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ORIGINAL RESEARCH

Conspecific interactions between corals mediate the effect of submarine groundwater discharge on coral physiology

Jamie R. Kerlin[1] · Danielle M. Barnas[2] · Nyssa J. Silbiger[3]

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Abstract

Land-based inputs, such as runoff, rivers, and submarine groundwater, can alter biologic processes on coral reefs. While the abiotic factors associated with land-based inputs have strong effects on corals, corals are also affected by biotic interactions, including other neighboring corals. The biologic responses of corals to changing environmental conditions and their neighbors are likely interactive; however, few studies address both biotic and abiotic interactions in concert. In a manipulative field experiment, we tested how the natural environmental gradient created by submarine groundwater discharge (SGD) affected holobiont and symbiont metabolic rates and endosymbiont physiology of *Porites rus*. We further tested how the effect of SGD on the coral was mediated by intra and interspecific interactions. SGD is a natural land-sea connection that delivers nutrients, inorganic carbon, and other solutes to coastal ecosystems worldwide. Our results show that a natural gradient of nutrient enrichment and pH variability as a result of acute SGD exposure generally benefited *P. rus*, increasing gross photosynthesis, respiration, endosymbiont densities, and chlorophyll *a* content. Conspecifics in direct contact with the a neighboring coral, however, altered the relationship between coral physiology and SGD, lowering the photosynthetic and respiration rates from expected values when the coral had no neighbor. We show that the response of corals to environmental change is dependent on the types of nearby neighbor corals and how neighbors alter the chemical or physical environment around the coral. Our study underscores the importance of considering biotic interactions when predicting the physiologic responses of corals to the environment.

Keywords Coral reefs · Land-based inputs · Species-interactions · Mo'orea · Conspecific · Submarine groundwater discharge · Biotic–abiotic interactions

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This study measures the interactive effect of abiotic and biotic conditions on coral physiology in Mo'orea, French Polynesia. We show that intraspecific interactions alter the physiologic responses of corals to acute natural changes in nutrients and pH via submarine groundwater discharge. Our results highlight the importance of considering species interactions when examining the effects of changing abiotic conditions on organismal physiology.

✉ Nyssa J. Silbiger
silbiger@hawaii.edu

[1] Department of Biology, California State University, Northridge, CA 91330, USA

[2] Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kaneohe, HI 96744, USA

[3] Department of Oceanography, Uehiro Center for the Advancement of Oceanography, University of Hawai'i at Mānoa, Honolulu, HI 96822, USA

Introduction

Uncovering the relative importance of biotic and abiotic interactions is a fundamental challenge in ecology. Species interactions and environmental conditions can each alter organismal physiology and structure communities, but the strength of one effect can be modified by the other. For example, the Menge-Sutherland model is a classic paradigm for how environmental context alters the importance of biotic interactions, where, for instance, competition is less important than physical stress in very harsh conditions (Menge and Sutherland 1987). Further, the stress-gradient hypothesis suggests that facilitative or positive interactions, where the presence of one organism enhances the physiology or survival of another, increase under stressful environmental conditions (Bertness and Callaway 1994; He et al. 2013), likely because these biotic interactions ameliorate physical stress. Given that environmental conditions and

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biodiversity are both rapidly changing throughout the world (Hooper et al. 2012; Cardinale et al. 2012; Lee and Romero 2023), there is a need for more studies that address the combined effects of biotic and abiotic interactions on organismal response.

Tropical corals are an excellent study system to uncover the combined effects of biotic and abiotic interactions as they persist in biodiverse (Hughes et al. 2002) and variable biophysical environments (Guadayol et al. 2014; Rivest and Gouhier 2015). Coral reefs, due to their proximity to coasts, experience a wide range of land-based inputs that create both natural and anthropogenic environmental gradients in many parameters, such as pH, temperature, and nutrient loading, that may affect coral physiology (Hofmann et al. 2011; Guadayol et al. 2014; Delevaux et al. 2018). Submarine groundwater discharge (SGD) is one such land-based process that is common on coral reefs (Santos et al. 2021) and alters multiple parameters of coastal seawater conditions (Nelson et al. 2015; Knee et al. 2016; Hagedorn et al. 2020; Silbiger et al. 2020).

SGD is freshwater or recirculated seawater that flows from land, across the sediment–seawater interface into the ocean (Moosdorf et al. 2015; Knee et al. 2016). The biogeochemical properties of SGD are unique relative to ambient seawater, and SGD often has lower salinity, temperature, and pH, and elevated nutrient concentrations (Paytan et al. 2006; Cyronak et al. 2014; Nelson et al. 2015; Lecher and Mackey 2018; Luijendijk et al. 2020). Coastal coral reefs exposed to SGD experience natural pulses of environmental variability in these parameters as the amount of SGD entering the ocean varies with location, tides, and seasons, with larger pulses during low tide and rainy seasons (Moosdorf et al. 2015; Dulai et al. 2016; Oehler et al. 2019; McKenzie et al. 2021). SGD is likely to have substantial effects on coral physiology (i.e., calcification, metabolism, endosymbiont physiology), as environmental conditions, such as pH and nutrient concentrations, can alter coral physiology through changes in both the endosymbionts and the coral host (Hoegh-Guldberg and Smith 1989; Marubini and Davies 1996; Anthony et al. 2008; Crawley et al. 2010; Edmunds 2012; Donovan et al. 2020; Fox et al. 2021; Becker et al. 2021).

SGD input into coastal waters may benefit corals, as nutrient enrichment could modify endosymbiont physiology, potentially altering coral metabolism (Hoegh-Guldberg and Smith 1989; Marubini and Davies 1996; Becker et al. 2021), or can have negative effects on corals, such as suppressing calcification and increasing algal growth (Kinsey 1988; Silbiger et al. 2018). The beneficial or harmful nature of the effect of nutrients depends on the nutrient concentrations, sources (i.e., natural or anthropogenic), and/or nutrient species (Marubini and Davies 1996; Gil 2013; Ezzat et al. 2015; Burkepile et al. 2020; Fox et al. 2021). For example, coral endosymbiont densities and chlorophyll concentrations may increase with increasing nitrogen concentrations (Hoegh-Guldberg and Smith 1989; Marubini and Davies 1996; Becker and Silbiger 2020; Fox et al. 2021), but elevated nutrients also decrease coral thermal performance (Becker and Silbiger 2020) and cause the corals to be more prone to bleaching (Vega Thurber et al. 2014; Donovan et al. 2020). The low pH environment created by SGD could also affect *Symbiodiniaceae* populations, where endosymbiont densities have been shown to decrease under acidified conditions (Reynaud et al. 2003; Kaniewska et al. 2012). Conversely, other studies have found endosymbiont density to be unaffected by similar pH changes (Crawley et al. 2010; Baghdasarian et al. 2017).

Coral photosynthesis and respiration rates may also change as a result of SGD-driven biogeochemistry, including decreased salinity, increased nutrient concentrations, and decreased pH. Decreases in salinity of 10 psu or more can decrease photosynthetic rates by approximately 50–65% (Muthiga and Szmant 1987; Alutoin et al. 2001) and respiration rates by approximately 50% in tropical reef corals (Muthiga and Szmant 1987). Photosynthesis and respiration are also affected by nutrient enrichment, with increases in photosynthesis being associated with nitrate enrichment (Marubini and Davies 1996), ammonium enrichment (Hoegh-Guldberg and Smith 1989), percent nitrogen measured from macroalgal tissue (Becker and Silbiger 2020), and combined inorganic nitrogen and phosphorus additions (Silbiger et al. 2018; Becker et al. 2021). Coral respiration can increase with elevated nitrate (Silbiger et al. 2018) or be unaffected by increases in nitrate (Marubini and Davies 1996) or ammonium (Hoegh-Guldberg and Smith 1989). Decreases in seawater pH can have varying effects on coral photosynthesis and respiration. For example, in low pH seawater, coral photosynthesis can increase (Biscéré et al. 2019) or decrease (Anthony et al. 2008; Kaniewska et al. 2012). In some studies, respiration was not affected by intermediate acidification (Reynaud et al. 2003; Edmunds 2012) but at lower pH coral respiration has been shown to either decrease (Kaniewska et al. 2012; Edmunds 2012) or increase (Crawley et al. 2010). Given our understanding of how these parameters affect coral physiology either individually or synergistically, we hypothesize that the multivariate shift in biogeochemistry of seawater reflected in SGD will alter coral physiology.

Physiologic changes in corals along an SGD gradient can shift the outcomes of biotic interactions between corals and their neighbors. Adjacent species can affect each other's physiology through direct physical interaction (i.e., coral competition mechanisms such as mesenterial filaments) or indirectly through alteration to the immediate chemical or physical environment (Jones et al. 1997; Baird and Hughes 2000; O'Neil and Capone 2008). Notably, there has been considerable attention on direct and indirect effects

of coral-algal interactions (Inagaki and Longo 2024), but coral-coral interactions are comparably less studied. These coral-coral interactions can be negative, positive, or neutral and the directionality of the effect could be dependent on the type of interacting organisms or the environmental context. For example, corals surrounded by, but not touching, conspecific monocultures grew less and had lower survivorship than corals surrounded by polycultures in a field experiment (Clements and Hay 2019). Conversely, corals directly in contact with other conspecific corals grew nearly twice as fast as corals in direct contact with heterospecific corals (Idjadi and Karlson 2007). SGD-related biogeochemistry can also influence these coral-coral interactions. For instance, acidified conditions can shift the competitive hierarchies among coral taxa, where conspecific, but not heterospecific neighbors, reduced coral growth when exposed to low pH (Horwitz et al. 2017). Further, corals interacting with conspecific neighbors have been shown to mitigate the negative effect of low pH on coral physiology by altering the flow environment around the corals on a cm scale (Evensen and Edmunds 2016, 2017). While these studies uncover concrete interactions between pH and coral neighbors on coral physiology, the compounding effect of coral interactions and multivariate abiotic conditions, like SGD, have yet to be tested.

In this study, we test how corals respond to an SGD-driven environmental gradient and how this response is mediated by the presence of conspecific or heterospecific corals. We hypothesize that (1) the unique biogeochemistry created by SGD influences coral holobiont physiology (endosymbiont density, chlorophyll *a* content, gross photosynthesis, and respiration) and (2) coral neighbors around a center ("focal") coral mediate the effect of SGD on coral holobiont physiology. We hypothesize that the neighbor treatment effects will differ between species interaction types (conspecific vs heterospecific). This study contributes to the current understanding of biotic–abiotic interactions by determining if coral neighbors mediate the effects of the environment on coral physiology.

Materials and methods

Site selection

Mo'orea, French Polynesia is a high volcanic island located in the South Pacific with known SGD influence (Knee et al. 2016; Haßler et al. 2019; Hagedorn et al. 2020). There are several active SGD seeps around Mo'orea, where water is flowing into the ocean from the coastal aquifer. Alongshore current velocities in Mo'orea peak at around 0.4–0.5 m s^{-1} and seawater motion in the lagoon is also driven by surface waves on the reef crest (Leichter et al. 2013). We chose a fringing reef site on the western side of Mo'orea in the town Varari based on local knowledge of active SGD seeps communicated with us by residents and confirmed by measurements of radon and salinity (Fig. 1A; Hagedorn et al. (2020)). The study site is shallow (< 2 m), has a unidirectional northwesterly current flow (0.15 ± 0.00092 m s^{-1}, mean and SE) (Silbiger et al. 2023), and has a total coral cover of approximately 13% that is dominated by *Porites, Pocillopora,* and *Montipora* (Silbiger et al. 2023). At this site, *Porites rus* is frequently seen next to colonies of *Pocillopora acuta* (Fig. 1C).

We chose 20 experimental locations (Fig. 1B) along a gradient of SGD influence based on preliminary spatial samples of seawater radon, salinity, and temperature during low tide in May 2021 (Hagedorn et al. 2024). Radon is commonly used as a tracer for SGD because it has high concentrations within groundwater, is unreactive, and has a short half-life (Burnett and Dulaiova 2003). Radon was measured using a RAD7 Radon Detector (measurement accuracy = ± 5%; calibrated by Durridge Radon Capture & Analytics, MA, USA) mounted to an inflatable boat and pushed along the reef in a zigzag pattern to capture the alongshore and inshore-offshore gradient of SGD. At the same time, salinity and temperature were measured using a spatial array of HOBO Conductivity loggers (U24-002-C Onset, MA, USA; conductivity resolution = 2 µS cm^{-1}, temperature resolution = 0.1 °C) along the reef for two days (Hagedorn et al. 2020, 2024). All 20 experimental locations were positioned at sites aimed at capturing a gradient of SGD influence. The experiments were permanently marked with rebar attached to dead coral skeletons at similar depths (0.32–0.83 m from the surface at low tide).

SGD gradient characterization

We characterized five environmental parameters commonly correlated with SGD across the site throughout the experiment (3-August to 17-August 2021): temperature, nitrate + nitrite, phosphate, salinity, and pH (Paytan et al. 2006; Cyronak et al. 2014; Moosdorf et al. 2015; Nelson et al. 2015; Knee et al. 2016; Santos et al. 2021). Continuous measurements of temperature were taken every 20 min with Onset HOBO Conductivity Loggers for the entirety of the 2-week experiment. For the biogeochemistry data, detailed collection methods and biogeochemical results can be found in Silbiger et al. (2023). In brief, 500-mL discrete water samples were collected at four time points (high tide midday, high tide midnight, low tide dawn, low tide dusk) in an approximately 72-h period (5-Aug-2021 through 8-Aug-2021) at each experimental location with sub-surface automated dual water samplers (Enochs et al. 2020) or by hand into acid-washed HDPE bottles. Water samples collected with the autosamplers were either filtered in situ with a 0.22-µm Sterivex filter into dark mylar bags for nutrient

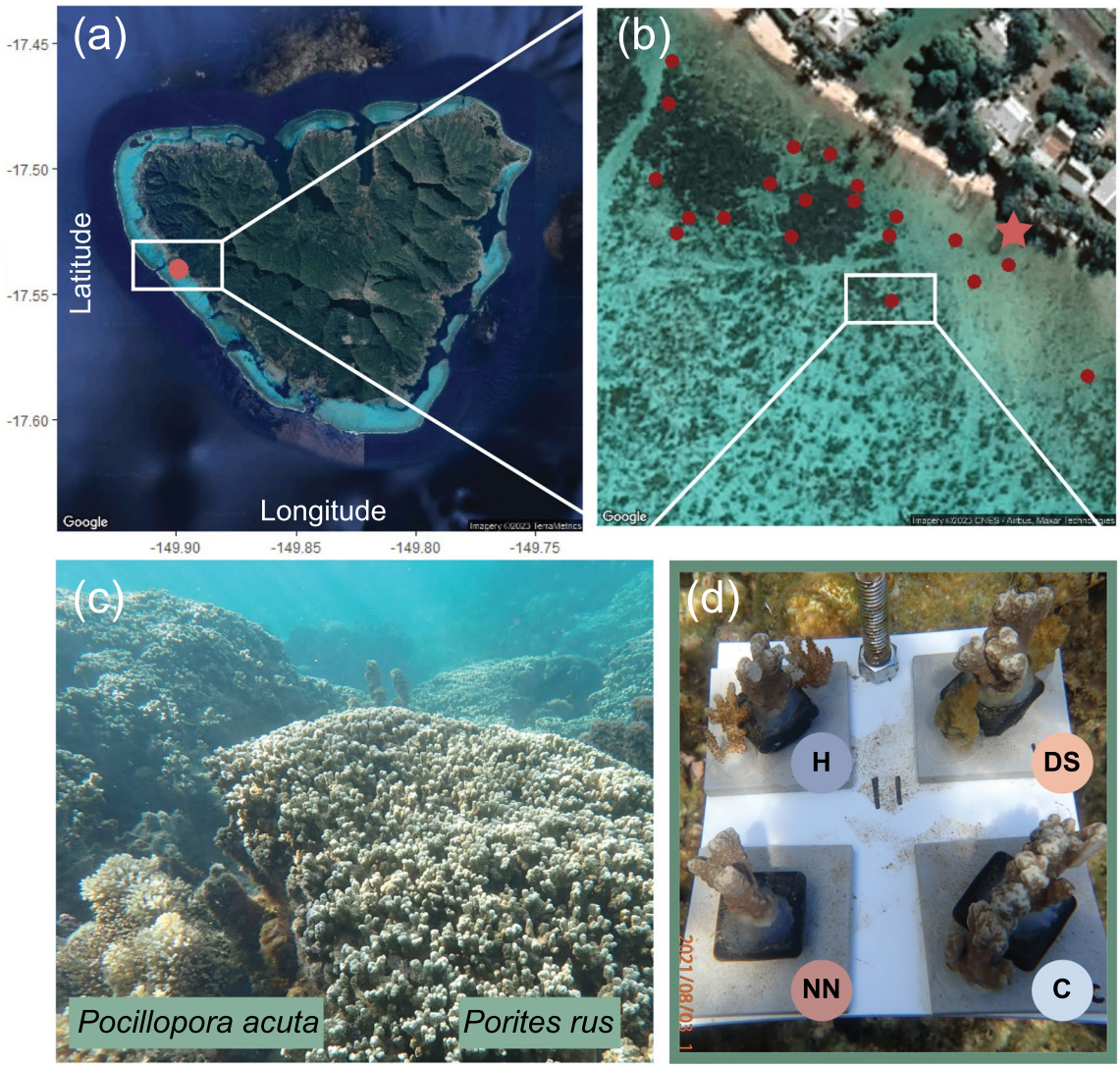

Fig. 1 **a** Map of the site on the west coast of Mo'orea. **b** Experimental locations (dark red) and the seep (light red star) at the site. **c** Photograph taken at the site of a *Porites rus* adjacent to a *Pocillopora acuta* colony. *P. rus* at the site is commonly touching or near dead coral skeleton, conspecifics, or heterospecifics, like *Pocillopora acuta*. **d** Experimental design of neighborhood treatment plates placed at experimental location. *NN* no neighbor, *DS* dead skeletal neighbor, *C* conspecific neighbor, *H* heterospecific neighbor

chemistry determinations or pumped into a polyvinyl fluoride bag (Tedlar, DuPont) pre-fixed with $HgCl_2$ for pH (Enochs et al. 2020). Hand-collected nutrient samples were filtered through a 0.22-µm Sterivex filter immediately after collection. All nutrient samples were immediately frozen at -20 °C in 50 mL falcon tubes and sent to SOEST Laboratory for Analytical Biogeochemistry (Hawai'i, USA) for analysis (level of detection: nitrate + nitrite = 0.009 µmol L^{-1}, phosphate = 0.008 µmol L^{-1}, silicate = 0.065 µmol L^{-1}). pH and salinity were measured immediately after collection using an Orion Star Multiparameter Meter (Thermo Fisher Scientific) with Orion Ross Ultra Low Maintenance pH/ATC Triode Combination Electrodes (pH precision = 0.01 and accuracy = 0.03), and DuroProbe 4-cell Conductivity Electrodes probes, respectively. pH probes were calibrated with a Tris buffer (purchased from Dickson Laboratory, Scripps Institution of Oceanography) of known pH prior to use (Dickson et al. 2007) and measured in combination with temperature using a Thermo Scientific trace digital thermometer (5-077-8, accuracy = 0.05 °C, resolution = 0.001 °C; Control Company, Friendswood, TX, USA). In situ pH (total scale) was back-calculated using in situ temperature from the HOBO

conductivity and temperature loggers using the R package *seacarb* (Gattuso et al. 2019).

Experimental design

Porites rus was chosen as the focal species for this experiment as it is common on tropical coral reefs worldwide (Darling et al. 2012), it is one of the dominant coral species at the study site, and it is often found in direct contact with both conspecific and heterospecific coral species (Fig. 1c). To test the hypothesis that coral neighbors mediate the effect of SGD on coral host and endosymbiont physiology, we placed living *P. rus* corals into four neighbor treatments placed at each of the 20 experimental locations, which included: (1) no neighbors (a solitary *P. rus*), (2) two dead skeletal fragments of *P. rus*, (3) two conspecific fragments (*P. rus* from a different colony than the focal colony), and (4) two heterospecific fragments (*Pocillopora acuta*) (Fig. 1). The dead skeletal fragments acted as a non-coral control, but were not cleaned during the experiment; thus, algal growth mimicked the natural succession on dead coral.

Fragments (3 cm in height and 2 cm in width) of *P. rus* and *P. acuta* were collected haphazardly approximately 200–650 m up current of the SGD seep in ambient seawater conditions. Six fragments were collected from each of 20 putative *P. rus* colonies (i.e., colonies at least 20-m apart from each other) for center ("focal") coral fragments ($n = 80$), pre-deployment metabolism sampling fragments ($n = 20$), and pre-deployment endosymbiont measurement fragments ($n = 20$). All physiological measurements described below were conducted on these 120 *P. rus* fragments. Neighbor fragments of *P. rus* ($n = 80$) and *P. acuta* ($n = 40$) were collected from an additional 20 colonies of each species (two fragments from each colony). All coral fragments were collected using a chisel and hammer, placed in Ziploc bags underwater, and transported to Richard B. Gump South Pacific Research Station ("Gump Research Station"). At the Gump Research Station, fragments were placed in outside flow-through seawater tables and resized to 3 cm height by 2 cm width using bone cutters, as needed.

All deployment fragments were randomly assigned to an experimental location, with the four focal fragments from the same putative colonies assigned to each neighbor treatment within an experimental location. The focal *P. rus* fragments were hot glued with Gorilla Glue Hot Glue (Dizon and Yap 2005; Wall et al. 2017; Becker and Silbiger 2020; Becker et al. 2021) to a nylon bolt connected to a 5-cm^2 PVC plate. The neighbor fragments were hot glued to the PVC plate as close as possible to the focal fragment, with the neighbor corals in direct contact with the focal fragment (Fig. 1). Four 5-cm^2 plates, one of each neighborhood treatment, were then attached to a larger 25-cm^2 PVC plate using bolts. Each plate was deployed at its experimental location for two weeks by attaching the plate to rebar epoxied to hard benthos and then collected to measure post-deployment response variables.

Endosymbiont density and chlorophyll a

Endosymbiont density and chlorophyll *a* content were measured following methods within Becker and Silbiger (2020) at the start of the experiment from the pre-deployment fragments and at the end of the 2-week SGD exposure period from each of the deployed center fragments. Coral fragments were frozen at -40 °C immediately after collection for the pre-deployment corals or after respirometry measurements (described below) for the center corals. The fragments were thawed and airbrushed to remove tissue using an Iwata Eclipse HP-BCS airbrush (Oregon, USA) with 0.2-µm filtered seawater collected from the lagoon offshore of Gump Research Station. Coral tissue was transferred into falcon tubes, homogenized with a PRO Scientific Bio-Gen PRO200 Homogenizer (Oxford, Connecticut), and aliquoted into two 1 mL microcentrifuge tubes for endosymbiont density and chlorophyll *a* content. Samples were frozen again at -40 °C until processing, and final tissue blastate volume was recorded for each coral fragment prior to aliquoting.

Samples aliquoted for chlorophyll *a* content were centrifuged (13,000 rpm for 3 min) (Labnet Spectrafuge 24D) and the supernatant was discarded to isolate the algal pellet. Acetone was added to extract the chlorophyll and the sample was vortexed and placed in 4 °C in the dark for 24 h. The samples were again vortexed and centrifuged at the same settings to separate out the debris and the extract was collected. The extract samples were processed on a Synergy HTX Multi-Mode Microplate Reader (BioTek, California, USA). Chlorophyll *a* content was calculated using equations from Jeffrey and Humphrey (1975) and normalized to surface area and endosymbiont density. *E* indicates the extinction at each wavelength (663 nm or 630 nm).

$$\text{Chlorophyll } a = 11.43\left(E_{663}\right) - 0.64(E_{630}).$$

Aliquot tissue slurries for endosymbiont density were sent to the University of Hawai'i at Mānoa and measured by flow cytometry following methodology from Fox et al. 2021. For each coral fragment, one sample of 150 µL was analyzed on a flow cytometer (Beckman Coulter CytoFLEX S) at a rate of 60 µL $minute^{-1}$ with excitation wavelengths of 375 nm, 405 nm, 488 nm, and 561 nm. Due to the uneven distribution of tissue blastate at the beginning of each run, the first 30 µL of each sample was removed from the analysis. Endosymbiont density was normalized to tissue blastate volume and coral surface area.

Surface area

After removing the coral tissue using the airbrush methods described above, skeletal fragments were placed in a drying oven at 60 °C to prepare for surface area measurements using the wax dipping method (Stimson and Kinzie 1991). First, a calibration curve ($r^2 > 0.9$) of mass change of weight against surface area was created by wooden dowels of known surface area. Coral fragments were then weighed, dipped in a 65 °C Minerva paraffin wax bath (Georgia, USA) for two seconds, and then rotated in the air for 2 s at a constant rate. Fragments were set for 10 min to cool and then weighed again to obtain the mass change from wax dipping. The surface area of each coral fragment was calculated using the calibration curve obtained with wooden dowels.

Coral metabolism

All metabolism measurements were conducted following methods within Silbiger et al. (2019). We first characterized the relationship between net photosynthesis and photon flux density, commonly known as a photosynthesis-irradiance (PI) curve, to ensure photosynthesis rates in the experimental fragments were measured at saturating light conditions. For the PI curve, additional fragments from six of the donor colonies were collected and placed in flow-through seawater tables for approximately 48 h to recover from the collection process and handling. Fragments were then placed in 650 mL acrylic chambers full of seawater (collected from the flow-through system at the Gump Research Station and filtered to 5 µm) at ambient temperature (28.4 ℃) with no air bubbles, a stir bar, a fiber-optic oxygen probe (Presens Oxygen Dipping Probes DP-PSt7; calibrated by Presens; Regensburg, Germany), and a temperature probe (Presens Pt1000, Regensburg, Germany, precision: ± 0.1 °C). The two probes were connected to a Presens Oxygen Meter [OXY-10 SMA (G2)], which measures oxygen percentage saturation and temperature (°C) at a frequency of 1 Hz. Oxygen concentrations (µmol L^{-1}) were estimated from percent saturation accounting for a seawater salinity of 35 psu and standard oxygen solubility (Weiss 1970). Net photosynthesis was measured at eight light levels (µmol m^{-2} s^{-1}) using an LED light (Mars Aqua 300w LED Brand Epistar, LongGang District, ShenZhen, China) for 20 min at each light level: 0, 57, 144, 219, 300, 435, 573, and 809 µmol m^{-2} s^{-1}. Photosynthetically active radiation (PAR) was measured above each coral fragment with a cosine corrected MQ-510 Quantum Meter (error ± 2% and ± 5% at 45° and 75° from the light source, respectively; Apogee Instruments, Logan, UT, USA).

To calculate photosynthetic rates, the first two minutes of each run were removed to exclude the initial responses of the corals to changing light conditions and to ensure that the oxygen has reached equilibration within the chamber. The data were then thinned from every second to every 20 s to reduce noise in the data and to allow for processing of local linear regressions through the large dataset. Repeated local linear regressions were then used to calculate oxygen flux rates in the chambers using the R package *LoLinR* (Olito et al. 2017). Rates were normalized to the surface area (cm^2) of each fragment after accounting for chamber seawater volume and blank control chamber rates. Saturating light (I_k) is the irradiance at which photosynthesis will no longer continue to increase. I_k was calculated (Online Resource Figure S1) following methods from Marshall and Biscoe (1980) for a non-linear least squares regression of a non-rectangular hyperbola, with the following equation:

$$A_n = \left\{ \frac{[A_{max} + (\alpha PPFD) - [A_{max} + (\alpha PPFD))^2 - (4\alpha\theta \mathrm{PPFD} \bullet A_{max})]^{0.5}}{(2\theta)} \right\} - R_d$$

The parameters included in this equation are as follows: net photosynthetic rate (A_n), maximum gross photosynthetic rate (A_{max}), photosynthetic photon flux density (PPFD), dark respiration (R_d), curvature parameter (Θ; a dimensionless measure of the resistance to CO_2 diffusion), and apparent quantum yield, or the low-light photochemical efficiency of photosynthesis (AQY, α). The saturating light (I_k) was calculated by dividing A_{max} by AQY (Online Resource Figure S1; $I_k = 362.9$ µmol photons m^{-2} s^{-1}; Marshall & Biscoe (1980)).

Oxygen evolution was measured in all pre- and post-deployment coral fragments in 5 µm-filtered, ambient seawater (28 ℃) first in saturating light (approximately 590 µmol m^{-2} s^{-1}) for 20 min to measure the net photosynthesis and then in complete darkness for 20 min in the same seawater to measure light-adapted dark respiration. Ten chambers were measured at a time, with nine chambers having coral fragments and one chamber acting as a control seawater-only chamber to account for background fluctuation in oxygen. The volume of seawater in each chamber was measured with a graduated cylinder after each respirometry measurement. Metabolic rates were calculated using the same methods outlined above for the photosynthesis-irradiance curve. Gross photosynthesis was calculated by summing net photosynthesis and respiration rates (as absolute values).

Statistical design

As SGD directly reduces salinity through the input of freshwater into the reef, the correlation of biogeochemical parameters with salinity was measured to gain insight into the effect of SGD at the site. Pearson's correlations were used to test the correlations between biogeochemical parameters to understand correlation of the multivariate changes in SGD-driven biogeochemistry at the site. We then used a

model selection approach based on Akaike's Information Criterion (AIC) to determine the dominant SGD-related environmental driver for each coral response variable in the absence of a neighbor (Sakamoto et al. 1986; Richards 2005; Anderson 2007). One outlier was removed for the chlorophyll *a* content cell^{-1} model selection as the outlier was 200% higher than the next highest value of chlorophyll *a* content cell^{-1}. The model selection included individual linear models of all SGD predictor variables (temperature, salinity, pH, nitrate + nitrite, and phosphate) as a function of scaled (z-score) means, minimums, maximums, and ranges to rank multiple aspects of the altered groundwater biogeochemistry on coral physiology. To account for colony-level differences in each of the measured coral parameters, initial coral physiology measurements were included as a covariate in the models if they were a significant predictor of the post-deployment measurements, otherwise they were dropped (Online Resource Table S1).

To test if neighbors mediate the effect of SGD on coral physiology, we compared the expected response values from the no neighbor models (SGD effect only) to the observed response values in neighbor-present treatments (neighbor-mediated SGD effect). We ran individual linear mixed effect models for each physiological parameter with calculated residuals (i.e., the difference between SGD-only and neighbor-mediated effect) as the response variable, neighbor treatment as a fixed factor, and plate ID as a random factor to account for the four neighbor treatments co-located within each plate. Linear mixed models were assessed using the R packages *lme4* (Bates et al. 2014) and *emmeans* (Lenth 2022) for post-hoc analysis. Assumptions were visually and statistically checked for all models using the R package *performance* (Lüdecke et al. 2021). All statistical tests and figures were made in R (R Core Team 2021). All data and code are publicly available at https://github.com/njsilbiger/Neighborhood_effects_and_SGD.

Results

SGD alters reef biogeochemistry

Salinity varied from 36.4 to 37.2 psu across the 20 locations, with the most variable location having a 7 times higher within location salinity range (range = 0.64 psu) than the most stable location (range = 0.09 psu) (Fig. 2A, B). Salinity had a strong negative correlation with nitrate + nitrite ($r = -0.60$, $P < 0.001$; Online Resource Figure S2), a strong negative correlation with phosphate ($r = -0.55$, $P < 0.001$), and a weak, but significant negative correlation with temperature ($r = -0.24$, $P < 0.05$) along the spatial gradient. The coldest site was approximately 0.6 °C cooler than the site with the highest minimum temperature (Fig. 2I), and the daily temperature range varied from 2.12 to 2.92 °C (Fig. 2J). SGD directly increased nutrients at the site, with nitrate + nitrite ranging from 0.23–1.34 µmol L^{-1} and phosphate ranging from 0.18–0.31 µmol L^{-1} across the site (Fig. 2C, D). The daily range in nitrate + nitrite and phosphate increased by approximately 14-fold (0.88 vs 0.06 µmol L^{-1}) and tenfold (0.1 vs 0.01 µmol L^{-1}) across all sites, respectively (Fig. 2E, F). pH ranged from 7.97–8.10 (Fig. 2G) and the daily range quadrupled across the 20 locations (Fig. 2H). pH was not significantly correlated with salinity; however, pH was positively correlated with both nitrate + nitrite ($r = 0.35$, $P < 0.01$) and phosphate ($r = 0.49$, $P < 0.001$; Online Resource Figure S2). Minimum pH had a strong negative correlation with pH range ($r = -0.84$, $P < 0.001$; Online Resource Figure S2) and high pH range values were largely driven by the low minimum pH values at these experimental locations. Conversely, the range of nitrate + nitrite at the experimental site was driven by maximum nitrate + nitrite values, as there was a strong positive correlation between maximum and range of nitrate + nitrite ($r = 0.94$, $P < 0.001$; Fig. 2; Online Resource Figure S2).

SGD alters coral and endosymbiont physiology

A total of eight out of 80 center fragments (10%) and 13 out of 120 neighbor fragments (10.8%) were lost due to a large wave event that occurred during the experimental period. Replicate focal corals that were missing any neighboring coral fragments at the end of the experiment were removed from the analysis. The resulting sample sizes are an *N* of 15–16 per treatment (out of the original 20). All measured physiological response variables, except for chlorophyll *a* content cell^{-1}, were significantly affected by SGD-associated parameters (Online Resource Table S2). However, the dominant environmental driver differed between the biological responses (Fig. 3). Endosymbiont density was most strongly associated with the minimum concentration of nutrients (nitrate + nitrite), while chlorophyll *a* content per cm^{-2}, gross photosynthesis, and respiration were most strongly related to pH range (Fig. 3; Online Resource Table S2). The second best-fit model for gross photosynthesis was minimum pH with a ΔAIC value of 0.45. A ΔAIC value less than two indicates the fit of the models is indistinguishable from one another (Richards 2005), therefore minimum pH and pH range were both included as the dominant drivers for gross photosynthesis. For all other response variables, the second-best parameter always had a ΔAIC greater than two. There was no significant relationship between initial and post-deployment measurements for endosymbiont density, gross photosynthesis, and respiration and were thus dropped from those models (Online Resource Table S1). However, there was a significant positive relationship ($F_{1,56} = 9.04$, $P < 0.01$) between the initial and post-deployment values

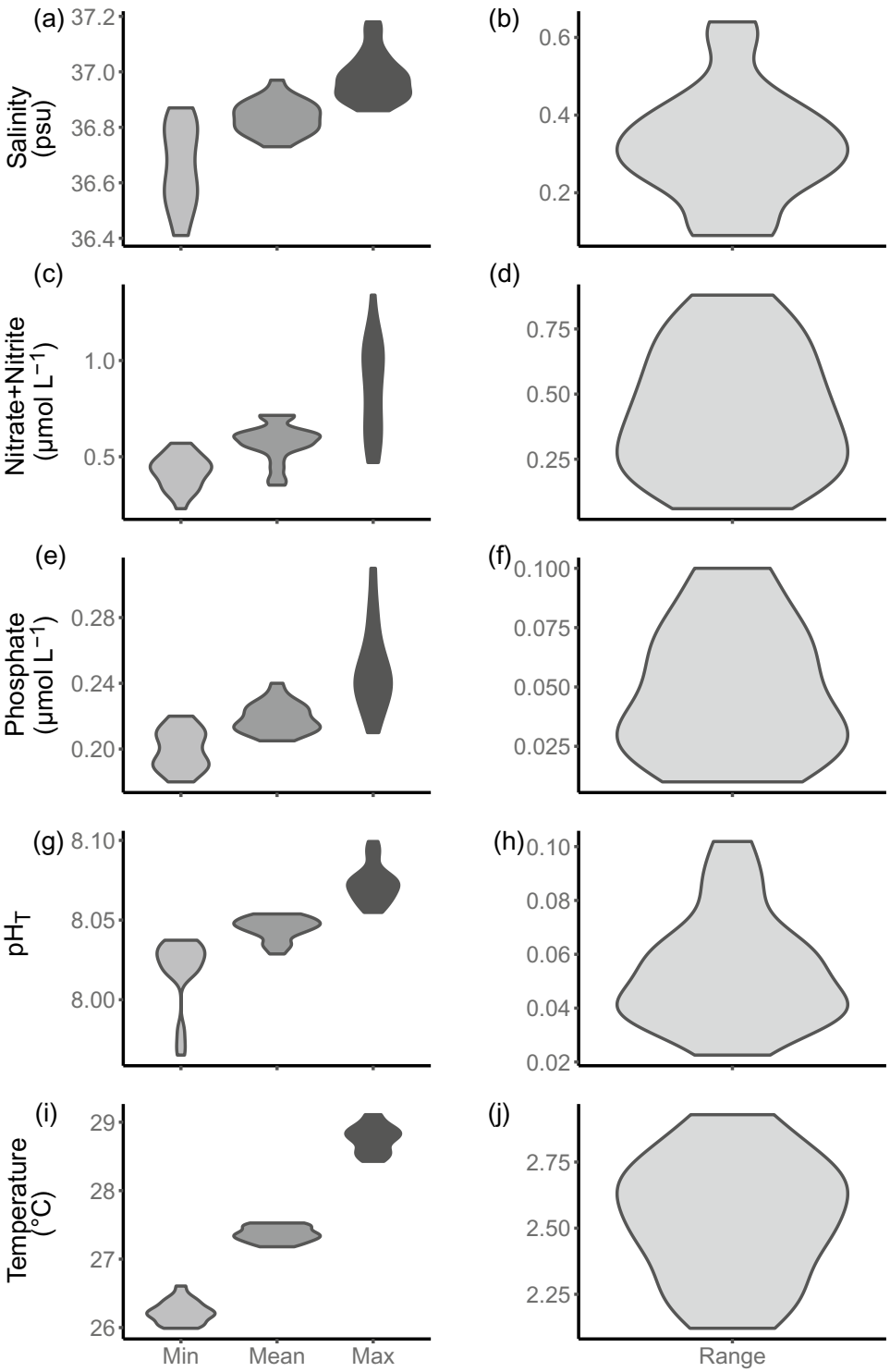

Fig. 2 Violin plots of SGD related biogeochemical parameters showing (**a**, **c**, **e**, **g**, **i**) minimums, means, maximums, and (**b**, **d**, **f**, **h**, **j**) ranges of each parameter across all 20 experimental locations

for chlorophyll *a* content per cm^{-2}, and thus initial values were included as a covariate for the chlorophyll *a* content per cm^{-2} models.

Final endosymbiont density ranged from 0.02 to 0.58×10^6 cells cm^{-2} across all center *P. rus* fragments (Fig. 4A). The nutrients at the site increased endosymbiont density within the coral hosts by $0.44 \pm 0.17 \times 10^6$ cells cm^{-2} per µmol L^{-1} of nitrate + nitrite ($F_{1, 13} = 6.5$, $r^2 = 0.28$, $P < 0.05$; Fig. 4A; Online Resource Table S3), which equated to a 4.2-fold increase in endosymbiont density in response to the 2.5-fold increase in minimum nitrate + nitrite along the SGD gradient. Chlorophyll *a* content per cm^{-2} ranged from 0.76 to 5.7 µg cm^{-2} across the site and increased by 29.8 ± 8.6 µg cm^{-2} per unit change of pH range ($F_{2, 12} = 8.0$,

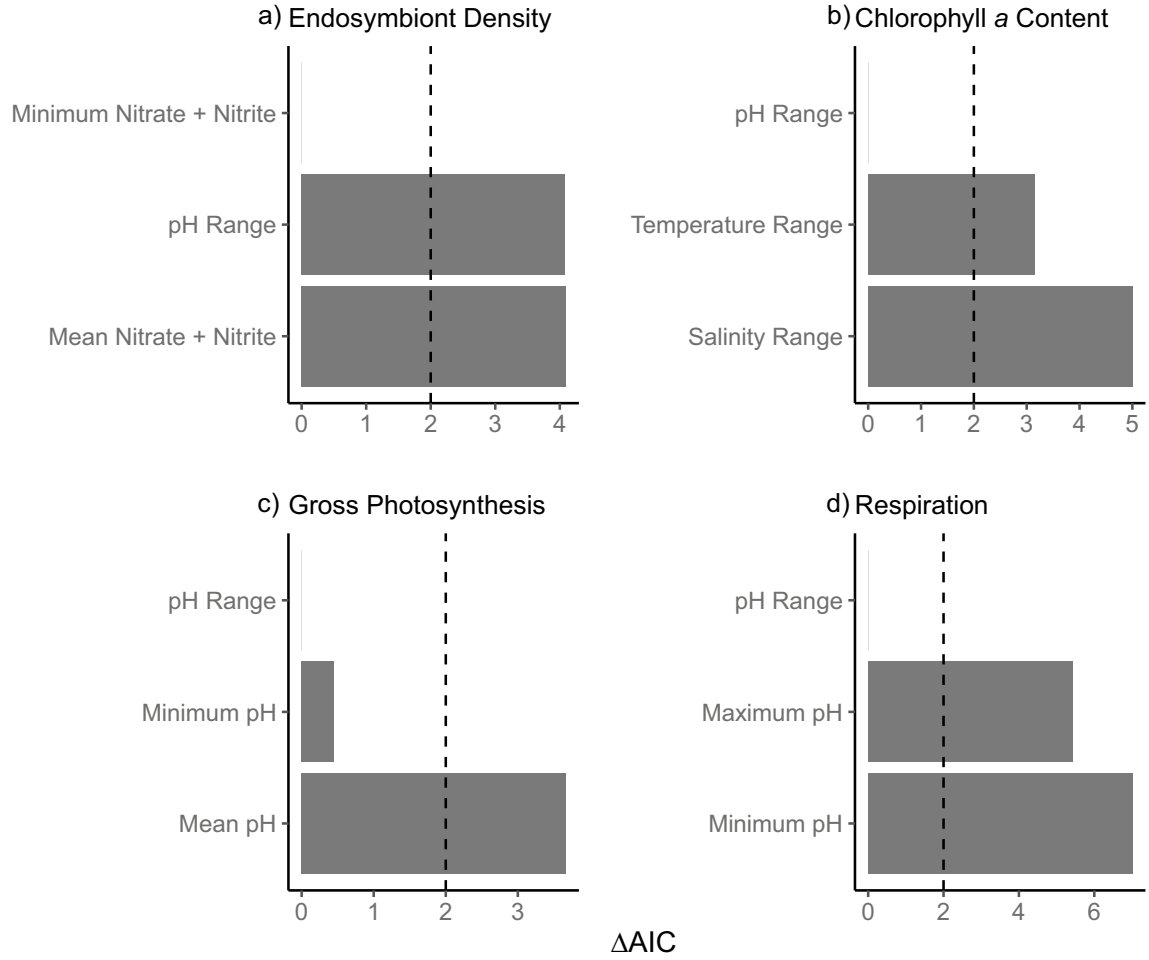

Fig. 3 ΔAIC (Akaike's Criterion Information) values from the top three ranking SGD biogeochemistry models for **a** endosymbiont density, **b** chlorophyll a content (μg cm^{-2}), **c** gross photosynthesis, and **d** respiration of *Porites rus* coral fragments. Parameters with a ΔAIC value of zero were considered the top parameter and were used for the subsequent analysis. The vertical dashed lines represent a ΔAIC value of 2, where ΔAIC values less than or equal to 2 represent models that are similar in their fit

$r^2 = 0.50$, $P < 0.01$; Fig. 4B; Online Resource Table S3) and 0.23 ± 0.16 μg cm^{-2} per unit change of initial chlorophyll *a* content (μg cm^{-2}). Chlorophyll *a* content was 113% greater at the site with the highest pH range relative to the site with the lowest pH range. When normalized to endosymbiont density, final chlorophyll *a* content ranged from 5.68 to 92.5 pg $cell^{-1}$ across the site. Notably, five of the more extreme values, which ranged from 33.9 to 92.5 pg $cell^{-1}$, were associated with low endosymbiont densities (0.02–0.07 cells 10^6 cm^{-2}). While the best-fit model for chlorophyll content $cell^{-1}$ was minimum nitrate + nitrite, the relationship was not statistically significant for this parameter or any of the other SGD parameters (Online Resource Figure S3).

pH range had the strongest association with coral metabolism (Figs. 3C, D and 4C, D). Gross photosynthesis ranged from 0.53 to 2.1 μmol O_2 cm^{-2} h^{-1} across all center fragments and had a marginally significant association with pH range ($P = 0.054$; Fig. 4C). Gross photosynthesis increased by 15.1 ± 7.1 μmol O_2 cm^{-2} h^{-1} per unit change of pH range ($F_{1, 13} = 4.5$, $r^2 = 0.20$, $P = 0.054$; Fig. 4C; Online Resource Table S3), where the rate nearly doubled between the highest and lowest pH range site. Respiration varied from 0.13 to 0.96 μmol O_2 cm^{-2} h^{-1} across the site and increased by 8.97 ± 2.7 μmol O_2 cm^{-2} h^{-1} per unit change of pH ($F_{1, 13} = 11$, $r^2 = 0.42$, $P < 0.01$; Fig. 4D; Online Resource Table S3). Respiration was 464% greater at the highest pH range site compared to the lowest pH range site.

Neighbors mediate the effect of SGD

Gross photosynthesis and respiration were significantly reduced by nearly 20% and 23%, respectively, in the conspecific neighbor treatment relative to the no neighbor treatment (Fig. 5; Online Resource Figure S4; Table S4). Specifically, gross photosynthesis and respiration decreased an average of 0.20 ± 0.09 μmol O_2 cm^{-2} h^{-1} ($t = -2.17$, df = 39, $P < 0.05$;

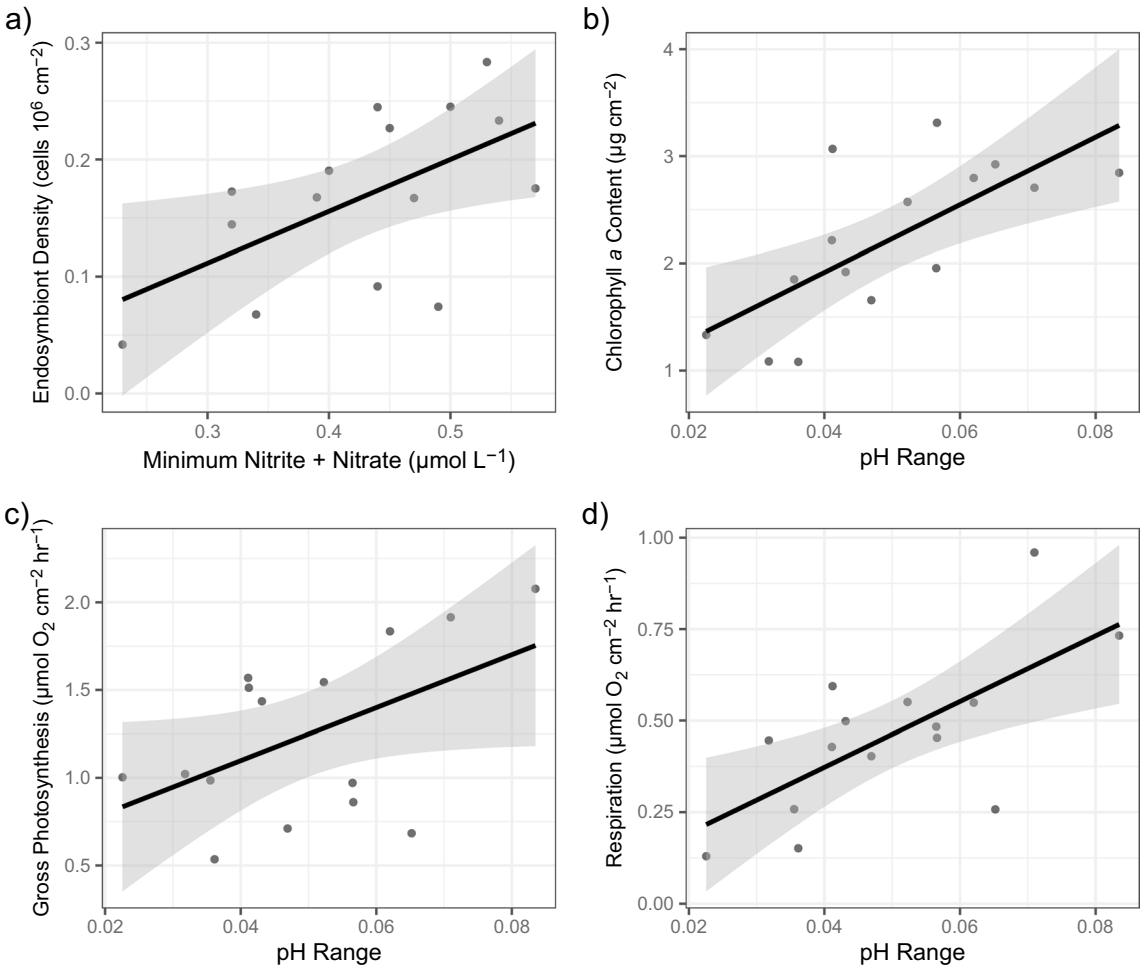

Fig. 4 Regression plots of top-ranking SGD biogeochemical model for each coral physiological response variable when no neighbor was present. Subsets include **a** endosymbiont density (cells × 10^6 cm^{-2}) as a function of minimum nitrate + nitrite (µmol L^{-1}), **b** chlorophyll a content (µg cm^{-2}) as a function of pH range, **c** gross photosynthesis (µmol O_2 cm^{-2} h^{-1}) as a function of pH range, and **d** respiration (µmol O_2 cm^{-2} h^{-1}) as a function of pH range. Lines are best-fit lines and shaded areas are 95% confidence intervals ($N = 15$)

Fig. 5D & Online Resource Table S4) and 0.09 ± 0.04 µmol O_2 cm^{-2} h^{-1} ($t = -2.14$, df = 36, $P < 0.05$; Fig. 5E & Online Resource Table S4), respectively, when in competition with conspecific neighbors relative to being alone. Endosymbiont density and chlorophyll *a* content were not significantly affected by neighbor treatment.

Discussion

Our research showed that SGD-driven biogeochemistry affected coral physiology and that the relationship between local biogeochemistry and coral physiology was mediated by intraspecific interactions. We found that SGD-driven biogeochemistry increased endosymbiont density, chlorophyll *a* content, photosynthesis, and respiration. While SGD caused multivariate changes to the seawater, the model selection showed that pH range and inorganic nitrogen concentrations were the dominant drivers of changes in coral physiology along the SGD gradient. SGD is an important source of exogenous inorganic nutrients (Burnett et al. 2003; Paytan et al. 2006; Zhang and Mandal 2012) and is known to increase the flux of nitrate + nitrite to coastal ecosystems (Moosdorf et al. 2015; Santos et al. 2021). Our data also showed a strong relationship between nitrate + nitrite concentration and salinity, a proxy for SGD. SGD typically decreases pH in the nearby water column (Cyronak et al. 2014; Silbiger et al. 2020), but the indirect effect of SGD-driven nutrients increasing reef metabolism and thus diel pH outweighed the direct flux of CO_2 from the groundwater. The stronger indirect effect of SGD on pH has also been shown in Hawai'i (Silbiger et al. 2020), Mo'orea (Silbiger et al. 2023), and the Great Barrier Reef (Santos et al. 2011).

Endosymbiont density was positively associated with nutrient concentrations, which was expected as previous studies have also found nutrient enrichment increased

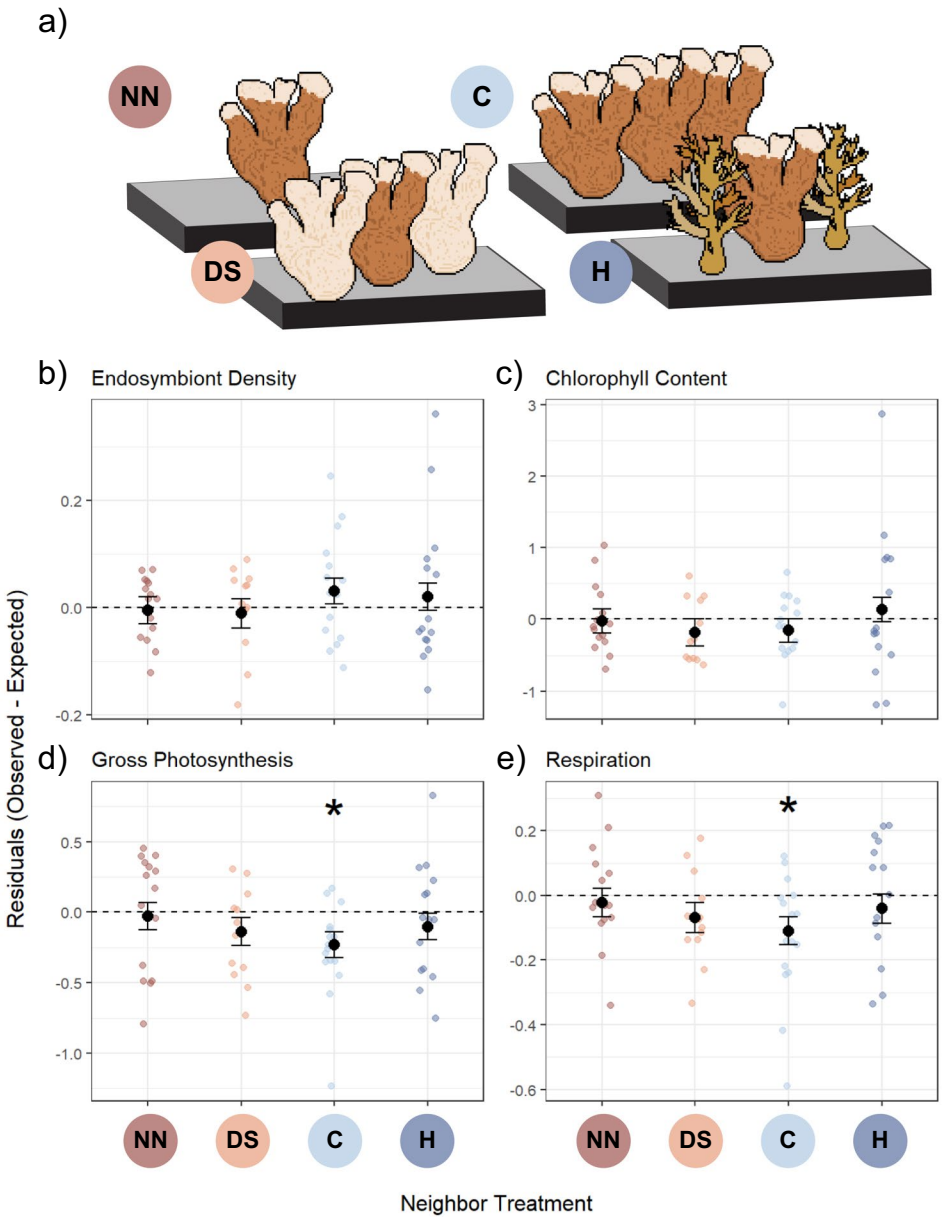

Fig. 5 **a** Diagram showing neighbor treatments. **b–d** Residual plots for each neighbor treatment showing observed values of coral physiological responses minus expected values calculated from the no neighbor treatment. **b** endosymbiont density (cells × 10^6 cm^{-2}), **c** chlorophyll *a* content (µg cm^{-2}), **d** gross photosynthesis (µmol O_2 cm^{-2} h^{-1}), and **e** respiration (µmol O_2 cm^{-2} h^{-1}). Black dots represent the mean ± SE of the residuals for each neighbor treatment. Asterisks represent neighbor treatments significantly different from the no neighbor treatment for that response variable. *NN* no neighbor, *DS* dead skeleton, *C* conspecific, *H* heterospecific neighbor ($N = 15–16$)

endosymbiont densities (Marubini and Davies 1996; Reynaud et al. 2003; Becker and Silbiger 2020; Becker et al. 2021). *In hospite* symbiotic dinoflagellates are normally nitrogen-limited due to the oligotrophic nature of coral reefs, leading to increases in population density, growth rates, and photosynthetic performance when supplied with exogenous nitrogen (Davy et al. 2012). Increases in endosymbiont densities can increase photosynthetic potential of the coral (Scheufen et al. 2017), which could lead to a beneficial effect of exogenous inorganic nitrogen from SGD.

Chlorophyll *a* measurements can be used as a proxy of endosymbiont photosynthetic efficiency (Suggett et al. 2010). As many symbiotic tropical reef corals receive much of their energy through photosynthates from endosymbionts, chlorophyll *a* measurements can also be used to estimate coral fitness. Chlorophyll *a* content normalized to the coral surface area increased with increasing pH range. If the increase in chlorophyll *a* content cm^{-2} was due to an increase in the biosynthesis of chlorophyll pigments directly, we would expect to see a positive association between chlorophyll *a* content $cell^{-1}$ and pH range. However, chlorophyll *a* content per algal cell was not significantly associated with any of the SGD parameters, indicating that SGD input is likely indirectly increasing chlorophyll *a* content by increasing endosymbiont density.

Metabolism of *Porites rus* was affected by the seawater pH, where both gross photosynthesis and respiration were positively associated with pH range. As both chlorophyll *a*

content and gross photosynthesis increased with increasing pH range, it is likely that gross photosynthesis was partially driven by increased light absorption by the increase in endosymbiotic chlorophyll. Respiration could have increased in corals experiencing high ranges of pH due to increased energetic costs for physiological processes (Erez et al. 2011). As pH range increased both photosynthesis and respiration, it is possible that due to the tight cycling of products from each metabolic process within the coral holobiont, respiration increased due to increasing photosynthesis (or vice versa).

Conspecific corals placed adjacent to the focal colony suppressed the metabolism of *Porites rus* relative to isolated colonies. Neighboring organisms can alter the physical environment around a coral, such as by altering seawater flow and thereby modulating the seawater chemistry around the focal fragment (Evensen and Edmunds 2017). However, as no effect was seen by dead skeletal neighbors or heterospecific neighbors, conspecific neighbors were likely further altering the chemical environment around the focal fragments in conjunction with altered flow. While the suppression of photosynthesis by conspecifics could indicate a negative interaction due to less photosynthates transferred to the host (Scheufen et al. 2017), the corresponding suppression of respiration could also indicate positive interaction. For example, lower coral respiration when in conspecific treatments could indicate lower energetic expenditure by the coral for processes like calcification when conspecific neighbors buffer the local seawater chemistry (Erez et al. 2011). Future studies should incorporate both respiration and calcification in the study design to determine if reduced respiration does indeed benefit coral calcification under stressful environmental conditions.

Many marine and aquatic organisms experience density-dependent metabolic suppression (i.e., negative relationship between metabolism and the number of nearby conspecifics), but the mechanisms leading to this relationship are debated (DeLong et al. 2014; Yashchenko et al. 2016; Ghedini et al. 2017; Lovass et al. 2020). For example, gregarious damselfish have been shown to release chemical cues that induce a "calming effect", which reduces overall oxygen uptake of the group (Nadler et al. 2016). Phytoplankton can decrease both photosynthesis and respiration with increasing conspecific density as a possible adaptive strategy to increase competitive ability (Malerba et al. 2017). In bryozoans, a sessile and colonial marine organism, food-limitation and water-borne chemical cues may be important mechanisms leading to metabolic suppression while with conspecifics (Lovass et al. 2020). Further, changes to the abiotic environment, such as flow and/or oxygen availability, as a result of increased conspecific density have also been shown to reduce metabolic rates in gorgonians (Kim and Lasker 1997) and bryozoans (Ferguson et al. 2013).

In the context of our study, we highlight two mechanisms that could explain the suppression of SGD effects by conspecific corals: (1) intraspecific competition between *P. rus* individuals is suppressing the increase in photosynthesis from SGD input via competition for resources (i.e., nutrients or CO_2 for photosynthesis), further suppressing respiration due to reduced tissue O_2 concentrations. The congener *Porites cylindrica* has been shown to take-up nitrate at a rate of 34 nmol cm^{-2} d^{-1} at a concentration of 2 µmol L^{-1} nitrate (Tanaka et al. 2006), a concentration slightly higher than what we see at our SGD site. Using this uptake rate and the size of *P. rus* in our experiment, the corals could have the capability to reduce the nitrate concentration by ~ 0.68 µmol L^{-1} d^{-1} if no new nutrients were being added to the system. Since SGD at the site is continuously supplementing the reef with exogenous inorganic nitrogen and CO_2, it is less likely that intraspecific competition for resources is the mechanism by which conspecific neighbors suppress the positive metabolic effects of SGD. Therefore, we posit that (2) conspecific corals could buffer the nearby pH range through their metabolism and by creating a microhabitat refuge that reduces groundwater influx, thus suppressing the focal coral respiration and further reducing photosynthesis. A prior study showed that corals can increase their local pH environment by ~ 0.15 pH units during the day under ambient conditions and by nearly 0.2 pH units under nitrate concentrations that are commonly found in SGD (Silbiger et al. 2018), which could help alleviate the low pH conditions as a result of SGD. Further, a study focused on *Pocillopora* in Mo'orea showed that conspecific interactions may alleviate the negative effects of low pH environments on coral metabolism, possibly by increasing water retention within the coral branches (Evensen and Edmunds 2016, 2017). The possible refuge created by conspecific corals decreases the need for elevated respiration, reducing energy expenditure by the coral, and decreasing photosynthesis via reduced tissue CO_2.

The heterospecific neighbor treatment did not have measurable effects on the focal coral for any of the response variables, indicating that heterospecific neighbors neither buffer from, nor exacerbate, the effects of SGD on coral physiology, at least in the short-term. Therefore, while having conspecific neighbors mediates the effect of acute SGD exposure by suppressing metabolism, having a *P. acuta* neighbor or a dead skeletal neighbor is similar to having no neighbor present. The absence of a difference between the no neighbor and the heterospecific treatments could be dependent on the species or morphology of the heterospecific neighbor, likely due to differences in physiological responses of species to SGD biogeochemistry. Likewise, the dead skeletal neighbor treatment had no effect on the responses of *P. rus* to SGD, but this effect may have been different depending on the microbial community or algae that settled on the skeletal

fragments. However, in this study, this lack of difference between the no neighbor, dead skeletal, and heterospecific neighbor treatments represents that the biotic effects of the heterospecific and skeletal neighbors were not as strong as the effect of SGD biogeochemistry on *P. rus* responses.

While the results of this study indicate beneficial effects of SGD through increased nutrient concentrations and pH variability, the physiological responses of corals to SGD will depend on the composition and concentration of different biogeochemical parameters in the SGD, which can vary considerably between nearby watersheds and over time (Taniguchi and Iwakawa 2004; Nelson et al. 2015; Silbiger et al. 2020, 2023). For example, a previous study in Hawai'i showed a nonlinear response to SGD, where SGD increased growth rates of a massive *Porites* species at low to moderate SGD input (0–4% SGD) but decreased growth rates at high SGD input (>4% SGD), thought to be due to salinity stress (Lubarsky et al. 2018). Additionally, studies highlight that nitrogen species can have varying impacts on coral health, where nitrate addition had a stronger negative effect on coral susceptibility to bleaching than urea (i.e., ammonium) (Burkepile et al. 2020). Notably both nitrate and ammonium are both common in the SGD (Silbiger et al. 2023), but the concentrations of ammonium likely vary with levels of human influence.

Seasonality could also modify the relationships seen in the current study. Interestingly, a six-week study on *P. rus* at our same study site in Mo'orea, but conducted during the rainy season (February–March) when SGD fluxes are highest, showed a negative effect of SGD on coral growth (Barnas et al. 2024). The present study was conducted during the dry season (August), with the weekly cumulative rainfall ranging between 0 and 14 mm in the eight weeks leading up to and during the experiment (Washburn and Brooks 2022), as well as during a large offshore wave event. Low precipitation and large waves are two factors that reduce the amount of SGD entering the coastal reefs because SGD flow is dependent on the hydraulic gradient of the aquifer (Dulaiova et al. 2010). The differences in responses of the same coral genera across sites and seasons highlights the context dependency of SGD-coral interactions.

Notably, the length of exposure to SGD may also affect the results. The length of the current experiment was limited to two weeks due to logistical constraints from COVID-19, which was enough time to see significant changes in the physiological responses measured in this study and is a similar duration to time points in other studies that have shown an effect of environmental conditions on coral physiology and/or survivorship (Nordemar et al. 2003; Yap 2004; Ezzat et al. 2015; Comeau et al. 2016; Fox et al. 2021). Indeed, chronic exposure to the SGD biogeochemistry may have altered the results. Regardless of the exposure time, our results align with previous findings that small to intermediate amounts of SGD are beneficial to corals, while high concentrations are detrimental (Lubarsky et al. 2018; Barnas et al. 2024).

Studying the ecological effects of SGD on coral reefs allows us to gain a better understanding of how coral physiology responds to multivariate shifts in seawater biogeochemistry, including pH and nutrient concentrations, along a chronic natural gradient. As SGD shifts the biogeochemistry and thermal environment of coastal seawater (Nelson et al. 2015; Knee et al. 2016; Hagedorn et al. 2020; Silbiger et al. 2020), the effect of SGD on corals could either exacerbate or buffer the effects of other environmental stressors, by decreasing seawater temperature (Utsunomiya et al. 2017), stimulating community metabolism, (Silbiger et al. 2020), or directly lowering pH (Cyronak et al. 2014). SGD is globally present (Santos et al. 2021) and the effect of SGD on seawater biogeochemistry and ecosystem responses will vary due to differences in the groundwater sources and locations (Silbiger et al. 2020, 2023). The current study shows that the type of neighbor around a coral can also alter the response of coral metabolism to SGD input. Multivariate shifts in environmental conditions with climate change (Harley et al. 2006; Stott 2016) are causing worldwide changes in coral reef community composition (Hughes et al. 2003, 2018). As communities change with the environment, this can shape and alter the frequencies and types of biotic interactions that organisms experience (Tylianakis et al. 2008), thereby further mediating coral physiological response to environmental conditions.

Availability of data, material, and code

All data and code are available on GitHub at https://github.com/njsilbiger/Neighborhood_effects_and_SGD and Zenodo https://zenodo.org/records/14262764.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00442-024-05660-6.

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Author contributions JRK and NJS conceived and designed the experiments, JKR and DMB performed the experiments, JKR and NJS wrote the manuscript, all authors edited and approved the final draft.

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Declarations

Conflict of interest We declare no conflict of interests.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors. Research was completed under permits issued by the French Polynesian Government (Délégation à la Recherche) and the Haut-commissariat de la République en Polynésie Française (DTRT) (Protocole d'Accueil 2005–2022).

Consent to participate N/A.

Consent for publication N/A.

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