

**THE ROLE OF SUBMARINE GROUNDWATER IN SHAPING NEARSHORE CORAL  
PHYSIOLOGY**

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## ABSTRACT

Although coral reefs evolved in oligotrophic waters, corals are now distributed across a variety of biogeochemical environments that shape their physiology. Allochthonous sources of nutrients – such as coastal runoff, rivers, and submarine groundwater discharge (SGD) – increased nutrient availability and altered carbonate dynamics. To investigate the influence of SGD on coral physiology, we conducted a seven-week field experiment along an SGD gradient in Moorea, French Polynesia. This gradient was characterized by tidally-regulated pulses of cooler, less saline water with lower pH, higher alkalinity, and elevated macronutrient concentrations (phosphate, N+N, and silicate). We evaluated the physiological responses of two common fringing reef corals, *Porites rus* and *Pocillopora acuta*, by examining changes in the holobiont (percent change in buoyant weight), endosymbiont photopigmentation (total chlorophyll content), and nutrient partitioning ( $\delta^{15}\text{N}_{\text{H-S}}$  and  $\delta^{13}\text{C}_{\text{H-S}}$ ) when exposed to SGD influence for 7-8 weeks across 20 stations on the exposed reef. In *P. acuta*, total chlorophyll content and  $\delta^{15}\text{N}_{\text{H-S}}$  both displayed a significant relationship with SGD influence, highlighting the sensitivity of the symbiont physiology to SGD. There were no effects of SGD on any of the measured parameters for *P. rus*. Isotope analyses showed *P. rus* and *P. acuta* display different feeding strategies: *P. acuta* relied more on heterotrophy (67% overlap in isotopic niche between the host and symbiont) while *P. rus* relied more on autotrophy (93% overlap in isotopic niche between the host and symbiont).  $\delta^{15}\text{N}$  values of zooplankton and particulate organic matter within and outside the seep indicated heterotrophic contributions to corals were predominantly derived from non-seep sources outside the seep. These results indicate that the complex biogeochemical inputs from SGD drive contrasting physiological responses within coral holobionts. Our findings reveal that submarine groundwater discharge, an often-overlooked coastal input, can drive differential physiological responses that may ultimately influence species composition and trophic dynamics on coral reefs.

# TABLE OF CONTENTS

<b>ABSTRACT .....</b>	<b>III</b>
<b>LIST OF TABLES .....</b>	<b>V</b>
<b>LIST OF FIGURES .....</b>	<b>VI</b>
<b>1. INTRODUCTION .....</b>	<b>1</b>
<b>2. MATERIALS AND METHODS .....</b>	<b>4</b>
<b>2.1 STUDY SITE AND GRADIENT CHARACTERIZATION .....</b>	<b>4</b>
<b>2.2 EXPERIMENTAL DESIGN .....</b>	<b>6</b>
<b>2.3 CORAL GROWTH .....</b>	<b>7</b>
<b>2.4 TOTAL CHLOROPHYLL DENSITY .....</b>	<b>8</b>
<b>2.5 STABLE ISOTOPE ANALYSIS .....</b>	<b>8</b>
<b>2.6 ISOTOPIC CHARACTERIZATION OF ENERGETIC RESOURCE .....</b>	<b>9</b>
<b>2.7 DATA ANALYSES .....</b>	<b>10</b>
<b>3.0 RESULTS .....</b>	<b>12</b>
<b>3.1 ENDOSYMBIONT RESPONSE .....</b>	<b>12</b>
<b>3.2 HOLOBIONT RESPONSE .....</b>	<b>12</b>
<b>3.3 NUTRITIONAL PLASTICITY .....</b>	<b>13</b>
<b>3.4 CAGING TREATMENT .....</b>	<b>15</b>
<b>4.0 DISCUSSION .....</b>	<b>15</b>
<b>5.0 REFERENCES .....</b>	<b>25</b>

## LIST OF TABLES

**Table 1.** Trophic discrimination factors (TDF) for zooplankton, POM, and symbionts adopted from Wang et al., 2024.

**Table 2.** Summary statistics of univariate models of low tide water chemistry parameters associated with SGD against the  $\delta^{15}\text{N}_{\text{H-S}}$  in *P. acuta*.

## LIST OF FIGURES

**Figure 1.** (A) Map of experimental stations with insets depicting (B) a windrose plot displaying ADCP current speed and direction data collected in March 2023 and (C) the location of the site on the western coast of Moorea. Colors on (A) represent the interpolation of principal component axis 1, shown in (D). The source of SGD is marked SEEP, and experimental stations named in descending alphabetical order by geographical distance to the seep of SGD, except for pin T, which was presumed to be upstream of the labeled seep. (E) depicts the experimental set-up at each station.

**Figure 2:** Univariate model depictions of coral physiology response variables against the principal components axis for *P. acuta* (A-D) and *P. rus* (E-H).

**Figure 3.** SIBER for (A) *P. acuta* and (D) *P. rus*. Isotope biplot for (B) *P. acuta* and (E) *P. rus* host samples and their potential isotopic sources. Proportional contributions as determined by MixSIAR are represented as whisker plots for (C) *Pocillopora acuta* and (F) *Porites rus*.

## 1. INTRODUCTION

The symbiotic relationship between the coral animal host and its micro-algal endosymbionts (family Symbiodiniaceae (LaJeunesse et al., 2018)) is tightly regulated by biogeochemical conditions. Disruptions to this balance - whether from changes in nutrient availability, temperature, pH, or alkalinity - can fundamentally alter coral physiology, affecting growth, physiological resilience, and thermal tolerance (Davy et al., 2012; Rådecker et al., 2015). While the effects of changes in seawater chemistry and nutrient loads on the coral holobiont have been meticulously studied in manipulative experiments (Krämer et al., 2022; Nalley et al., 2023; N. J. Silbiger et al., 2018), field-based studies that evaluate the multivariate responses of corals to these conditions remain limited (but see Barnas et al., 2025; Kerlin et al., 2025; Shantz & Burkepile, 2014). Given the complexity of biogeochemical shifts *in situ*, corals likely experience and respond to chemical and nutrient changes differently than in controlled settings where key environmental variables are isolated. For example, the effects of nitrogen and phosphorus enrichment are highly interactive. Moderate levels of either nutrient can enhance coral photosynthesis and growth (Bucher & Harrison, 2000; Davy et al., 2012; Godinot et al., 2011; Marubini & Davies, 1996; Morris et al., 2019; Nalley et al., 2023), excess nitrogen without sufficient phosphorus can disrupt symbiosis and reduce resilience (Donovan et al., 2020; Rosset et al., 2017; Wooldridge, 2016), and balanced nutrient enrichment (i.e., conserved stoichiometric relationship) may mitigate some negative effects observed on coral physiology (Morris et al., 2019; Zhao et al., 2021). However, the broader ecological implications of these nutrient interactions remain unclear, particularly in the context of real-world biogeochemical fluctuations.

Nutrient fluctuations are rarely unidirectional in coral reef ecosystems; instead, they occur as dynamic, multivariate shifts driven by tidal cycles, wave action, and land-sea interactions (Adam et al., 2021; Guadayol et al., 2014; Liu et al., 2018; Wang et al., 2018). One prominent source of such variability is submarine groundwater discharge (SGD), defined as the flow of water from land through the marginal

seabed into the coastal ocean (Johannes, 1980). SGD serves as a major conduit for nutrient delivery to nearshore reefs, particularly on high volcanic islands (Moosdorf et al., 2015), where SGD fluxes of chemical weathering products can exceed that from rivers (Schopka & Derry, 2012). SGD alters the water chemistry of nearshore environments, typically by altering carbonate chemistry, decreasing salinity, decreasing temperature, and increasing nutrient availability (Santos et al., 2021). The nutrient concentration and alkalinity of SGD is influenced by geologic composition and land-based processes, including agricultural runoff and/or wastewater intrusion (Taniguchi et al., 2002, 2019), and the flux of SGD varies with subsurface geology, rainfall (Burnett et al., 2006; Wu et al., 1996), and seawater level (tide and wave run-up) (Li et al., 1999; Li et al., 2009). Once discharged into coastal waters, the extent to which SGD influences reef ecosystems depends on its mixing dynamics, which vary spatially and temporally with hydrodynamic processes (Hagedorn et al., 2024; Monismith, 2007). Consequently, corals exposed to SGD experience high-frequency variability in alkalinity, nutrients, and other environmental conditions (e.g. salinity, temperature, pH). Understanding how corals respond to such naturally fluctuating conditions is essential for predicting their resilience in an era of accelerating environmental change.

Prior studies indicate that intermediate fluxes of SGD have been found to increase coral growth (Lubarsky et al., 2018), as well as community taxonomic and functional richness (Barnas et al., 2025a; La Valle et al., 2021). In areas with significant SGD flux, low salinity and high variability in pH negatively impact coral survival (Lubarsky et al., 2018); however, the mechanisms behind these physiological limitations remain unclear. Decades of experimental work have revealed how shifts in water chemistry associated with SGD can shape coral physiological performance. For instance, chronic reductions in pH—mimicking ocean acidification—impair coral calcification (Erez et al., 2011) and enhance bioerosion, weakening reef accretion ([Silbiger et al., 2014](#); [Silbiger & Donahue, 2015](#); [Wisshak et al., 2012](#)). Conversely, highly alkaline conditions promote coral growth by increasing the availability of carbonate ions for skeletal deposition (Marubini et al., 2008; Schneider & Erez, 2006; Wall & Edmunds,

2013). Moderate and persistent exposure to lower salinity reduces coral growth (Ferrier-Pagès et al., 1999) and autotrophic capacity (Moberg et al., 1997), potentially compromising coral resilience to environmental stress (True, 2012). Similarly, temperature fluctuations from SGD can act as both stressors and buffers. Cooler water generally slows coral growth (P. A. Baker & Weber, 1975), however, SGD-driven temperature moderation has been hypothesized to provide localized refugia during marine heatwaves, helping corals maintain thermal conditions closer to their physiological optima ([Jokiel & Coles, 1977](#)).

Although coral trophic plasticity has been studied in the context of thermal stress and nutrient enrichment, changes in response to the altered resource regimes of SGD systems have yet to be examined. Beyond physicochemical shifts, SGD also modifies reef trophodynamics by introducing distinct microbial assemblages (McClintock, 2022), which may serve as an additional food source for corals. Stable isotope analysis is a widely used method for investigating nutritional exchanges in ecological studies, particularly in food webs. Isotopes of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) are commonly used because their relative abundances can provide insights into an organism's dietary sources and trophic level (Deniro & Epstein, 1981). Specifically,  $\delta^{13}\text{C}$  values help differentiate between carbon sources, such as those derived from autotrophic versus heterotrophic production, while  $\delta^{15}\text{N}$  values are often used to infer trophic position, as nitrogen isotope values become enriched with each trophic transfer. In corals, heterotrophic feeding increases the nitrogen and carbon isotope values of the host ( $\delta^{15}\text{N}_{\text{host}}$ ,  $\delta^{13}\text{C}_{\text{host}}$ , respectively) relative to the symbiont, which can be detected as increases in the difference between host and symbiont values of these isotopes ( $\delta^{15}\text{N}_{\text{H-S}}$  and  $\delta^{13}\text{C}_{\text{H-S}}$ ) (Muscatine et al 1989; Conti-Jerpe et al., 2020), though these signals may be weakened by internal nutrient recycling between holobiont fractions (Reynaud et al., 2009). The extent to which corals rely on heterotrophic or autotrophic food sources varies depending on the ability to produce phototrophic nutrition (Grottoli et al., 2006), the availability of heterotrophic food sources (Fox et al., 2018), and species-specific constraints in trophic plasticity (Conti-Jerpe et al., 2020; Wall et al., 2021). Increased heterotrophy may offer corals an opportunity to increase their energy reserves during

stress (Grottoli et al., 2006), with limitations (Wall et al., 2019), meaning that the increased opportunities for nutrition from SGD-derived sources may support coral host performance during adverse conditions.

Building on these insights, this study examines physiological plasticity in nearshore corals as a response to SGD exposure. We tested two common reef coral species for physiological impacts of SGD-driven variability in water chemistry over a two month outplanting along a SGD gradient to determine whether exposure to SGD is beneficial or detrimental to coral performance. Given the complexity of SGD as a contributor to reef biogeochemistry, we examined a combined SGD signal while also identifying which aspects of altered groundwater biogeochemistry most influence coral physiology.

## **2. MATERIALS AND METHODS**

### **2.1 Study site and gradient characterization**

This study took place on the western coast of Moorea<sup>1</sup>, a high volcanic island within the Society Archipelago of French Polynesia, known to have SGD under microtidal conditions (Hagedorn et al., 2020, 2024; Haßler et al., 2019; Knee et al., 2016). This site has been previously described (Hagedorn et al., 2024; N. J. Silbiger et al., 2025), where a seep of SGD was confirmed with preliminary radon and salinity surveys. Results from an acoustic doppler current profiler (ADCP) showed near-unidirectional northwestward flow averaging 0.15 m/s (N. J. Silbiger et al., 2025). Using this information, 20 experimental stations were chosen between ca. 12 m and 140 m from the source (Figure 1A), ranging from 0.3 m – 0.8 m deep with an average depth of 0.6 m.

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<sup>1</sup> With respect to the spelling of Moorea, we followed the Raapoto transcription system that is adhered to by a large segment of the Tahitian community, but also recognize other community members follow the Te Fare Vanā‘a transcription system where the island name is spelled with an ‘eta (Mo‘orea) (see [mcr.lternet.edu/spelling\\_of\\_Tahitian\\_place\\_names](http://mcr.lternet.edu/spelling_of_Tahitian_place_names)).

The gradient of SGD influence was characterized through discrete water samples collected at the seep and each experimental location at high and low tide in day and night conditions (n = 4 samples per survey location) in March and August of 2022 (N. J. Silbiger et al., 2025). During each sampling event, water quality variables were measured including macronutrient concentrations of nitrate plus nitrite (N+N), ammonia ( $\text{NH}_4^+$ ), silicate ( $\text{SiO}_3^{2-}$ ), and phosphate ( $\text{PO}_4^{3-}$ ) and indicators of submarine groundwater discharge (SGD), including salinity, total alkalinity, and temperature (Moosdorf et al., 2015; Paytan et al., 2006; Santos et al., 2021), as reported by Silbiger et al. (2025).

Sampling followed standardized protocols to ensure consistency across time points, detailed collection methods of which can be found in Silbiger et al. (2025). In summary, water was collected in acid-washed, triple-rinsed high-density polyethylene (HDPE) bottles and immediately processed for *in situ* measurements of temperature (accuracy  $\pm 0.3^\circ\text{C}$ , precision =  $0.1^\circ\text{C}$ ), salinity (accuracy  $\pm 1.0\%$  psu, precision =  $0.1$  psu), and  $\text{pH}_T$  (tris-calibrated [total scale] ROSS double junction electrode, accuracy  $\pm 0.002$ , precision =  $0.001$ , Orion Star A325, Thermo Fisher Scientific, Massachusetts). *In situ*  $\text{pH}_T$  measurements were corrected for temperature using the *seacarb* package (Gattuso et al., 2023). Samples used for nutrient analysis were passed through  $0.22\text{-}\mu\text{m}$  Sterivex filters and frozen at  $-20^\circ\text{C}$  until laboratory analysis was completed on a Seal Analytical AA3 High-Resolution Nutrient AutoAnalyzer by the the UH SOEST Laboratory for Analytical Biogeochemistry (Hawai'i, USA) (level of detection: nitrate + nitrite =  $0.009\ \mu\text{mol L}^{-1}$ , phosphate =  $0.008\ \mu\text{mol L}^{-1}$ , silicate =  $0.065\ \mu\text{mol L}^{-1}$ ). Samples used for total alkalinity were fixed using a 50% saturated mercuric chloride solution with deionized (DI) water, following Dickson et al., (2007). Total alkalinity was determined using open-cell potentiometric titrations performed on a Mettler Toledo T5 autotitrator. To ensure analytical quality, a certified reference material (CRM Reference Material for Oceanic CO<sub>2</sub> Measurements, A. Dickson, Scripps Institution of Oceanography) was analyzed at the start of each sample set. Titrations were consistently within  $<0.5\%$  of CRM values, with a precision of  $\pm 5\ \mu\text{mol kg}^{-1}$ .

## 2.2 Experimental Design

Six colonies of *Porites rus* (Forsskål et al., 1775) and *Pocillopora acuta* (Lamarck, 1815) were collected from the experimental region upstream of SGD influence on either February 7<sup>th</sup>, 2023 (for *P. rus*) or February 12<sup>th</sup>, 2023 (for *P. acuta*). *Porites rus* is a common perforate reef building coral in tropical reefs (Darling et al., 2012) found in all reef zones in Moorea (Moorea Coral Reef LTER & Edmunds, 2024), where it creates complex structures in the lagoon supporting ecosystem resilience (Adam et al., 2011; Brooks et al., 2007). *Pocillopora acuta* is a highly studied weedy and imperforate coral species that is known to colonize disturbed habitats (Darling et al., 2012) and common across fringing reefs in Moorea (Burgess et al., 2024; Johnston et al., 2022; Moorea Coral Reef LTER & Edmunds, 2024).

Six intact colonies of each species were transported to flow-through water tables at the Richard B. Gump South Pacific Research Station (Gump Research Station), where they were fragmented using a Gryphon AquaSaw Diamond Band Frag Saw and adhered to plastic tiles with All Fix marine epoxy. Three fragments (ramets) of a single parent colony (genet) were deployed at each experimental station, with each parent colony represented at 3 or 4 stations. *Pocillopora acuta* colonies were deployed on February 11<sup>th</sup>, 2023 and *P. rus* colonies were deployed on February 16<sup>th</sup>, 2023. Preliminary surveys revealed that experimental stations were located within territorial damselfish (*Stegastes* spp.) territories, which can exert grazing pressure on coral colonies in their territories to ‘farm’ preferred algal food species (Ceccarelli et al., 2001). To minimize coral fragment mortality from *Stegastes* while assessing their potential effects, we used three caging treatments (Figure 1E; Supplemental Figure 1): a fully enclosed cage using 1 cm<sup>2</sup> wire mesh (caged), a partially enclosed cage facing the prevailing current (cage control), and an uncaged fragment. The exclusion of fish through caging is a frequently used experimental method for evaluating the impact of fish predation on the health of coral colonies (Baria et al., 2010; Lirman, 2001; Raker et al., 2023); however, cages may introduce physical effects in addition to the exclusion of

predators (cage artifacts, see Connell, 1997; Hindell et al., 2001; Virnstein, 1978, 1980). Therefore, we designed our cage control treatment to mimic the physical effects of the full cage while allowing fish predation and included tests for cage effects to our response variables (Steele, 1996). Fragments were then allowed to incubate for 7 (*P. acuta*) or 8 (*P. rus*) weeks *in situ*, with cages cleaned twice weekly. All fragments were collected on April 18<sup>th</sup>, 2023 and transported to Gump Research Station for post-deployment measurements.

### 2.3 Coral Growth

Coral growth was quantified as the percent change in buoyant weight before and after exposure to the SGD gradient using methods outlined in (Jokiel et al., 1978). The submerged weight of the corals with the plate attached were determined for each coral at each time point, in seawater with temperature and salinity measured using an Orion Thermo Scientific Star A329 pH/ISE/Cond/RDO/DO HH Meter STARA. These measurements were then used to calculate the density of seawater for each coral using the *rho* function from the R seacarb package (version 4.3.2, Gattuso et al., 2023). Buoyant weight was then converted to dry weight, assuming the density of aragonite to be the density of the coral skeleton ( $D_{\text{aragonite}} = 2.93 \text{ g cm}^{-3}$ ) following (Jokiel et al., 1978):

$$W_{dry} = \frac{W_{buoyant}}{\left(1 - \frac{D_{seawater}}{D_{aragonite}}\right)}$$

The percent change in buoyant weight was calculated as the change in dry weight pre- and post-deployment normalized to the starting dry weight of the coral ramet (Lubarsky et al., 2018; Sebens et al., 2003; Yap et al., 1998).

## 2.4 Total Chlorophyll Density

Chlorophyll content was measured following methods outlined in (Becker & Silbiger, 2020b). Coral fragments for each parent colony pre-deployment and of all experimental colonies post-deployment were frozen, thawed, and coral tissue was subsequently removed with an airbrush using deionized (DI) water, consistent with Baker et al., (2018). Tissue aliquots were centrifuged (5,000 xg for 3 min), keeping the algal pellet, which was suspended in 100% acetone and incubated in the dark at -20 °C for 24 hours.

Following extraction, the supernatant was measured at 750 nm, 663 nm, and 630 nm in a glass well plate reader whose path length is 0.71 cm. Final chlorophyll content per sample aliquot (µg/ml) was calculated using equations from Jeffrey & Humphrey, 1975:

$$\begin{aligned}\text{Chlorophyll } a &= 11.43 (A_{663} - A_{750} / \text{Path Length}) - 0.64 (A_{630} - A_{750} / \text{Path Length}) \\ \text{Chlorophyll } c2 &= 27.09 A_{663} - A_{750} / \text{Path Length} - 3.63 (A_{630} - A_{750} / \text{Path Length}) \\ \text{Total chlorophyll} &= \text{Chlorophyll } a + \text{Chlorophyll } c2\end{aligned}$$

Total chlorophyll content per sample was normalized to the live fragment surface area and is represented as total chlorophyll per cm<sup>2</sup>. To calculate the surface area of live tissue over the coral skeleton, after airbrushing coral skeletons were dried at 60°C in a drying oven (Thermo Scientific Heratherm General Incubator) for at least 12 hours. Surface area was determined through the wax dipping method, as outlined by Stimson & Kinzie, 1991, using one dip as is recommended by Veal et al., 2010 and converted to a known area through a conversion curve (R<sup>2</sup> = 0.92) generated off of a single observer measuring the wax weight of wooden dowels of various sizes.

## 2.5 Stable Isotope Analysis

An aliquot of coral tissue blastate was kept on ice, briefly homogenized, and filtered through 20-µm mesh to remove skeletal debris (Wall et al., 2020). To assess filtration effectiveness, we tested for a correlation between sample C:N ratios and δ<sup>13</sup>C values, observing no relationship (Supplemental Figure 2). Coral host fraction and symbiont pellet were separated by repeated centrifugation (5,000 xg for 3 min) and

ddH<sub>2</sub>O rinses (Muscatine et al., 1989) before being concentrated on pre-combusted (450°C, 4 h) 25 mm GF/F filters (0.7µm pore size)), dried (60°C, 24 h) and transported to the Biogeochemical Stable Isotope Facility at the University of Hawai‘i at Mānoa for analysis. Filters were subsampled, packed in tin capsules, and measured on a Costech elemental combustion system coupled to a Thermo-Finnigan Delta Plus XP isotope ratio mass spectrometer. Sample analytical accuracy and precision ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) was <0.2‰. Reported isotopic values are in delta values ( $\delta$ ) using per mill (‰) notation relative to standard materials (Vienna Pee-Dee Belemnite [V-PDB] and atmospheric N<sub>2</sub> [Air] for carbon and nitrogen, respectively). Only the caged coral at each station were included in the isotope analysis.

We use the difference between the isotopic values of the host and symbiont tissue fractions ( $\delta^{13}\text{C}_{\text{H-S}}$ ,  $\delta^{15}\text{N}_{\text{H-S}}$ ) as proxies for heterotrophy (Lesser et al., 2022). More positive  $\delta^{13}\text{C}_{\text{H-S}}$  values suggest tighter nutrient recycling within coral and host tissue and greater relative proportion of autotrophic nutrition relative to heterotrophy, while more negative values suggest greater heterotrophy (Grottoli et al., 2006; Muscatine et al., 1989). Similarly, heterotrophy increases  $\delta^{15}\text{N}$  in the coral host relative to ambient nitrate at the base of the food web assimilated by the coral’s endosymbionts, leading to more positive  $\delta^{15}\text{N}_{\text{H-S}}$  in corals relying on heterotrophic nutrition (Conti-Jerpe et al., 2020; Nahon et al., 2013).

## **2.6 Isotopic Characterization of Energetic Resource**

Samples of particulate organic matter (POM) and zooplankton adjacent to and outside of influence of the SGD seep were sampled in April 2024. At each location, plankton nets were repeatedly thrown and retrieved for five minutes and plankton samples (63-200 µm) were collected, filtered onto pre-combusted 47mm GF/F filters (preparation described above), and dried (60°C) for analysis. Due to a high potential of carbonate contamination during collection, zooplankton samples were run as two subsamples: one acidified (dropwise addition of 0.1N HCl) for  $\delta^{13}\text{C}$  analysis and another non-acidified sample for  $\delta^{15}\text{N}$

analysis. An additional 2 L of seawater was filtered to  $<63 \mu\text{m}$  and collected at each location for POM. Water samples were subsequently filtered onto GF/F filters (as above) and dried ( $60^\circ\text{C}$ ).

## 2.7 Data Analyses

All analyses were conducted using R version 4.4.1 (R Core Team, 2023), and all data and code are available at GitHub ([https://github.com/CallieStephenson/Moorea\\_Coral\\_Physiology](https://github.com/CallieStephenson/Moorea_Coral_Physiology)) and archived at Zenodo (xxx - will update following peer review). To quantify pulses of nearshore nutrients associated with SGD, we summarized the mean values of SGD-associated water quality variables including nutrients ( $\text{N+N}$ ,  $\text{PO}_4^{3-}$ ), altered carbon chemistry (pH, TA), and two conservative SGD tracers ( $\text{SiO}_3^{2-}$ , Salinity) from low tide water samples across both sampling seasons ( $n=4$ ). We reduced collinearity in the water quality variables through principal components analysis (PCA) (Figure 1D), and used the first PC axis (PC1), which described 67.4% of the variance, as a predictor variable in subsequent analyses. Using a linear mixed model, each coral response parameter (percent change in buoyant weight, chlorophyll content,  $\delta^{13}\text{C}_{\text{H-S}}$ ,  $\delta^{15}\text{N}_{\text{H-S}}$ ) was regressed against PC1, with colony genet and caging treatment treated as random effects, where applicable. Separately, we tested for the effect of caging treatments on coral response variables using linear mixed models, including random effects of parent colony and experimental location. All models were run using the lme4 package (Bates et al., 2015). Additionally, we regressed each response variable against water quality parameters in univariate linear mixed models with appropriate random effects and ranked these models by akaike information criterion (AIC) value to evaluate mechanisms driving these relationships. Diseased ( $n = 1$ ) and physically damaged ( $n = 2$ ) colonies were removed from all analysis.

To better understand nutritional strategies used by both species within SGD environments, we characterized the isotopic niche of each species using stable isotope Bayesian ellipses (Layman et al., 2012). This method estimates the core isotopic niche of a population by modeling the distribution of

individuals in isotope space, providing a measure of niche width and overlap, and has been used across different systems (see Manlick et al., 2017; Vázquez-Liñero et al., 2025; Yuille et al., 2015 for examples). In corals, the trophic strategy of a population can be inferred through the proportion of the host standard ellipse area corrected for small sample size ( $SEA_C$ ) that overlaps with the  $SEA_C$  of the symbiont (see Conti-Jerpe et al., 2020; Price et al., 2021; Thibault et al., 2021; Wang et al., 2024 for examples). We created these maximum likelihood ellipses for the host and symbiont fraction of each species using the R package SIBER (Stable Isotope Bayesian Ellipses in R) (Jackson et al., 2011), and evaluated the trophic strategy based off the  $SEA_C$  encompassing 40% (Syväranta et al., 2013) and 95% (Thibault et al., 2021) of the variation in each species, as is recommended for populations spanning heterogeneous environments. Additionally, to quantify whether the host and symbiont fraction occupied separate niche spaces, we used the Hotelling  $T^2$  test from the R package Hotelling, using 999 permutations and a significance threshold of  $p = 0.05$  (Turner et al., 2010).

To see the proportionate contribution of potential food sources, we used Bayesian isotope mixing models using the R package MixSIAR (Stock et al., 2018). In these models, coral host samples were treated as a population of consumers with five potential food sources: an autotrophic source from the symbiont and four types of heterotrophic sources derived from either POM or zooplankton, originating from the seep or from ambient seawater. To produce a mean and standard deviation prior to modeling, each food source was averaged within its respective category across all relevant sampling environments. Specifically, all symbionts were pooled together, while POM and zooplankton were split by samples influenced and outside of the influenced area, resulting in five distinct food sources. Trophic discrimination factors (TDF) for zooplankton, POM, and symbionts were adopted from Wang et al., 2024, wherein the TDF for POM and zooplankton samples are taken from assumed values of trophic enrichment in marine invertebrates (Minagawa & Wada, 1984; Zanden & Rasmussen, 2001) while a lower value is used for the TDF of  $\delta^{15}N$  in coral symbionts to account for nitrogen recycling between the host and symbiont (Reynaud et al., 2009; Table 1). Though MixSIAR was developed to handle the uncertainty of TDFs,

model outputs are heavily reliant on inputted TDF values. Thus, we conducted a sensitivity analysis varying the TDFs and evaluated how these values altered our results (Supplemental Table 1).

**Table 1.** Trophic discrimination factors (TDF) for zooplankton, POM, and symbionts adopted from Wang et al., 2024.

	Symbiont	Zooplankton	POM
$\delta^{13}\text{C}$ TDF	$0.5 \pm 1.3$	$0.5 \pm 1.3$	$0.5 \pm 1.3$
$\delta^{15}\text{N}$ TDF	$1.5 \pm 1.3$	$2.3 \pm 1.5$	$2.3 \pm 1.5$

### 3.0 Results

#### 3.1 Endosymbiont response

Total chlorophyll content ranged from 0.61 - 4.2  $\mu\text{g cm}^{-2}$  in *P. acuta* (Supplemental Table 3) and 0.56  $\mu\text{g cm}^{-2}$  in *P. rus* (Supplemental Table 4). PC1 (Figure 1D) was positively associated with total chlorophyll in *P. acuta* (Figure 2B), and there was no effect in *P. rus* (Figure 2F). Subsequent analysis of each water quality parameter in univariate models indicated that the chlorophyll response was in part attributable to the increase in N+N ( $p = 0.004$ ) and decrease in pH ( $p = 0.026$ ) across the gradient (Supplementary Table 5).

#### 3.2 Holobiont response

Percent change in coral net calcification (i.e., skeletal growth) ranged from 2.3% to 23% in *P. acuta* (Table S1) and 0.64% to 33% in *P. rus* (Table S2). There was no relationship between water quality PC1 and coral growth in either coral species (Figure 2A, E). Additionally, growth in *P. acuta* was not related to any individual water chemistry parameter when tested in univariate models (Supplemental Table 6). In

*P. rus*, growth increased with mean salinity at low tide ( $p < 0.001$ ,  $\beta = 39.1$ ) and showed no response to other water quality parameters when tested in univariate models (Supplemental Table 7).

### 3.3 Nutritional plasticity

In *P. acuta*, the difference in the isotopic value of the host and symbiont ( $\delta^{15}\text{N}_{\text{H-S}}$ ) declined with associated water quality PC1 ( $p = 0.006$ , Figure 2D)  $\delta^{15}\text{N}$  values in *P. acuta* host samples ranged from 6.1 to 7.7‰ and showed a slight, non-significant decrease with increasing SGD exposure ( $\beta = -0.054\text{‰}$  per unit increase in SGD,  $p = 0.183$ ). Concurrently, *P. acuta* symbiont samples showed a slight, non-significant increase with SGD exposure ( $\beta = 0.039\text{‰}$  per unit increase in SGD,  $p = 0.246$ ). The net effect was that the more SGD-exposed symbionts in *P. acuta* had higher  $\delta^{15}\text{N}$  values relative to their hosts. Investigating univariate relationships between potential drivers, we found that changes in the low tide pulses of phosphate best described this relationship, though changes in pH, N+N, salinity, and silicate values were also significant (Table 2). For *P. rus*, there was no effect of water quality PC1 on  $\delta^{15}\text{N}_{\text{H-S}}$  ( $p = 0.127$ , Figure 2H). Neither coral species displayed a response in  $\delta^{13}\text{C}_{\text{H-S}}$  (Figure 2C, G).

**Table 2.** Summary statistics of univariate models of low tide water chemistry parameters associated with SGD against the  $\delta^{15}\text{N}_{\text{H-S}}$  in *P. acuta*. Bold values indicate values where the model has statistical significance ( $p < 0.05$ ).

Parameter	Beta Value	p	$\Delta\text{AIC}$	Marginal $R^2$	Conditional $R^2$
Phosphate	<b>- 20.73</b>	<b>0.002</b>	<b>0</b>	<b>0.225</b>	<b>0.610</b>
pH	<b>13.39</b>	<b>0.029</b>	<b>3.86</b>	<b>0.110</b>	<b>0.592</b>
Salinity	<b>2.50</b>	<b>0.015</b>	<b>6.34</b>	<b>0.189</b>	<b>0.576</b>

N+N	- 1.525	0.010	7.11	0.177	0.637
Silicate	- 0.170	0.006	10.86	0.167	0.633
TA	- 0.003	0.788	20.55	0.003	0.410

When pooled by species, *P. rus* and *P. acuta* displayed different nutritional strategies. Overlap values for host and symbiont fractions of *P. acuta* samples were 21.94% for 40% SEA<sub>C</sub> (i.e., small-sample corrected Standard Ellipse Area) and 66.60% for 95% SEA<sub>C</sub> (Figure 3A). For *P. rus*, 40% SEA<sub>C</sub> had 72.18% overlap, while 95% SEA<sub>C</sub> had 92.69% overlap (Figure 3D). Hotelling T<sup>2</sup> test demonstrated significantly different isotopic niches for host and symbiont fraction for *P. acuta* ( $p < 0.001$ ), but not for *P. rus* ( $p = 0.160$ ).

Sources of heterotrophic nutrition from SGD-influenced and non-influenced waters varied in their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotopic composition (Figure S2), allowing for mixing models to determine the proportional contributions of these sources to coral nutrition. The  $\delta^{13}\text{C}$  of POM samples was significantly higher at SGD seep stations compared to those from outside the SGD plume, with an average difference of 1.9‰ ( $-19.6\text{‰}$  at seep vs.  $-21.5\text{‰}$  out;  $p = 0.001$ ; Figure S2A). There was no significant difference in  $\delta^{15}\text{N}$  of POM across stations ( $p = 0.206$ ; Figure S2E), with mean values of 7.5‰ at the seep and 6.6‰ outside. Conversely, zooplankton  $\delta^{15}\text{N}$  values were significantly higher in samples from the SGD seep, averaging 1.3‰ higher than those from outside the plume (7.2‰ vs. 5.9‰;  $p = 0.003$ ; Figure S2B). There was no significant difference in zooplankton  $\delta^{13}\text{C}$  between locations ( $p = 0.261$ ; Figure S2F), with mean values of  $-19.8\text{‰}$  at the seep and  $-18.8\text{‰}$  outside.

We found no relationship between symbiont  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  and PC1 for either species. MixSIAR results suggested coral hosts shared isotopic values primarily with their symbionts. *Pocillopora acuta* symbionts

contributed  $80.6\% \pm 6.4\%$  of the coral host's nutrition (Figure 3C). The next highest contribution ( $10.4\% \pm 7.6\%$ ) was from non-seep zooplankton, followed by  $3.1\% \pm 2.7\%$  from non-seep POM,  $3.0\% \pm 2.7\%$  from seep zooplankton, and  $2.9\% \pm 2.7\%$  from seep POM (Figure 3C; Supplemental Table 2). Similarly, *P. rus* had  $85.0\% \pm 4.7\%$  of its  $\delta^{13}\text{C}$  contributed from its symbionts,  $6.4\% \pm 2.5\%$  from non-seep zooplankton,  $3.6\% \pm 3.0\%$  from non-seep POM,  $2.5\% \pm 2.3\%$  from seep-derived zooplankton, and  $2.5\% \pm 2.5\%$  from seep-derived POM (Figure 3F; Supplemental Table 2).

### 3.4 Caging treatment

Caging treatment was not a significant contributor to variation in any response variable, with the exception of total chlorophyll content in *P. rus*, which was significantly higher in caged corals compared to uncaged corals ( $p = 0.033$ , marginal  $R^2 = 0.115$ ; Supplemental Table 8). In this relationship, partially caged corals were intermediate in value and not significantly different from either caged ( $p = 0.465$ ) or uncaged ( $p = 0.278$ ) corals. For all other species–response combinations, the effect of caging was not significant ( $p > 0.05$ ) and explained little variance (marginal  $R^2 = 0.001$ – $0.053$ ; Supplemental Table 8).

### 4.0 Discussion

Our findings underscore the variable effects of submarine groundwater discharge on coral holobiont physiology. The lack of consistent responses observed between *P. acuta* and *P. rus* highlight species-specific sensitivities to SGD-driven environmental fluctuations, particularly in relation to pH, alkalinity, salinity, and nutrient availability. While *P. acuta* increased photopigmentation in response to SGD conditions, these shifts did not translate into enhanced growth over the seven week study. Conversely, *P. rus* displayed stability in its growth, photopigmentation, and isotopic ratios across the SGD gradient, suggesting a degree of resistance that may be attributable to its physiological strategy and symbiont association. However, the absence of effects in responses measured here does not necessarily indicate an absence of SGD effects, as counteracting environmental influence on different physiological traits may have masked more subtle changes (e.g., P:R balance, cellular homeostasis, biomass changes, skeletal

dissolution vs. accretion). For example, in a previous study at this location, *P. rus* fragments subjected to a range of SGD conditions over two weeks displayed increased total chlorophyll concentrations in those experiencing higher SGD exposure (Kerlin et al., 2025). Therefore, the response of corals to SGD can be dynamic, and different traits may respond quickly (photopigmentation) or slowly (net calcification) to these effects. These results emphasize the need for species-specific assessments when evaluating the impacts of SGD on coral physiology, as different taxa may exhibit fundamentally distinct responses to similar environmental drivers.

Our results indicate that *P. acuta* symbionts exhibit pronounced sensitivity to submarine groundwater discharge, evident by a marked increase in total chlorophyll along the SGD gradient. This increase was significantly associated with environmental variables, including positive associations with changes in N+N and silicate versus negative trends across changes in pH. Positive relationships between N+N and coral total chlorophyll content have also been identified in prior lab (Fox et al., 2021; Marubini & Davies, 1996) and field experiments (Becker & Silbiger, 2020a), including along the same SGD gradient as the current study (Kerlin et al., 2025). While N+N concentrations within our study were the <5  $\mu\text{M}$  threshold shown to simulate symbiont populations (Nalley et al., 2023), low levels of nutrient enrichment and/or episodic pulses of nutrients along our study gradient nevertheless shaped physiological responses.

Although coral total chlorophyll and silicate show some correlation, this likely reflects nutrient delivery via submarine groundwater discharge (SGD), since silicate is frequently used as a tracer for SGD (Oehler et al., 2019). Rather than indicating a direct physiological mechanism, this relationship offers more support to the possibility that SGD may be an important source of nutrients fueling coral chlorophyll. In contrast, we observed a negative association between pH and total chlorophyll content. pH can have a range of effects on corals, primarily influencing growth through ocean acidification, but also potentially affecting photopigmentation, symbiont density, or photochemical efficiency in variable ways (Crawley et al., 2010; Krief et al., 2010; Meron et al., 2012; but see Wall et al., 2014). Our data do not allow us to distinguish whether changes in total chlorophyll were driven by shifts in symbiont density or chlorophyll

content per cell, as we did not measure symbiont counts. However, our findings ultimately demonstrate only that total chlorophyll content varied along a gradient in pH, in conjunction with nutrient enrichment, and should be taken as evidence of a physiological response, not a mechanistic explanation. Taken together, these results indicate that even subtle environmental gradients driven by SGD can influence coral symbiont physiology of some species in ecologically-relevant ways.

Although *P. acuta* showed increased photopigmentation in response to SGD-driven nutrient and pH changes, this did not lead to enhanced net calcification. This disconnect highlights that while SGD can strongly affect symbiont physiology, such changes do not automatically benefit coral growth, at least over an 8-week time period. Instead, the results point to potential trade-offs or other limiting factors that constrain the positive impacts of altered photopigmentation on calcification.

In contrast, *P. rus* exhibited relative physiological stability despite exposure to SGD. Variation in *P. rus* physiology could not be explained as a response to SGD parameters collectively in PC1; however, univariate models showed more nuanced responses. *Porites rus* is characterized as weedy coral taxa with a high capacity for colonizing disturbed environments (Darling et al., 2012) able to physiologically acclimatize to increased turbidity over time scale similar to this experiment (Padilla-Gamiño et al., 2012). Notably, this 8-week experiment represents the longest duration study conducted along this gradient to date, while two shorter-term studies have reported significant physiological changes in *P. rus*. First, another experiment performed on a compressed time scale (2 weeks, Kerlin et al., 2025) found significant differences in *P. rus* gross photosynthesis, respiration, endosymbiont densities, and chlorophyll *a* content related to shifts in water quality from SGD. An experiment at this same location across a 5-6 week time scale (Barnas et al., 2025) found significantly decreased growth in *P. rus* between an area immediately adjacent to the seep and one presumed outside of SGD influence. Therefore, it is possible that these experiments captured the acclimation of *P. rus* to these changes, after which, as in our experiment, *P. rus* may be acclimated to its environment and not show significant patterns in coral growth.

Differences in coral host and symbiont stable isotope values are commonly applied as proxies for nutritional states and photosynthetic function (Price et al., 2021). In our study, we found no clear shift in values of  $\delta^{13}\text{C}_{\text{H-S}}$  in *P. acuta* or *P. rus* in response due to SGD exposure. However,  $\delta^{15}\text{N}_{\text{H-S}}$  did show a linear decrease to our combined SGD-PC1 axis in *P. acuta* (Figure 2D), but not *P. rus*. When we explored potential mechanistic relationships through univariate models, we found significant changes in  $\delta^{15}\text{N}_{\text{H-S}}$  as a response to all SGD-associated water chemistry parameters except total alkalinity (Table 2), suggesting that the observed  $\delta^{15}\text{N}_{\text{H-S}}$  response in *P. acuta* was symptomatic of a broader response to SGD exposure rather than a specific driver. Additionally, results from the MixSIAR framework did not reveal any isotopic contributions from SGD-enriched food sources to the coral host in either species (Figure 3C, F). This result indicates that such food sources may have been inaccessible to corals, potentially due to limited mixing between the SGD layer and surrounding seawater, consumption by fish predators (Zeff, In Prep), or restricted temporal availability of SGD-driven resources associated with tidal cycles. Instead, our results suggest that  $\delta^{15}\text{N}_{\text{H-S}}$  decreased in areas of high-SGD influence. This greater similarity between  $\delta^{15}\text{N}$  in the host and symbiont may indicate a decrease in heterotrophy as exposure to SGD increases, or greater N-cycling in the holobiont, thereby reducing differences between animal and algal partners.

Since we observed concurrent increases in total chlorophyll content, it is possible to interpret our findings as evidence that *P. acuta* fragments shifted their trophic strategy to become more autotrophic with the increased nutrients as a result of SGD exposure; however, this is not supported by the lack of change in our values  $\delta^{13}\text{C}_{\text{H-S}}$  values. Though some studies have suggested  $\delta^{15}\text{N}$  is a better proxy for heterotrophy than  $\delta^{13}\text{C}$  (Conti-Jerpe et al., 2020), there is need to consider whether environmental conditions may alter the availability of  $^{15}\text{N}$  relative to  $^{14}\text{N}$  for the symbiont. Although we were unable to directly measure  $\delta^{15}\text{N}$  of nitrate in water samples from the seep, it is possible that the seep carries seawater enriched in  $\delta^{15}\text{N}$  based on high  $\delta^{15}\text{N}$  from *Turbinaria ornata* samples collected adjacent to the seep (Silbiger Unpublished Data). In other regions, groundwater has been shown to have elevated  $\delta^{15}\text{N}$  of nitrate (Biddau et al., 2019;

Wong et al., 2014), and in our data, zooplankton and particulate organic matter samples from the seep generally exhibited higher  $\delta^{15}\text{N}$  levels than those found in ambient conditions (Supplemental Figure 3). Since *P. acuta*  $\delta^{15}\text{N}_{\text{H-S}}$  approached zero with increasing SGD, *P. acuta* may have maintained a mixotrophic strategy across SGD exposure, though  $\delta^{15}\text{N}$  of the symbiont may have increased from  $\delta^{15}\text{N}$ -enriched SGD seawater. In contrast, *P. rus* did not show this response, possibly due to its stronger reliance on autotrophy across the gradient, as evidenced by our SIBER results showing high overlap in both 40% and 95% ellipses (Figure 3D). More efficient nitrogen recycling between host and symbiont, as indicated by higher levels of autotrophy, may have prevented the differential accumulation of  $\delta^{15}\text{N}$ , obscuring any detectable signal in *P. rus*. These findings highlight the complexity of coral holobiont responses to SGD, emphasizing the role of nutrient dynamics and host-symbiont interactions in shaping physiological outcomes beyond shifts in trophic strategy.

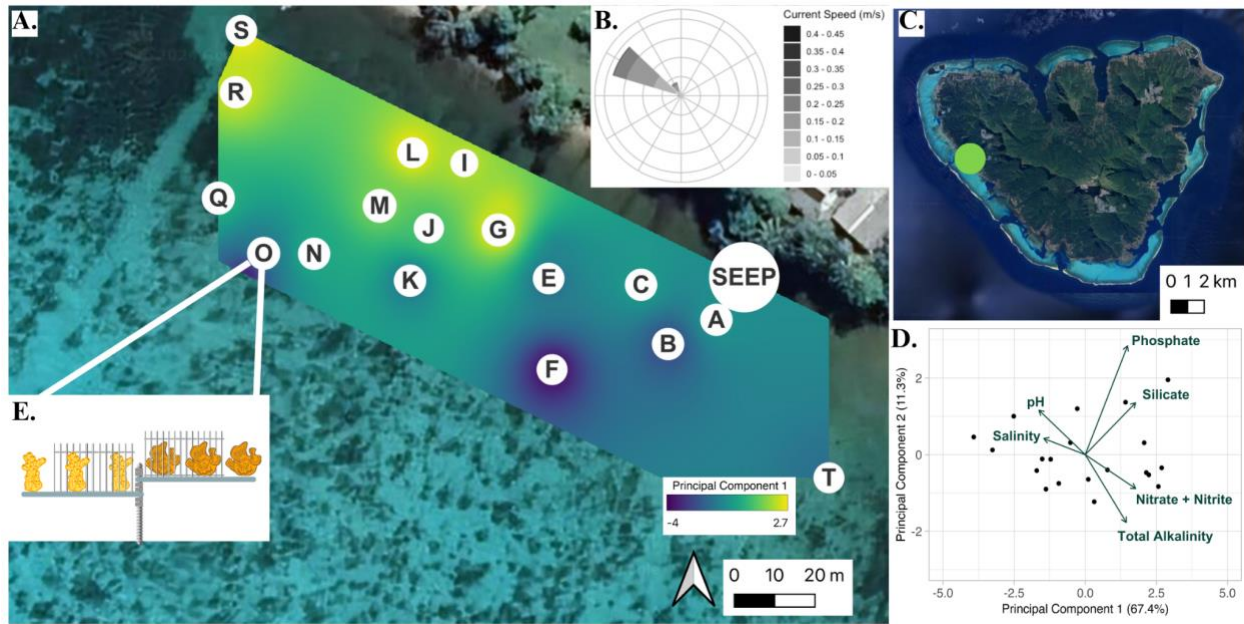
The elevated  $\delta^{15}\text{N}$  values observed in zooplankton and particulate organic matter, along with additional microbial data from the site (McClintock, 2022), provide evidence of wastewater intrusion along the gradient. These higher  $\delta^{15}\text{N}$  signatures are typically associated with anthropogenic nutrient sources, such as sewage, and reflect the transfer of these pollutants through the food web. The incorporation of these elevated  $\delta^{15}\text{N}$  values into coral tissues highlights a direct impact of human activities on coral reef physiology, though we did not measure adverse physiological impacts to the corals from cycling these nutrients. Moreover, understanding the mechanisms behind the incorporation of anthropogenic nitrogen into coral tissues can inform future research into the physiological and biochemical processes that enable corals to uptake and assimilate these nutrients. Clarifying how nitrogen from different food web sources impacts both the host and the symbiont is essential for interpreting isotopic signals in the context of coral nutritional ecology.

The physiological responses observed in our study reflect the specific environmental conditions of our SGD site—namely, lower nutrient concentrations and higher water flow—that differ from those in previous studies. In our experiment, nutrient concentrations were lower but still within the range of values reported in other SGD-influenced systems (Supplemental Table 9). For instance, while some studies have documented extremely high dissolved inorganic nitrogen to dissolved inorganic phosphorus (DIN:DIP) ratios exceeding 16 (Moosdorf et al., 2015; Santos et al., 2021), the highest DIN:DIP ratio in our dataset was 3.49—comparable to conditions used as unenriched controls in another study (Bednarz et al., 2020). Similarly, mean concentrations of N+N ( $0.5 \mu\text{mol L}^{-1}$ ) and phosphate ( $0.19 \mu\text{mol L}^{-1}$ ) in our study align closely with those reported in Lubarsky et al. (2018), where nonlinear physiological responses in *Porites* were observed at slightly higher nitrate ( $0.73 \mu\text{mol L}^{-1}$ ) and slightly lower phosphate ( $0.13 \mu\text{mol L}^{-1}$ ). Further context is provided by two recent studies conducted at the same SGD site: Barnas et al. (2025) and Kerlin et al. (2025). Barnas et al. exposed corals to extreme SGD conditions for six weeks, finding no change in growth for *P. acuta*, while *P. rus* exhibited reduced growth. In contrast, Kerlin et al. reported enhanced physiological metrics in *P. rus*—including gross photosynthesis, respiration, endosymbiont densities, and total chlorophyll—after just two weeks of exposure across an SGD gradient. Additionally, high water flow at our site (averaging  $0.15 \text{ m/s}$ ) likely limits the mixing of SGD into the surrounding marine water, resulting in sharp nutrient gradients between seep and ambient waters (Figure S1C). Despite relatively low nutrient input and high water flow, our results demonstrate that SGD can still alter coral physiology, though the effects may be more subtle than in systems with more intense SGD exposure.

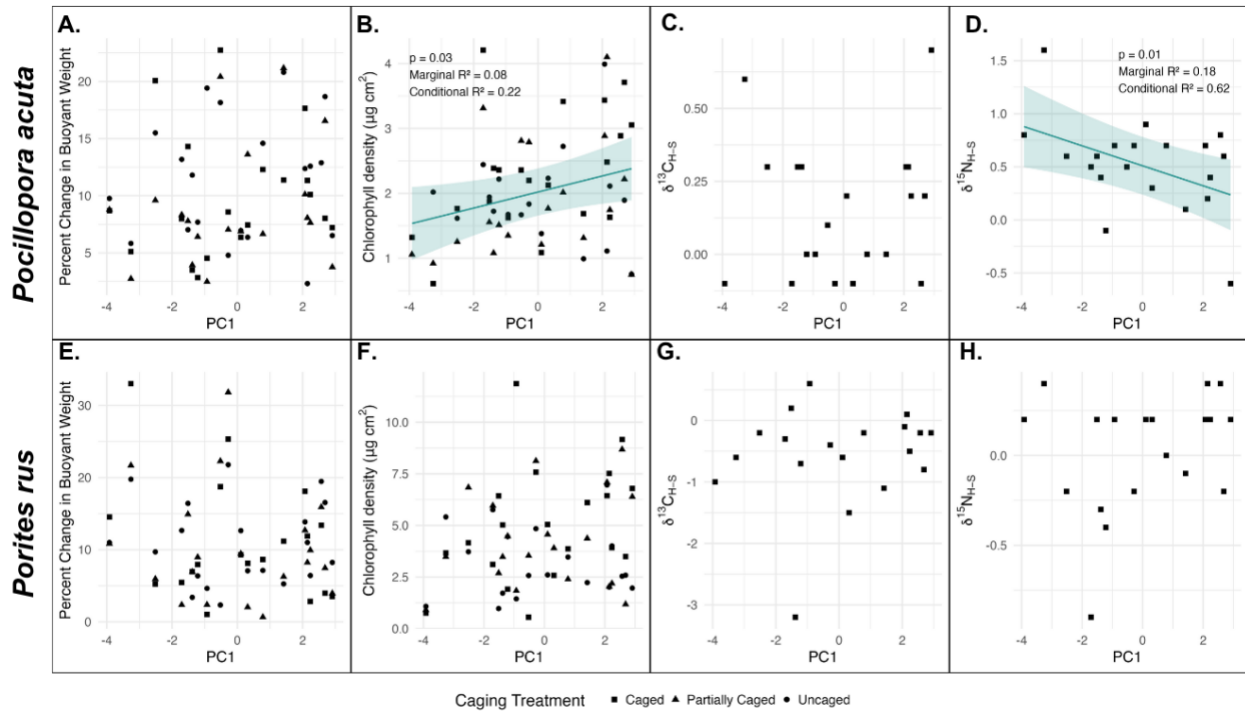
Collectively, our findings reveal that SGD exposure elicits species-specific physiological responses in corals, with *P. acuta* symbionts displaying sensitivity to SGD-driven environmental changes, while *P. rus* maintained relative physiological stability of tightly coupled host and symbiont. Despite the potential for novel food sources, neither species exhibited a shift toward heterotrophy, and instead our isotope results

underscore the complexity of nutrient assimilation within the coral holobiont. Given that SGD can introduce both beneficial and detrimental environmental shifts, understanding the mechanisms underlying species-specific responses is critical for predicting coral persistence in SGD-impacted ecosystems. Future research should investigate the long-term energetic trade-offs associated with chronic SGD exposure, particularly in the context of global climate change, where altered groundwater dynamics may further modulate coastal reef environments.

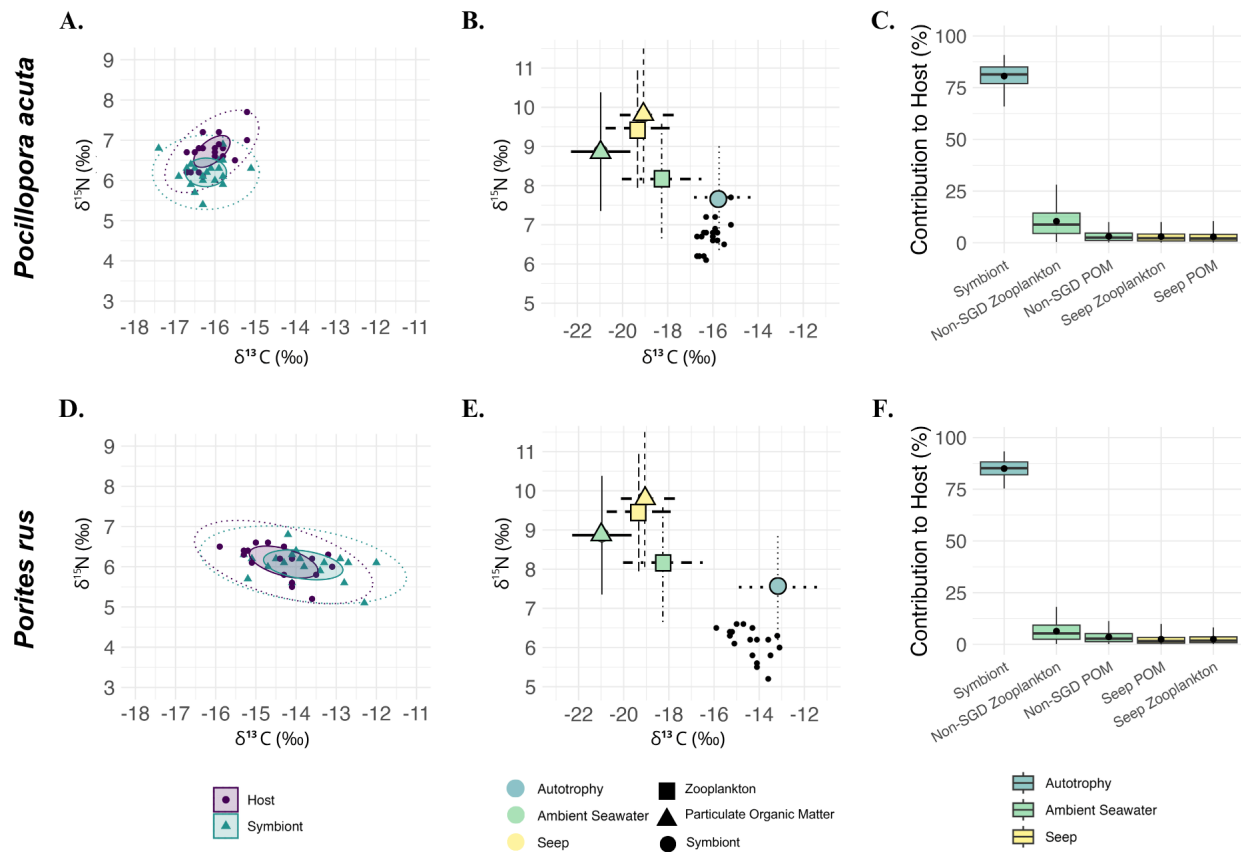
**Figures:**



**Figure 1.** (A) Map of experimental stations with insets depicting (B) a windrose plot displaying ADCP current speed and direction data collected in March 2023 and (C) the location of the site on the western coast of Moorea. Colors on (A) represent the interpolation of principal component axis 1, shown in (D). The source of SGD is marked SEEP, and experimental stations named in descending alphabetical order by geographical distance to the seep of SGD, except for pin T, which was presumed to be upstream of the labeled seep. (E) depicts the experimental set-up at each station.



**Figure 2: *Pocillopora acuta* symbionts respond to a combined signal of SGD.** Univariate model depictions of coral physiology response variables against the principal components axis for *P. acuta* (A-D) and *P. rus* (E-H).



**Figure 3. Stable Isotopes show heterotrophic contributions differ between species.** SIBER for (A) *P. acuta* and (D) *P. rus*. Solid and shaded ellipses encompass 40% of the variability in host and symbiont fractions. Dotted ellipses encompass 95% of the variation. Isotope biplot for (B) *Pocillopora acuta* and (E) *Porites rus* host samples and their potential isotopic sources. Host samples are represented as black dots. The mean isotopic value of each source is represented as a colored dot, with the color of the dot representing whether the source is derived from autotrophy or heterotrophy. Sources are plotted with trophic discrimination factors (TDF, see Table 1) considered. Proportional contributions as determined by MixSIAR are represented as whisker plots for (C) *Pocillopora acuta* and (F) *Porites rus*.

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