e., negative values) producing both at low tide. These differences in 2020 occurred at the same seawater pH, and dissolved oxygen values as measured in 2018, but in 2020 the temperature was much higher, being the highest ever recorded at Bouraké. Similarly, photosymbiont photosynthetic activity was negatively affected during low tide in 2020. Our result suggests that while the combination of extreme levels of acidification and deoxygenation seem not to affect *R. globostellata* metabolism and the sponge loop, temperature may be a key driver in metabolic shifts, likely when combined with extreme levels of acidification and deoxygenation.

4.1. Changes in sponge organic matter recycling

Our results demonstrate that although the values of acidification and deoxygenation at our study site are extremes, the massive sponge *R. globostellata* preferentially produces detritus, which is a prerequisite for the sponge loop pathway. All the incubations we performed under both normal (high tide, HT) and extreme conditions (low tide, LT) confirmed the first step of the sponge loop, i.e., sponge DOC uptake, which is in agreement with the trend reported for many other species, both encrusting and emergent forms (e.g., Yahel et al., 2003; Hoer et al., 2018; McMurray et al., 2018; Wooster et al., 2019), and recently reported for the same study species (Hildebrand et al., 2022). In addition, we found a positive correlation between DOC consumption and its initial

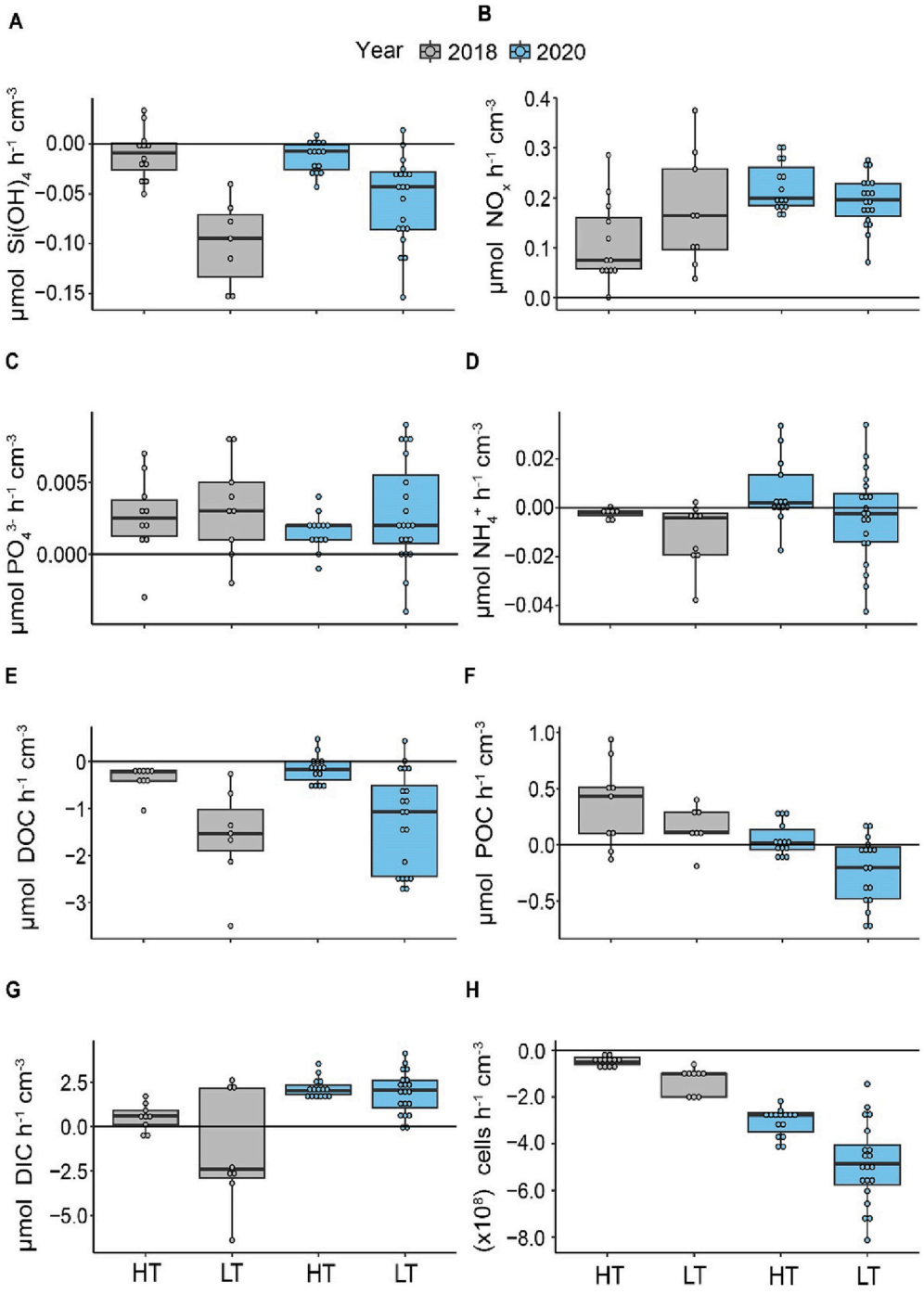

Fig. 3. Nutrients and organic matter consumption/production per sponge volume measured during the incubations in the dark at high tide (HT) and low tide (LT) in 2018 and 2020. (A) $Si(OH)_4$, (B) NO_x, (C) PO_4^{3-}, (D) NH_4^+, (E) Dissolved organic carbon (DOC), (F) Particulate organic carbon (POC), (G) Dissolved inorganic carbon (DIC), and (H) Bacteria abundance. Data are the difference between the beginning and the end of the incubations. Boxes represent the interquartile range (25th and 75th percentile); the horizontal line is the median, and the whiskers represent the data range (i.e., minimum and maximum).

concentration (Fig. S3), as also found in previous studies (i.e., Mueller et al., 2014; McMurray et al., 2016; Morganti et al., 2017; McMurray et al., 2018). However, DOC uptake at low tide in 2020 was not higher than in 2018 (Fig. 3E), even though the amount of available organic matter was almost double in 2020 (129.10 vs 219.83 µmol C L^{-1}). This could suggest that the positive relationship between DOC uptake and DOC availability (as in Archer et al., 2017) only exists up to a certain DOC level, which likely corresponds to the optimum organic matter uptake for the sponge.

Furthermore, all the sponges incubated in 2018 and the ones incubated at HT in 2020 produced both POC and/or detritus (Fig. 3F, 4A; Table S3), therefore also confirming the second step of the sponge loop, i.e., DOM transformation to both POC and detritus (e.g., De Goeij et al., 2013; Rix et al., 2018). The detritus production we reported (in average 0.06 µmol h^{-1} cm^{-3}) was higher compared to the majority of massive sponges in the Caribbean for which only small amounts of detritus production were reported (< 0.032 µmol h^{-1} cm^{-3}, from McMurray et al., 2018). While DOM transformation is common in encrusting and deep-sea sponges from the Caribbean and Red Sea, with net detritus production found for 19 out 22 species (reviewed by De Goeij et al., 2017), to the best of our knowledge, our study is the first demonstrating high detritus production (i.e., sponge loop pathway) in a massive sponge in shallow-waters from the Pacific Ocean (Table S3).

In contrast, during the LT (extreme conditions) in 2020 (Figs. 3F, 4A; Table S3), we found negative values of both POC and detritus, which means that neither POC nor detritus were produced by the sponges. This

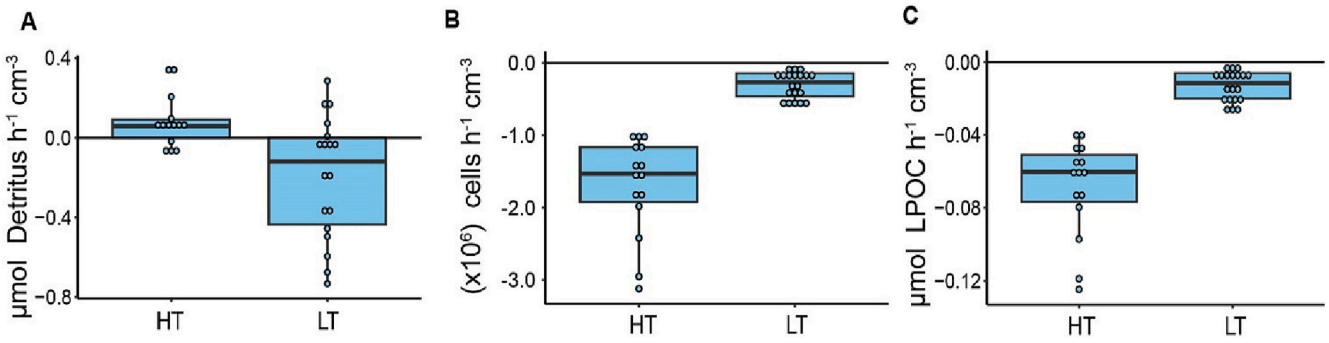

Fig. 4. Nutrients and organic matter consumption/production per sponge volume measured during the incubations in the dark at high tide (HT) and low tide (LT) in 2020. (A) Detritus (POC-LPOC), (B) phytoplankton abundance, (C) Life particulate organic carbon (LPOC). Data are the difference between the beginning and the end of the incubations. Boxes represent the interquartile range (25th and 75th percentile); the horizontal line is the median, and the whiskers represent the data range (i.e., minimum and maximum).

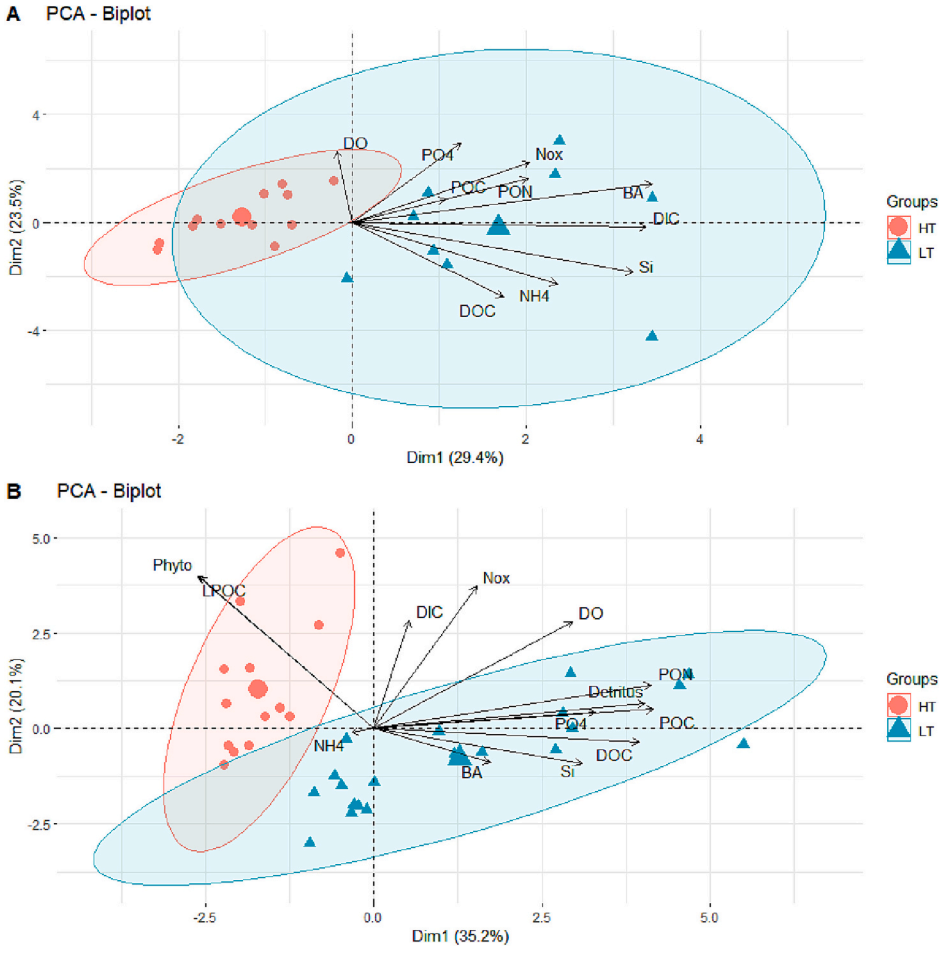

Fig. 5. Principal Component Analyses (PCA) on the parameters measured in the incubation medium A) in 2018, B) in 2020 at both high tide (HT) and low tide (LT). Each dot in red indicates one single sponge incubation made during HT, while triangles in blue indicate incubations during LT. Arrows indicate variables and their length approximates the variance of the variables. The ellipses represent the 95 % interval confidence. Large triangles or dots indicate multiple incubations at the same point. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

result is consistent with recent studies reporting examples of emergent sponges that consumed detritus. For example, the giant barrel sponge *Xestospongia muta* consumed 0.11 ± 0.16 µmol h^{-1} cm^{-3} of detritus in Key Largo, Florida, and 0.016 ± 0.009 µmol h^{-1} cm^{-3} in Belize (McMurray et al., 2018). The causes of the disruption of detritus production during low tide in 2020, and the consequent interruption of the sponge loop, could be the result of the extreme physical conditions in pH, DO, and temperature. When considering only the condition and results from 2020, we are unable to disentangle the contribution of the single parameters on the sponge loop since pH, temperature, and dissolved oxygen are significantly correlated with the detritus production/consumption (Fig. S6), and all were negative at LT. Based on these results, we conclude that the combination of these extreme parameters may have caused the disruption of the second step of the sponge loop in *R. globostellata* during the LT in 2020.

We also analyzed the regression between POC and the main physical parameters measured at the beginning of the incubation at both 2018 and 2020. Indeed, since POC is mainly composed of detritus, as LPOC comprises a maximum of 24 % of POC (Table 1), POC production could be a good proxy to assess the second step of the sponge loop, and to compare data between years (Fig. S7). In this case, temperature seem to be the main factors driving the reduction in POC (i.e., detritus)

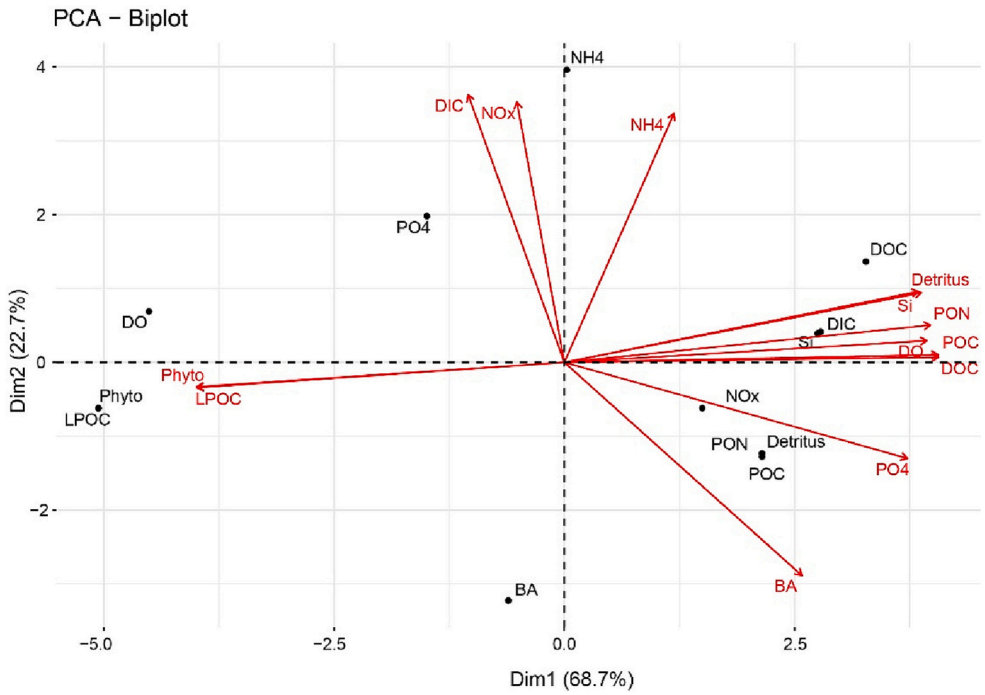

Fig. 6. Principal Component Analyses (PCA) on a Spearman correlation matrix between the seawater chemical parameters measured at the beginning of the incubations, and the absolute values of their changes (i.e., consumption and production) during the incubations. Data were collected in 2020. Dots indicate the sponge metabolic specific parameters while arrows indicate the variable, and their length approximates the variance of the variables.

Table 2
Summary of the gross photosynthesis (P_g), dark respiration (R_{dark}), and their ratio (P:R) measured in situ, the initial photosynthetic efficiency (F_v/F_m) and $rETR_{max}$ measured ex situ. For in situ, $n = 9$ and $n = 8$ at high tide (HT) and low tide (LT), respectively; while for ex situ, $n = 9$. Data are expressed as mean ± SD.

	HT	LT	HT	LT	HT	LT
	R_{dark}		P_g		P:R	
In situ	−1.91 ± 0.19	−1.79 ± 0.29	1.25 ± 0.29	0.38 ± 0.33	0.32 ± 0.07	0.10 ± 0.09
	F_v/F_m		$rETR_{max}$			
Ex situ	0.5 ± 0.04	0.5 ± 0.06	27.6 ± 7.0	12.6 ± 6.5		

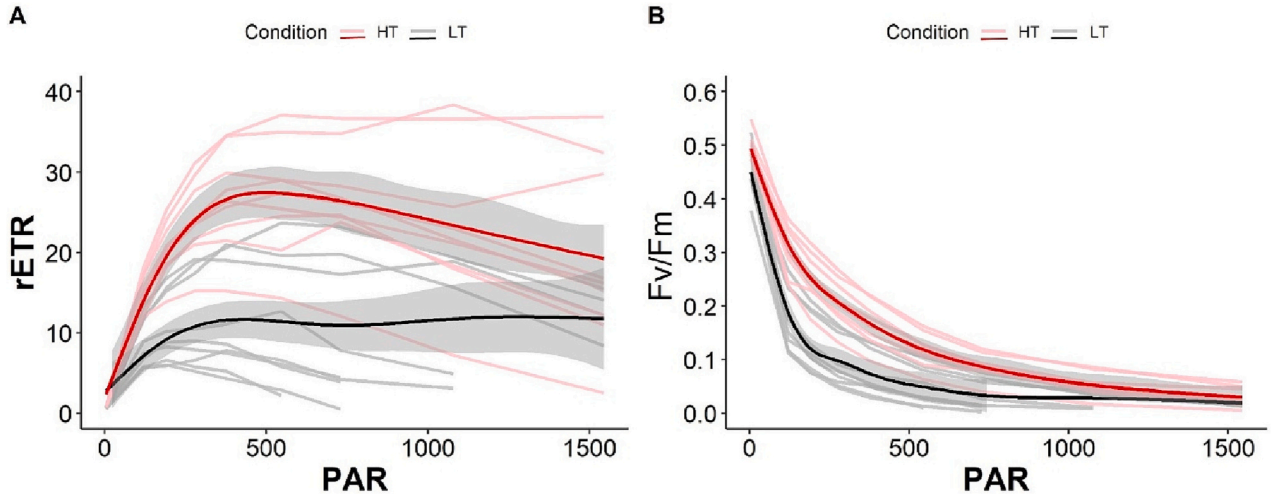

Fig. 7. Generalized Additive Models (GAM) on (A) relative ETR (rETR) and (B) the effective quantum yield (F_v/F_m) versus irradiance (PAR). Data were obtained from dark-adapted sponges during the ex situ incubations in 2020 under high tide (HT; n = 9 in red) and low tide (LT; n = 9 in black) conditions. The shaded areas indicate the 95 % confidence intervals of the GAM model. Individual measurements were also reported. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

production, clearly showing that while POC was always produced in 2018 at temperature of ca 26–28 °C, it was mostly consumed during the low tide in 2020 at temperature of ca 31–33 °C ($p < 0.001$, Fig. S7). Further laboratory experiments are needed to confirm the effect of temperature on sponge loop pathway.

Another possible explanation for the change in the detritus production we measured during the LT in 2020 is a reduction in sponge pumping rates as demonstrated in previous studies (e.g., Massaro et al., 2012; Stevenson et al., 2020). However, if there were a halt in pumping rates during extreme conditions, sponges would simply stop recycling nutrients and carbon, which was not the case. Although we did not measure this parameter, our data showed that even at LT in 2020 sponges continued to recycle DOC, as well as other nutrients (Fig. 3), and respired at the same rates as at HT in the same year, therefore the sponge was not stressed and had a normal basal metabolism (Fig. 2; Table S3). However, sponge respiration rates were higher in 2020 than in 2018 (Table S3), possibly as a mechanisms to cope with the high temperatures (Table 1).

We also hypothesize that this break in the detritus production at LT in 2020 was due to the lower concentration of LPOC and phytoplankton found at LT (Table 1; Fig. 5; Fig. S3), while both were more abundant and more consumed during HT. However, given LPOC was a very small part of the POC pool, the POC mainly comprised detritus (Fig. 3F, 4A), and both POC and detritus were always higher at LT (Table 1), and therefore available for sponge nutrition. Although our 1 h incubations were too short to measure division of filter cells, which take place every five to six hours (De Goeij et al., 2013), both at HT and LT in 2018 and HT in 2020 *R. globostellata* produced POC (Fig. 3F) but this stopped at LT in 2020.

The finding that sponges stopped producing POC and detritus during the extreme conditions measured at LT in 2020 means that they reduced cell turnover, which is energetically costly and may represent 75 % of the daily energy (DOC and POC) consumed (Kahn and Leys, 2016). Lower detritus production was also found in mesophotic sponges where it is seems that sponges preferentially invest in their growth rather than in cell turnover, when compared with the same species in shallower water, probably due to a change in food quality and availability (Hadas et al., 2009; De Goeij et al., 2017; Lesser et al., 2020). This hypothesis, which needs to be experimentally validated with others techniques (e.g., NanoSIMS and stable isotope analyses) is also in agreement with findings for Caribbean massive sponges where less carbon is released as detritus (e.g., Pawlik et al., 2015, 2016; McMurray et al., 2018). Sokolova et al. (2012) also suggested that when food is not limiting, high growth rates and biomass accumulation can be supported even under stressful conditions. This might partially explain why our study species is so massive and abundant across Bouraké, covering up to 40 % of the reef area (Maggioni et al., 2021), but is rare and forms small colonies outside the lagoon.

In conclusion, several hypotheses could explain the change in sponge organic matter recycling, and further studies are needed to understand the processes that occur when carbon is no longer released as detritus. However, based on the environmental conditions measured in Bouraké, our observations suggest that high temperature, in combination with acidification and deoxygenation, may be the main factor driving the break.

4.2. Effect of extreme conditions on sponge holobiont nutrient recycling and feeding

Beyond their role in carbon recycling on coral reefs, sponges likely have a key influence on nutrient biogeochemistry (e.g., De Goeij et al., 2017; Pawlik and McMurray, 2020). Sponges are important sources of dissolved inorganic nitrogen (DIN), such as ammonium, nitrite and nitrate; and also phosphate through their metabolism (Jiménez and Ribes, 2007), and through the inextricable activity of their associated microbial communities. Sponges typically remove ammonium from seawater, as a nitrogen source for chemo- and phototrophic bacteria and an energy source for ammonium oxidizing bacteria and archea. For instance, both the sponges *Tethya citrina* and *Xestospongia muta* produced NO_x, and the latter consumed NH_4^+ (Fiore et al., 2013; López-Acosta et al., 2019), reflecting the diverse nitrogen metabolic pathways within the sponge holobiont (Archer et al., 2017). In agreement also with previous findings for *R. globostellata* (Hildebrand et al., 2022), and notwithstanding the extreme conditions experienced in Bouraké, we measured a net production of NO_x, especially in 2020, and a consumption of NH_4^+ (Fig. 3B, D; Table S3). Since both aerobic and anaerobic ammonia-oxidizing microbes have been found in sponges (Bayer et al., 2008), these results could be due to both the photosymbionts and anaerobic activity of the associated bacteria. Microbial symbionts may also sequester a significant amount of phosphorus in the form of polyphosphate (Zhang et al., 2015), however we found a net, and consistent production of PO_4^{3-} during incubations (Fig. 3C; Tables S3; S4), which was comparable to the sponge *Tethya citrina* that released 0.005 ± 0.004 μmol h^{-1} mL^{-1} of PO_4^{3-} (López-Acosta et al., 2019).

Most sponges rely on silicic acid (DSi), such as $Si(OH)_4$ to produce their silica skeletons and to grow. We found that *R. globostellata* always consumed $Si(OH)_4$, with higher rates during extreme conditions (low tide) when the DSi concentration in Bouraké was the highest (Fig. 3A; Table S3). Average DSi consumption was 0.10 ± 0.043 and 0.057 ± 0.043 μmol h^{-1} cm^{-3} during low tide in 2018 and 2020 respectively, which corresponded to a $Si(OH)_4$ concentration of 19.37 ± 5.01, and 21.03 ± 1.07 μmol L^{-1}, respectively. A positive correlation between DSi concentration and uptake was found (Fig. S3), which is in agreement with other studies where consumption of DSi was reported at a similar rate and correlated with DSi availability (Maldonado et al., 2012, 2020; López-Acosta et al., 2019). The high concentration of DSi during low tide in the Bouraké lagoon could be due to the elevated acidification level (minimum $pH_T = 7.2$), which prevents dissolution of $Si(OH)_4$ and increases its concentration in seawater. This chemical condition results in high DSi availability in the Bouraké lagoon, thus facilitating the skeletal growth of *R. globostellata*.

Although the effect of tide and tidally-driven changes in the seawater plankton and bacterial community have yet to be investigated in Bouraké, our measurements in 2020 clearly showed that the abundance of phytoplankton vs bacteria during the tide had a great effect on sponge metabolism (see Maggioni et al., 2021 for further discussion on the Bouraké functioning). Both the live particulate organic carbon (LPOC) and phytoplankton were more concentrated at high tide (Table 1; Table S5), corresponding to the new water from the open lagoon, while bacteria and detritus concentrations were high at low tide, corresponding to the water coming from the mangrove. Differences in the PCA between 2018 and 2020 were likely because in 2020 the incubations were always done at HT and LT and not close to them as in 2018. In agreement with this diurnal variability in the water quality of Bouraké, *R. globostellata* feeds more on LPOC and phytoplankton during the high tide, and inversely, more on detritus and bacteria during the low tide (Fig. 3H, Fig. 4). This result is in agreement with a recent study showing that *R. globostellata* efficiently filters bacteria cells (Hildebrand et al., 2022), although less than what we found in Bouraké. This difference may be simply due to the different methods used, or more likely because the Bouraké lagoon is eutrophic (Table 1) when compared to the study site in Guam by Hildebrand et al. (2022). These bacterial cells are likely a food source (Reiswig, 1975; Ribes et al., 1999) for this sponge, although it is well known that sponges are selective filter feeders preferring the relatively rarer but labile resource of phytoplankton compared to the numerical dominant heterotrophic bacteria (Maldonado et al., 2012; McMurray et al., 2016). In contrast, *R. globostellata* in Bouraké seems to change the food source regardless of the tide. For instance, ingestion rates of both the bacteria and phytoplankton groups increased or shifted from one group to another according to their composition based on the tide (Table S5). Food selection may result from either passive processes, in which the physical properties of the sponge

filtering cells leads to differential uptake of picoplankton cell types, or active processes, in which food selection is mediated by sponge behaviour (Jürgens and DeMott, 1995; Maldonado et al., 2010). Therefore, the abundance and metabolic plasticity that make this species highly competitive in Bouraké could be because food is never limited there, and that the passive filtration method is the one preferably used by *R. globostellata*.

4.3. Effect of extreme conditions on the sponge photosynthetic activity

Sponges form symbiotic relationships with many microbial groups (e.g., Thomas et al., 2016; Moitinho-Silva et al., 2017b), including some photosynthetic symbionts, which provide photosynthetically-derived carbon to their host (Wilkinson, 1983).

Some studies have reported that microbial photosynthetic symbionts are not significantly affected when exposed to both OW and OA (Wisshak et al., 2012; Morrow et al., 2015; Luter et al., 2020; Bell et al., 2022). However, earlier studies showed reduced photosynthetic functioning of associated photosymbionts when exposed to high temperature (Cebrian et al., 2011; Webster et al., 2012; Goodwin et al., 2014; Lesser et al., 2016; Beepat et al., 2020). For example, *Cliona orientalis* showed a significant reduction in photochemical efficiency when exposed to a temperature of 27 °C (Ramsby et al., 2018). Consistent with these earlier studies, our in situ measurements showed a negative effect of the low tide conditions on sponge symbiont photosynthesis, which corresponded to a drop in the symbiont photosynthetic activity on the sponge pinacoderm measured during the ex situ incubation. In fact, significantly lower values were found during low tide for P_g, P:R, F_v/F_m and rETR, while no differences in respiration was reported during in situ measurements between tides (Tables 2, S7; Fig. S5). This drop might be due to the extreme conditions experienced by the sponges during the low tide, especially seawater pH and temperature, since it has been already demonstrated that some sponges can be tolerant to reduced levels of oxygen (Micaroni et al., 2022). A similar response was observed in the giant barrel sponge (*X. muta*), where a decrease in the productivity of cyanobacteria symbionts was observed when sponges were exposed to high temperature and low pH (Lesser et al., 2016). The drop in photosynthesis could be due to the differences in the light levels between incubations (i.e., at low tide in the afternoon the light was less than at high tide in the morning). However, both the photosynthetic efficiency and the relative ETR measured on dark-adapted sponges in the lab confirmed the drop in the sponge symbiont photosynthesis between tides (Fig. 7; Table S7). Although long-term measurements should be done on the whole energy budget, it seems that even if the symbiosis of *R. globostellata* in Bouraké were greatly affected by the combination of extreme conditions, the effect may not be that large since sponges can rely on heterotrophy, which may plays a greater role in its survival. In fact, *R. globostellata* from Bouraké showed heterotrophy characteristics (P:R ratios <1.5; Table 2). To support this hypothesis some studies showed that eutrophic conditions could render bioeroding sponges less dependent on their photosymbionts (i.e., Webb et al., 2017).

5. Conclusion

In our study, we used the semi-enclosed lagoon of Bouraké as a natural laboratory to study for the first time the metabolism and organic carbon recycling in the sponge *R. globostellata* exposed to normal and extreme values in physical and chemical parameters. We found that *R. globostellata* can tolerate the combination of low seawater pH and dissolved oxygen during the low tidal phase, and it does not show any metabolic dysfunction in its ability to recycle both the organic matter and nutrients. In contrast, higher temperature coupled with extreme acidification and deoxygenation had a dual effect on the sponge: *(i)* instead of recycling organic matter into detritus and making it available to higher trophic levels, sponges showed no detritus production; *(ii)* the photosynthetic activity of the symbionts suffered during periods of thermal stress. On-going laboratory experiments using stable isotope analyses are testing the potential role of temperature as the driver of the break in the detritus production, and the processes that are involved when the detritus production stops. Our study further shows how important trophic pathways may change under extreme environmental conditions and provides insights into how other sponges may respond to ongoing climate change.

CRediT authorship contribution statement

Federica Maggioni and Riccardo Rodolfo-Metalpa designed the study and realize the in situ experiment. James J. Bell and Megan Shaffer conducted the ex-situ experiments. Mireille Pujo-Pay, Hugues Lemonnier and the IRD, LAMA laboratory performed the seawater sample analyses. Carlo Cerrano and Yves Letrourner intellectually contributed to the study. All data were analyzed by Federica Maggioni who wrote the original ms with Riccardo Rodolfo-Metalpa, and James J. Bell. All the authors contributed to the revision of the manuscript.

Declaration of competing interest

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.

Data availability

The original contributions presented in the study are included in the Supplementary Material, further inquiries can be directed to the corresponding author.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.114869.

References

Achlatis, M., Pernice, M., Green, K., Guagliardo, P., Kilburn, M.R., Hoegh-Guldberg, O., Dove, S., 2018. Single-cell measurement of ammonium and bicarbonate uptake within a photosymbiotic bioeroding sponge. ISME J. https://doi.org/10.1038/s41396-017-0044-2.

Alexander, B.E., Liebrand, K., Osinga, R., Van Der Geest, H.G., Admiraal, W., Cleutjens, J. P.M., Schutte, B., Verheyen, F., Ribes, M., Van Loon, E., De Goeij, J.M., 2014. Cell turnover and detritus production in marine sponges from tropical and temperate benthic ecosystems. PLoS ONE. https://doi.org/10.1371/journal.pone.0109486.

Archer, S.K., Stevens, J.L., Rossi, R.E., Matterson, K.O., Layman, C.A., 2017. Abiotic conditions drive significant variability in nutrient processing by a common Caribbean sponge, Ircinia Felix. Limnol. Oceanogr. https://doi.org/10.1002/lno.10533.

Azam, F., Fenchel, T., Field, J., Gray, J., Meyer-Reil, L., Thingstad, F., 1983. The ecological role of water-column microbes in the sea. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps010257.

Bart, M.C., Hudspith, M., Rapp, H.T., Verdonschot, P.F.M., de Goeij, J.M., 2021. A Deep-Sea sponge Loop? Sponges transfer dissolved and particulate organic carbon and nitrogen to associated Fauna. Front. Mar. Sci. https://doi.org/10.3389/fmars.2021.604879.

Bayer, K., Schmitt, S., Hentschel, U., 2008. Physiology, phylogeny and in situ evidence for bacterial and archaeal nitrifiers in the marine sponge aplysina aerophoba. Environ. Microbiol. https://doi.org/10.1111/j.1462-2920.2008.01582.x.

Beepat, S.S., Davy, S.K., Woods, L., Bell, J.J., 2020. Short-term responses of tropical lagoon sponges to elevated temperature and nitrate. Mar. Environ. Res. https://doi.org/10.1016/j.marenvres.2020.104922.

Bell, J.J., 2008. The functional roles of marine sponges. Estuar. Coast. Shelf Sci. https://doi.org/10.1016/j.ecss.2008.05.002.

Bell, J.J., Davy, S.K., Jones, T., Taylor, M.W., Webster, N., 2013. Could some coral reefs become sponge reefs as our climate changes? Glob. Chang. Biol. https://doi.org/10.1111/gcb.12212.

Bell, J.J., Rovellini, A., Davy, S.K., Taylor, M.W., Fulton, E.A., Dunn, M.R., Bennett, H.M., Kandler, N.M., Luter, H.M., Webster, N.S., 2018. Climate change alterations to ecosystem dominance: how might sponge-dominated reefs function? Ecology. https://doi.org/10.1002/ecy.2446.

Bell, J.J., Shaffer, M., Luter, H.M., Mana, R., Rodolfo-Metalpa, R., 2022. Phototrophic sponge productivity may not be enhanced in a high CO2 world. Glob. Chang. Biol. May, 1–12. https://doi.org/10.1111/gcb.16235.

Benner, R., Pakulski, J.D., McCarthy, M., Hedges, J.I., Hatcher, P.G., 1992. Bulk chemical characteristics of dissolved organic matter in the ocean. Science. https://doi.org/10.1126/science.255.5051.1561.

Bennett, H.M., Altenrath, C., Woods, L., Davy, S.K., Webster, N.S., Bell, J.J., 2017. Interactive effects of temperature and pCO2on sponges: from the cradle to the grave. Glob. Chang. Biol. https://doi.org/10.1111/gcb.13474.

Biggerstaff, A., Smith, D.J., Jompa, J., Bell, J.J., 2015. Photoacclimation supports environmental tolerance of a sponge to turbid low-light conditions. Coral Reefs. https://doi.org/10.1007/s00338-015-1340-9.

Biscéré, T., Rodolfo-Metalpa, R., Lorrain, A., Chauvaud, L., Thébault, J., Clavier, J., Houlbrèque, F., 2015. Responses of two scleractinian corals to cobalt pollution and ocean acidification. PLoS ONE. https://doi.org/10.1371/journal.pone.0122898.

Burt, J.A., Camp, E.F., Enochs, I.C., Johansen, J.L., Morgan, K.M., Riegl, B., Hoey, A.S., 2020. Insights from extreme coral reefs in a changing world. Coral Reefs. https://doi.org/10.1007/s00338-020-01966-y.

Camp, E.F., Suggett, D.J., Gendron, G., Jompa, J., Manfrino, C., Smith, D.J., 2016. Mangrove and seagrass beds provide different biogeochemical Services for Corals Threatened by climate change. Front. Mar. Sci. https://doi.org/10.3389/fmars.2016.00052.

Camp, E.F., Nitschke, M.R., Rodolfo-Metalpa, R., Houlbreque, F., Gardner, S.G., Smith, D. J., Zampighi, M., Suggett, D.J., 2017. Reef-building corals thrive within hot-acidified and deoxygenated waters. Sci. Rep. https://doi.org/10.1038/s41598-017-02383-y.

Camp, E.F., Schoepf, V., Mumby, P.J., Suggett, D.J., 2018. Editorial: the future of coral reefs subject to rapid climate change: lessons from natural extreme environments. Front. Mar. Sci. https://doi.org/10.3389/fmars.2018.00433.

Carlson, C.A., Giovannoni, S.J., Hansell, D.A., Goldberg, S.J., Parsons, R., Otero, M.P., Vergin, K., Wheeler, B.R., 2002. Effect of nutrient amendments on bacterioplankton production, community structure, and DOC utilization in the northwestern Sargasso Sea. Aquat. Microb. Ecol. https://doi.org/10.3354/ame030019.

Cebrian, E., Uriz, M.J., Garrabou, J., Ballesteros, E., 2011. Sponge mass mortalities in a warming mediterranean sea: are cyanobacteria-harboring species worse off? PLoS ONE. https://doi.org/10.1371/journal.pone.0020211.

De Goeij, J.M., Van Den Berg, H., Van Oostveen, M.M., Epping, E.H.G., Van Duyl, F.C., 2008. Major bulk dissolved organic carbon (DOC) removal by encrusting coral reef cavity sponges. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps07403.

De Goeij, J.M., Van Oevelen, D., Vermeij, M.J.A., Osinga, R., Middelburg, J.J., De Goeij, A.F.P.M., Admiraal, W., 2013. Surviving in a marine desert: the sponge loop retains resources within coral reefs. Science. https://doi.org/10.1126/science.1241981.

De Goeij, J.M., Lesser, M.P., Pawlik, J.R., 2017. Nutrient fluxes and ecological functions of coral reef sponges in a changing ocean. In: Climate Change, Ocean Acidification and Sponges: Impacts Across Multiple Levels of Organization.

Fan, L., Liu, M., Simister, R., Webster, N.S., Thomas, T., 2013. Marine microbial symbiosis heats up: the phylogenetic and functional response of a sponge holobiont to thermal stress. ISME J. https://doi.org/10.1038/ismej.2012.165.

Fiore, C.L., Baker, D.M., Lesser, M.P., 2013. Nitrogen biogeochemistry in the Caribbean sponge, Xestospongia muta: a source or sink of dissolved inorganic Nitrogen? PLoS ONE. https://doi.org/10.1371/journal.pone.0072961.

Genty, B., Briantais, J.M., Baker, N.R., 1989. The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. Biochim. Biophys. Acta Gen. Subj. https://doi.org/10.1016/S0304-4165(89)80016-9.

Goodwin, C., Rodolfo-Metalpa, R., Picton, B., Hall-Spencer, J.M., 2014. Effects of ocean acidification on sponge communities. Mar. Ecol. https://doi.org/10.1111/maec.12093.

Hadas, E., Shpigel, M., Ilan, M., 2009. Particulate organic matter as a food source for a coral reef sponge. J. Exp. Biol. https://doi.org/10.1242/jeb.027953.

Hall-Spencer, J.M., Rodolfo-Metalpa, R., Martin, S., Ransome, E., Fine, M., Turner, S.M., Rowley, S.J., Tedesco, D., Buia, M.C., 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. Nature. https://doi.org/10.1038/nature07051.

Hentschel, U., Usher, K.M., Taylor, M.W., 2006. Marine Sponges as Microbial Fermenters.

Hildebrand, T., Osterholz, H., Bunse, C., Grotheer, H., Dittmar, T., Schupp, P.J., 2022. Transformation of dissolved organic matter by two indo-Pacific sponges. Limnol. Oceanogr. 2483–2496. https://doi.org/10.1002/lno.12214.

Hoegh-Guldberg, O., Bruno, J.F., 2010. The impact of climate change on the world's marine ecosystems. Science. https://doi.org/10.1126/science.1189930.

Hoer, D.R., Gibson, P.J., Tommerdahl, J.P., Lindquist, N.L., Martens, C.S., 2018. Consumption of dissolved organic carbon by Caribbean reef sponges. Limnol. Oceanogr. https://doi.org/10.1002/lno.10634.

Hoey, A.S., Howells, E., Johansen, J.L., Hobbs, J.P.A., Messmer, V., McCowan, D.M., Wilson, S.K., Pratchett, M.S., 2016. Recent advances in understanding the effects of climate change on coral reefs. Diversity. https://doi.org/10.3390/d8020012.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C., Grosberg, R., Hoegh-Guldberg, O., Jackson, J.B.C., Kleypas, J., Lough, J.M., Marshall, P., Nyström, M., Palumbi, S.R., Pandolfi, J.M., Rosen, B., Roughgarden, J., 2003. Climate change, human impacts, and the resilience of coral reefs. Science. https://doi.org/10.1126/science.1085046.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., Bridge, T.C., Butler, I.R., Byrne, M., Cantin, N.E., Comeau, S., Connolly, S.R., Cumming, G.S., Dalton, S.J., Diaz-Pulido, G., Eakin, C.M., Figueira, W.F., Gilmour, J.P., Harrison, H. B., Heron, S.F., Hoey, A.S., Hobbs, J.P.A., Hoogenboom, M.O., Kennedy, E.V., Kuo, C.Y., Lough, J.M., Lowe, R.J., Liu, G., McCulloch, M.T., Malcolm, H.A., McWilliam, M.J., Pandolfi, J.M., Pears, R.J., Pratchett, M.S., Schoepf, V., Simpson, T., Skirving, W.J., Sommer, B., Torda, G., Wachenfeld, D.R., Willis, B.L., Wilson, S.K., 2017. Global warming and recurrent mass bleaching of corals. Nature. https://doi.org/10.1038/nature21707.

IPCC, 2013. Climate Change 2013-The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC.

IPCC, 2014. Climate Change 2014 Synthesis Report - IPCC.

IPCC, 2021. Climate Change 2021—The Physical Science Basis, Chemistry International. https://doi.org/10.1515/ci-2021-0407.

Jiménez, E., Ribes, M., 2007. Sponges as a source of dissolved inorganic nitrogen: nitrification mediated by temperate sponges. Limnol. Oceanogr. https://doi.org/10.4319/lo.2007.52.3.0948.

Jürgens, K., DeMott, W.R., 1995. Behavioral flexibility in prey selection by bacterivorous nanoflagellates. Limnol. Oceanogr. https://doi.org/10.4319/lo.1995.40.8.1503.

Kahn, A.S., Leys, S.P., 2016. The role of cell replacement in benthic-pelagic coupling by suspension feeders. R. Soc. Open Sci. https://doi.org/10.1098/rsos.160484.

Lesser, M.P., Fiore, C., Slattery, M., Zaneveld, J., 2016. Climate change stressors destabilize the microbiome of the Caribbean barrel sponge, Xestospongia muta. J. Exp. Mar. Biol. Ecol. https://doi.org/10.1016/j.jembe.2015.11.004.

Lesser, M.P., Mueller, B., Pankey, M.S., Macartney, K.J., Slattery, M., de Goeij, J.M., 2020. Depth-dependent detritus production in the sponge, Halisarca caerulea. Limnol. Oceanogr. https://doi.org/10.1002/lno.11384.

López-Acosta, M., Leynaert, A., Chavaud, L., Amice, E., Bihannic, I., Le Bec, T., Maldonado, M., 2019. In situ determination of si, N, and P utilization by the demosponge Tethya citrina: a benthic-chamber approach. PLoS ONE. https://doi.org/10.1371/journal.pone.0218787.

López-Legentil, S., Song, B., Mcmurray, S.E., Pawlik, J.R., 2008. Bleaching and stress in coral reef ecosystems: hsp70 expression by the giant barrel sponge Xestospongia muta. Mol. Ecol. https://doi.org/10.1111/j.1365-294X.2008.03667.x.

Luter, H.M., Andersen, M., Versteegen, E., Laffy, P., Uthicke, S., Bell, J.J., Webster, N.S., 2020. Cross-generational effects of climate change on the microbiome of a photosynthetic sponge. Environ. Microbiol. https://doi.org/10.1111/1462-2920.15222.

Maggioni, F., Pujo-Pay, M., Aucan, J., Cerrano, C., Calcinai, B., Payri, C., Benzoni, F., Letourneur, Y., Rodolfo-Metalpa, R., 2021. The Bouraké semi-enclosed lagoon (New Caledonia)- a natural laboratory to study the lifelong adaptation of a coral reef ecosystem to extreme environmental conditions. Biogeosciences 18 (18), 5117–5140. https://doi.org/10.5194/bg-18-5117-2021.

Maldonado, M., Zhang, X., Cao, X., Xue, L., Cao, H., Zhang, W., 2010. Selective feeding by sponges on pathogenic microbes: a reassessment of potential for abatement of microbial pollution. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps08411.

Maldonado, M., Ribes, M., van Duyl, F.C., 2012. Nutrient fluxes through sponges. Biology, budgets, and ecological implications. In: Advances in Marine Biology.

Maldonado, M., Acosta, M.L., Beazley, L., Kenchington, E., Koutsouveli, V., Riesgo, A., 2020. Cooperation between passive and active silicon transporters clarifies the

ecophysiology and evolution of biosilicification in sponges. Sci. Adv. https://doi.org/10.1126/sciadv.aba9322.
Massaro, A.J., Weisz, J.B., Hill, M.S., Webster, N.S., 2012. Behavioral and morphological changes caused by thermal stress in the great barrier reef sponge rhopaloeides odorabile. J. Exp. Mar. Biol. Ecol. https://doi.org/10.1016/j.jembe.2012.02.008.
McMurray, S.E., Johnson, Z.I., Hunt, D.E., Pawlik, J.R., Finelli, C.M., 2016. Selective feeding by the giant barrel sponge enhances foraging efficiency. Limnol. Oceanogr. https://doi.org/10.1002/lno.10287.
McMurray, S.E., Stubler, A.D., Erwin, P.M., Finelli, C.M., Pawlik, J.R., 2018. A test of the sponge-loop hypothesis for emergent Caribbean reef sponges. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps12466.
Micaroni, V., Strano, F., McAllen, R., Woods, L., Turner, J., Harman, L., Bell, J.J., 2022. Adaptive strategies of sponges to deoxygenated oceans. Glob. Chang. Biol. https://doi.org/10.1111/gcb.16013.
Moitinho-Silva, L., Steinert, G., Nielsen, S., Hardoim, C.C.P., Wu, Y.C., McCormack, G.P., López-Legentil, S., Marchant, R., Webster, N., Thomas, T., Hentschel, U., 2017a. Predicting the HMA-LMA status in marine sponges by machine learning. Front. Microbiol. https://doi.org/10.3389/fmicb.2017.00752.
Moitinho-Silva, L., Nielsen, S., Amir, A., Gonzalez, A., Ackermann, G.L., Cerrano, C., Astudillo-Garcia, C., Easson, C., Sipkema, D., Liu, F., Steinert, G., Kotoulas, G., McCormack, G.P., Feng, G., Bell, J.J., Vicente, J., Björk, J.R., Montoya, J.M., Olson, J.B., Reveillaud, J., Steindler, L., Pineda, M.C., Marra, M.V., Ilan, M., Taylor, M.W., Polymenakou, P., Erwin, P.M., Schupp, P.J., Simister, R.L., Knight, R., Thacker, R.W., Costa, R., Hill, R.T., Lopez-Legentil, S., Dailianis, T., Ravasi, T., Hentschel, U., Li, Z., Webster, N.S., Thomas, T., 2017b. The sponge microbiome project. GigaScience. https://doi.org/10.1093/gigascience/gix077.
Morganti, T., Coma, R., Yahel, G., Ribes, M., 2017. Trophic niche separation that facilitates co-existence of high and low microbial abundance sponges is revealed by in situ study of carbon and nitrogen fluxes. Limnol. Oceanogr. https://doi.org/10.1002/lno.10546.
Morrow, K.M., Bourne, D.G., Humphrey, C., Botté, E.S., Laffy, P., Zaneveld, J., Uthicke, S., Fabricius, K.E., Webster, N.S., 2015. Natural volcanic CO2seeps reveal future trajectories for host-microbial associations in corals and sponges. ISME J. https://doi.org/10.1038/ismej.2014.188.
Mueller, B., De Goeij, J.M., Vermeij, M.J.A., Mulders, Y., Van Der Ent, E., Ribes, M., Van Duyl, F.C., 2014. Natural diet of coral-excavating sponges consists mainly of dissolved organic carbon (DOC). PLoS ONE. https://doi.org/10.1371/journal.pone.0090152.
Pansini, M., Morri, C., Bianchi, C.N., 2000. The sponge community of a subtidal area with hydrothermal vents: Milos Island, Aegean Sea. Estuar. Coast. Shelf Sci. https://doi.org/10.1006/ecss.2000.0674.
Pawlik, J.R., McMurray, S.E., 2020. The emerging ecological and biogeochemical importance of sponges on coral reefs. Annu. Rev. Mar. Sci. https://doi.org/10.1146/annurev-marine-010419-010807.
Pawlik, J.R., McMurray, S.E., Erwin, P., Zea, S., 2015. A review of evidence for food limitation of sponges on Caribbean reefs. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps11093.
Pawlik, J.R., Burkepile, D.E., Thurber, R.V., 2016. A vicious circle? Altered carbon and nutrient cycling may explain the low resilience of Caribbean coral reefs. Bioscience. https://doi.org/10.1093/biosci/biw047.
Pita, L., Rix, L., Slaby, B.M., Franke, A., Hentschel, U., 2018. The sponge holobiont in a changing ocean: from microbes to ecosystems. Microbiome. https://doi.org/10.1186/s40168-018-0428-1.
R Core Team, 2019. R.studio Team, R Development Core Team.
Ralph, P.J., Gademann, R., Larkum, A.W.D., Schreiber, U., 1999. In situ underwater measurements of photosynthetic activity of coral zooxanthellae and other reef-dwelling dinoflagellate endosymbionts. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps180139.
Ramsby, B.D., Hoogenboom, M.O., Smith, H.A., Whalan, S., Webster, N.S., 2018. The bioeroding sponge Cliona orientalis will not tolerate future projected ocean warming. Sci. Rep. https://doi.org/10.1038/s41598-018-26535-w.
Reiswig, H.M., 1975. Bacteria as food for temperate-water marine sponges. Can. J. Zool. https://doi.org/10.1139/z75-072.
Ribes, M., Coma, R., Gili, J.M., 1999. Natural diet and grazing rate of the temperate sponge Dysidea avara (Demospongiae, Dendroceratida) throughout an annual cycle. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps176179.
Rix, L., De Goeij, J.M., Mueller, C.E., Struck, U., Middelburg, J.J., Van Duyl, F.C., Al-Horani, F.A., Wild, C., Naumann, M.S., Van Oevelen, D., 2016. Coral mucus fuels the sponge loop in warm-and cold-water coral reef ecosystems. Sci. Rep. https://doi.org/10.1038/srep18715.
Rix, L., de Goeij, J.M., van Oevelen, D., Struck, U., Al-Horani, F.A., Wild, C., Naumann, M.S., 2017. Differential recycling of coral and algal dissolved organic matter via the sponge loop. Funct. Ecol. https://doi.org/10.1111/1365-2435.12758.
Rix, L., De Goeij, J.M., Van Oevelen, D., Struck, U., Al-Horani, F.A., Wild, C., Naumann, M.S., 2018. Reef sponges facilitate the transfer of coral-derived organic matter to their associated fauna via the sponge loop. Mar. Ecol. Prog. Ser. https://doi.org/10.3354/meps12443.
Sokolova, I.M., Frederich, M., Bagwe, R., Lannig, G., Sukhotin, A.A., 2012. Energy homeostasis as an integrative tool for assessing limits of environmental stress tolerance in aquatic invertebrates. Mar. Environ. Res. https://doi.org/10.1016/j.marenvres.2012.04.003.
Stevenson, A., Archer, S.K., Schultz, J.A., Dunham, A., Marliave, J.B., Martone, P., Harley, C.D.G., 2020. Warming and acidification threaten glass sponge Aphrocallistes vastus pumping and reef formation. Sci. Rep. 10 (1), 1–11. https://doi.org/10.1038/s41598-020-65220-9.
Taylor, F.J.R., Hoppenrath, M., Saldarriaga, J.F., 2008. Dinoflagellate diversity and distribution. Biodivers. Conserv. https://doi.org/10.1007/s10531-007-9258-3.
Thomas, T., Moitinho-Silva, L., Lurgi, M., Björk, J.R., Easson, C., Astudillo-García, C., Olson, J.B., Erwin, P.M., López-Legentil, S., Luter, H., Chaves-Fonnegra, A., Costa, R., Schupp, P.J., Steindler, L., Erpenbeck, D., Gilbert, J., Knight, R., Ackermann, G., Victor Lopez, J., Taylor, M.W., Thacker, R.W., Montoya, J.M., Hentschel, U., Webster, N.S., 2016. Diversity, structure and convergent evolution of the global sponge microbiome. Nat. Commun. https://doi.org/10.1038/ncomms11870.
Vicente, J., Silbiger, N.J., Beckley, B.A., Raczkowski, C.W., Hill, R.T., 2016. Impact of high pCO2and warmer temperatures on the process of silica biomineralization in the sponge mycale grandis. ICES J. Mar. Sci. https://doi.org/10.1093/icesjms/fsv235.
Webb, A.E., van Heuven, S.M.A.C., de Bakker, D.M., van Duyl, F.C., Reichart, G.-J., de Nooijer, L.J., 2017. Combined effects of experimental acidification and eutrophication on reef sponge bioerosion rates. Front. Mar. Sci. https://doi.org/10.3389/fmars.2017.00311.
Webster, N.S., Luter, H.M., Soo, R.M., Botté, E.S., Simister, R.L., Abdo, D., Whalan, S., 2012. Same, same but different: symbiotic bacterial associations in GBR sponges. Front. Microbiol. https://doi.org/10.3389/fmicb.2012.00444.
Wilkinson, C.R., 1983. Net primary productivity in coral reef sponges. Science. https://doi.org/10.1126/science.219.4583.410.
Wisshak, M., Schönberg, C.H.L., Form, A., Freiwald, A., 2012. Ocean acidification accelerates reef bioerosion. PLoS ONE. https://doi.org/10.1371/journal.pone.0045124.
Wooster, M.K., McMurray, S.E., Pawlik, J.R., Morán, X.A.G., Berumen, M.L., 2019. Feeding and respiration by giant barrel sponges across a gradient of food abundance in the Red Sea. Limnol. Oceanogr. https://doi.org/10.1002/lno.11151.
Wulff, J.L., 2006. Ecological interactions of marine sponges. Can. J. Zool. https://doi.org/10.1139/z06-019.
Yahel, G., Sharp, J.H., Marie, D., We, A., Yahel, R., Ayalon, I., Ohevia, M., Wyeth, C., Munkes, B., Motro, R., Eckstein, S., Brandes, G., Shif, Y., Weil, D., Inditzky, A., Cohen, N., Hazan, E., Cohen, T., Gutman, L., Meallem, I., Savidge, K.B., Andrews, R., Canfield, D.E., Rinker, K., 2003. In Situ Feeding and Element Removal in the Symbiont-bearing Sponge Theonella swinhoei: Bulk DOC is the Major Source for Carbon.
Zhang, F., Blasiak, L.C., Karolin, J.O., Powell, R.J., Geddes, C.D., Hill, R.T., 2015. Phosphorus sequestration in the form of polyphosphate by microbial symbionts in marine sponges. Proc. Natl. Acad. Sci. https://doi.org/10.1073/pnas.1423768112.