

Coral reef benthic community structure is associated with the spatiotemporal dynamics of submarine groundwater discharge chemistry

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Abstract

Submarine groundwater discharge (SGD) is an important transporter of solutes and fresh water in coastal systems worldwide. In high island systems with a mixed semidiurnal tidal cycle driving SGD, coastal biogeochemistry is temporally and spatially variable. Past studies have shown that SGD covaries with the local species composition, diversity, and richness of biological communities on a scale of meters. Empirical orthogonal function analyses (EOF)—a method analogous to principal components analysis which finds spatial patterns of variability and their time variation period—were used to define both the spatial and temporal variation in SGD using spatially resolved time series of salinity. The first two EOFs represented variability at the tidal 12-h period and the daily 24-h period, respectively, and were responsible for more than 50% of the SGD-derived salinity variability. We used the first two EOFs to explore spatiotemporally explicit patterns in SGD variability and their relationships with benthic community structure in reef systems. Distance-based linear models found significant relationships between multivariate community structure and variability in SGD at different periods. Taxa-specific logistic regressions showed that zoanths and turf are more likely to be present in areas with high tidally driven SGD variability, while the inverse relationship is true for the invasive rhodophyte *Acanthophora spicifera*, calcifying macroalgae, the native rhodophyte *Pterocladia* sp., the cyanobacteria *Lyngbya* sp., and the invasive chlorophyte *Avrainvillea amadelpha*. These results show that benthic communities vary with respect to SGD derived salinity at the scale of hundreds of meters resulting in spatially heterogeneous biotic patches.

Submarine groundwater discharge (SGD) has been recognized as an important source of inorganic nutrients and fresh water in marine systems (Burnett et al. 2006; Zhang and Mandal 2012). This is especially true in volcanic high island systems surrounded by oligotrophic waters (Moosdorf et al. 2015). Most of the literature concerning SGD has been focused on characterizing its solutes and chemical composition, with the implication that these distinct water masses can be important vectors for inorganic nutrients, organic matter, metals, microbes, and pharmaceuticals (Nelson et al. 2015; Richardson et al. 2017b). However, fewer studies have looked at the impacts of SGD on coastal communities.

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The temporal delivery of SGD-derived solutes in a system that is tidally driven sees high fluxes of SGD at low tide, when there is weak hydrostatic pressure on the seeps, and low fluxes at high tide with more hydrostatic pressure on the seeps. Additionally, SGD in island systems has a large freshwater component with higher inorganic nutrient concentrations relative to the surrounding coastal water (Burnett et al. 2006; Moosdorf et al. 2015). This cyclical delivery of SGD with geochemical properties that are very different from coastal waters can occur at multiple time points throughout the day in a semidiurnal tidal system. In coral reef communities, it is often the interaction of persistent and multiple synergistic disturbances that cause stable community phase shifts (McClanahan et al. 2002). The different stressors that come with SGD and the chronic mode of its delivery causes reef systems to be vulnerable to stable ecological transitions to algal-dominated states (Houk et al. 2014).

The composition and abundance of the algal assemblage on a reef with SGD depend on which species can thrive in this specific chemical and physical environment (La Valle

et al. 2019). Marine primary producers have an optimal range of nutrient concentrations and salinity for growth and production. Both of these environmental variables control major physiological functions; salinity drives osmotic and solute regulation (Wiencke and Bischof 2012), while nutrient concentrations drive uptake rates and productivity (Thomas and Cornelisen 2003). Salinity in coastal areas can affect survival and growth of benthic organisms directly (Telesh et al. 2013), while different nutrient regimes (i.e., concentrations and delivery) shift competitive dominance between species (Worm et al. 1999).

Shallow coastal waters with SGD undergo both nutrient load and salinity changes on small time scales (i.e., tidal, hourly) (Johnson et al. 2008). Functioning under this highly variable nutrient and salinity environment at this time scale requires fast acclimation or adaptation to wide ranges of chemical parameters. These rapidly changing environmental conditions can preferentially spur the growth of certain algal species. In areas where the nutrient concentration of coastal groundwater has been increased by changing land use (i.e., agriculture, residential, commercial), nutrient loading via SGD has been associated with macroalgal blooms and shifts in community composition (McCook 1999; Lyons et al. 2014).

SGD is an understudied driver of biological and physiological processes, despite its ubiquity on nearshore coral reefs. Current work on SGD and its effects on biological community structure focuses on microbial, phytoplankton, and meiofaunal communities. Recent studies have found that microbial (Lee et al. 2017) and phytoplankton communities (Troccoli-Ghinaglia et al. 2010) associated with SGD are distinct from control sites and that species diversity and richness patterns vary by community type and SGD-associated chemistry. Studies focused on meiofaunal community structure associated with SGD have found that areas within tens of meters of SGD show increased abundance of mollusks (Leitao et al. 2015) and polychaetes (Encarnação et al. 2015), while studies that have looked at macroalgal and seagrass community structure show decreased abundance and diversity in areas with SGD (Kantún-Manzano et al. 2018; La Valle et al. 2019). These studies show that SGD can shape the local species composition, diversity, and richness of biological communities, although few studies have explored this in tropical coral reef settings.

There is a gap in knowledge in the role of SGD delivery in structuring coastal communities. This is the first study to quantify the frequency of fluctuations in salinity associated with SGD as causal in structuring benthic communities. We use empirical orthogonal functions to define the spatial and temporal variability of SGD. This statistical technique, used predominantly in atmospheric sciences, allows us to quantify the most important periods of variability in SGD beyond the tidal cycle. Other studies have inferred that community structure differs in areas close to SGD, but this spatially and temporally explicit approach allows us to (1) quantify whether the delivery of SGD has an effect on the structure of benthic

communities and (2) identify the species most affected by the spatiotemporal delivery of SGD at the scale of hundreds of meters.

Maunalua Bay, located on the southeastern shore of O'ahu, has algal-dominated fringing reefs with localized, tidally modulated SGD. The fringing reefs have well-characterized and biogeochemically distinct SGD from each other close to the seeps (e.g., different inorganic nutrient concentrations, different carbonate chemistry) (Nelson et al. 2015; Richardson et al. 2017a; Lubarsky et al. 2018). The bay experiences a mixed semi-diurnal tidal regime such that the SGD fluxes vary on several cyclical temporal scales. Fringing reef sites throughout the bay are dominated by macroalgae, whose presence and abundance vary across the reef flat, providing an appropriate study site for the interaction of SGD with macroalgal benthic communities. Therefore, the objectives for this study are to (1) define patterns in the spatiotemporal variability of SGD across reef flats which experience complex changes in magnitude and period of SGD-related biogeochemistry using salinity as the main tracer for SGD, (2) assess whether multi-variate community structure is related to the SGD spatiotemporal patterns of variation, and (3) elucidate what taxa or functional groups are driving these relationships.

Methods

Site descriptions and SGD characterizations

The study sites are located along the southern shoreline of O'ahu, Hawai'i, in Maunalua Bay (Fig. 1A; 21.2743°N, 157.7492°W). The two study sites, Black Point (21.2586°N, 157.7899°W) and Wailupe (21.2756°N, 157.7624°W), are on the western side of the bay (Fig. 1B) and are macroalgae-dominated, with 50% and 15% fleshy macroalgal benthic cover at Wailupe and Black Point, respectively, from the shoreline to the reef crest. Coral cover is less than 1% at both of the sites and the main species found at these sites are *Porites lobata* and *Montipora* spp. Benthic cover is further described in Table S1. There is a close to conservative relationship between SGD-derived inorganic nutrients (nitrate, phosphate, and silicate) and salinity at Black Point and Wailupe (linear regressions statistics described in table 1 of La Valle et al. 2019, included as Table S2). SGD fluxes and nutrient delivery was described in detail in Holleman (2011), Nelson et al. (2015), Richardson et al. (2017a, b), Lubarsky et al. (2018), and summarized in La Valle et al. (2019). SGD rates are 128 m³ d⁻¹ m⁻¹ of coast at Black Point compared to 20 m³ d⁻¹ m⁻¹ of coast at Wailupe (Holleman 2011). Dissolved inorganic nutrient concentrations at Black Point average 190 μM NO₃⁻ and 3 μM PO₄³⁻ resulting in groundwater derived nutrient fluxes of 8902 mol NO₃⁻ d⁻¹ km⁻¹ shoreline and 238 mol PO₄³⁻ d⁻¹ km⁻¹ shoreline (Holleman 2011). At Wailupe, SGD inorganic nutrient concentrations average 68 μM NO₃⁻ and 2 μM PO₄³⁻, resulting in groundwater-derived nutrient fluxes of 1090 and 51 mmol d⁻¹ of NO₃⁻ and PO₄³⁻, respectively (Holleman 2011; Richardson

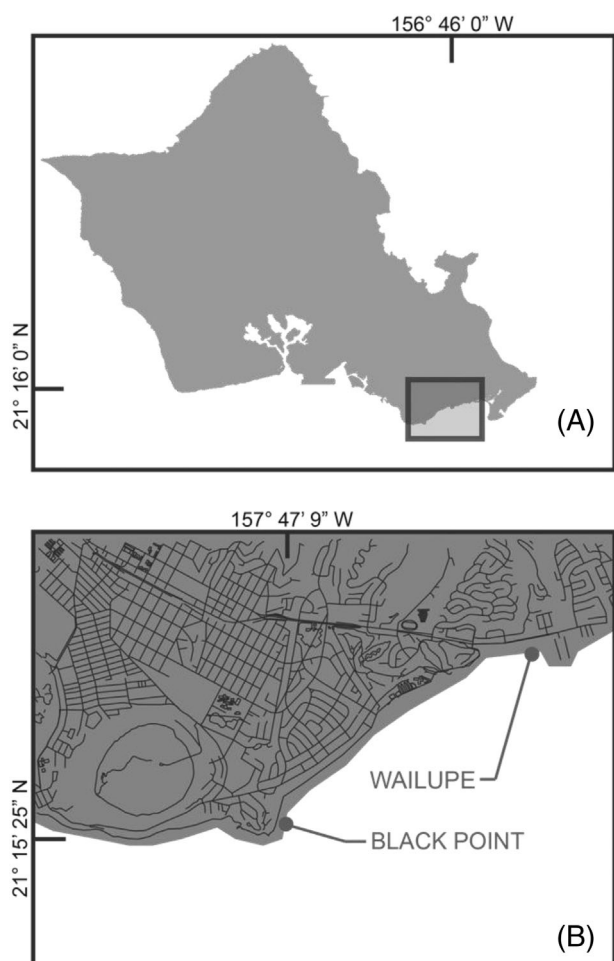


Fig. 1. Maps of the site locations. **(A)** Map of Oahu, Maunaloa Bay is enclosed in the gray box. **(B)** Close up of the coastline of the western half of Maunaloa Bay. Gray markers indicate Black Point and Wailupe.

et al. 2017a). Nutrient concentrations of SGD at both sites are at least 2 orders of magnitude higher than background levels. The SGD at both sites is high in inorganic N and P but approximately twice as concentrated at Black Point, possibly due to

the high density of nearshore cesspools in this area (Richardson et al. 2017b). Salinity and ^{222}Rn surveys of the bay's coastline indicated negligible surface water inputs (Richardson et al. 2017a) suggesting that SGD is the dominant source of nutrients and terrestrial freshwater inputs throughout the year, excluding rain.

Salinity time series and spatiotemporal analyses

Previous work has shown strong conservative relationships between salinity and SGD at both Black Point and Wailupe (Nelson et al. 2015; Lubarsky et al. 2018) therefore salinity was used as a proxy for SGD. Twenty-three autonomous salinity sensors (Odyssey Temperature and Conductivity loggers, $3\text{--}60\text{ mS cm}^{-1}$) were deployed in a sparse grid across each site (Fig. 2). The sensors were attached a few centimeters off of the benthos at Black Point for 30 d (29 May–29 June 2015) and for 27 d at Wailupe (4 April–21 May 2015) and took readings every 10 min. Two water samples were taken every week, synchronously with salinity sensor measurements, for the duration of the deployments at both sites and were analyzed using a Portasal Salinometer 8410A (accuracy 0.001) for quality control purposes and to check for sensor measurement drift. Data from rainy days ($n < 2$) at the sites were excluded from the analyses and time series were collated to restart at the same tidal height where the time series was interrupted. Fig. S1 shows the tidal charts for the salinity sensor deployments and benthic survey time periods. Previous ^{222}Rn surveys across the entire bay's coastline showed no freshwater input from surface runoff on non-rainy days. Thus, by taking out data from rainy days, we were left with SGD as the only source of freshwater and nutrients at both sites.

Empirical orthogonal functions (EOFs) were applied to the spatially indexed salinity time series at both sites. The continuous time series were inputted in the EOFs. EOFs were used to reduce dimensionality of the spatially explicit time series and to reveal the spatial structure of the time series data. EOFs are the spatiotemporal manifestation of principal components analysis (PCA) (Wikle et al. 2018). The output for EOFs

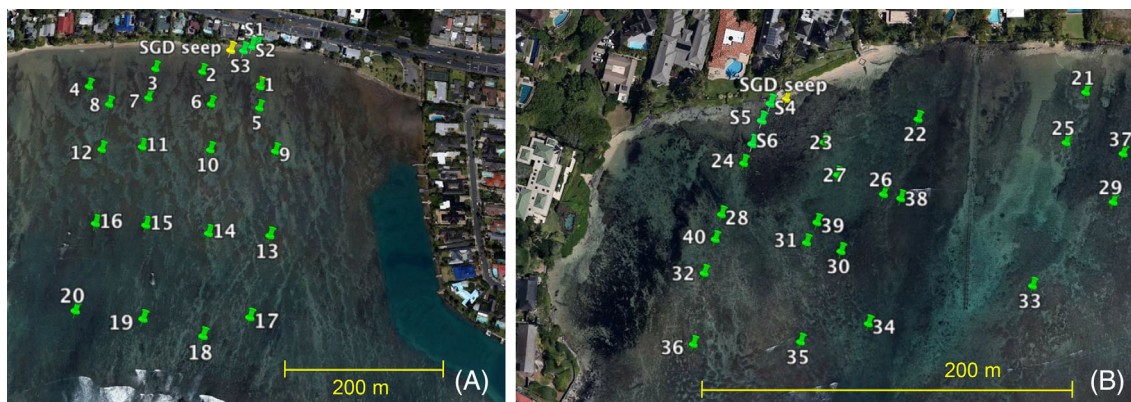


Fig. 2. Salinity sensor locations on reef flats **(A)** Wailupe **(B)** Black Point. Yellow marker indicates SGD seep in both locations.

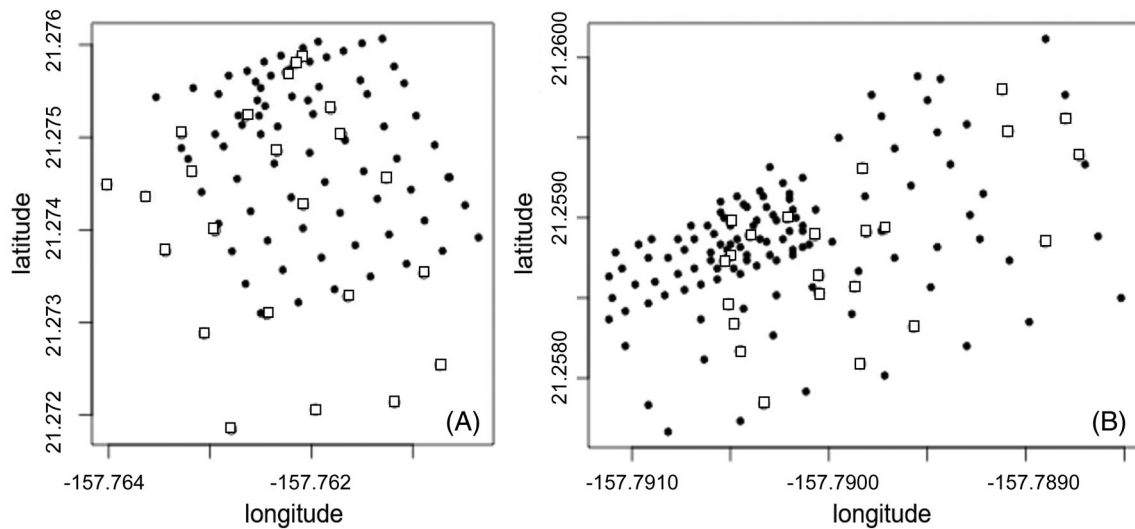


Fig. 3. Salinity sensor and benthic survey locations. Open squares represent salinity sensor locations and black filled-in circles represent benthic survey locations at (A) Wailupe and (B) Black Point.

includes a spatial map of loadings and an associated normalized principal-component time series for the salinity dataset obtained using a singular value decomposition of a space-wide matrix. The singular value decomposition was done using the function `svd` in the base library in RStudio (version 1.0.44, R Core Team 2016). The spectral density of the principal component time series was calculated for each EOF using the `spectrum` function in the `stats` library in RStudio (R Core Team 2016). The output for the spectral analysis includes a periodogram (Fig. S1), from which the most important period can be back calculated from the largest spectral peak (Wikle et al. 2018).

The salinity sensor locations (Fig. 2) and benthic survey areas (described in the next section) generally overlapped, but some benthic surveys (~25% of quadrat samples) fell outside of the bounds of the salinity sensor locations (Fig. 3). We used Kriging in order to extrapolate the EOF values for the benthic surveys outside the bounds of the EOF maps while accounting for spatial autocorrelation; we used the function `variogram` in the R library `spatial` (Venables and Ripley 2002) as well as the function `krige` applied as ordinary kriging in the R library `gstat` (Gräler et al. 2016).

Benthic surveys and community structure analyses

The spatial extent of the survey for each site was set to bracket a previously characterized gradient of SGD from seep to background oceanic waters (Nelson et al. 2015). The area covered for Black Point was 8.51 Ha (230 m offshore by 370 m alongshore) and 9.00 Ha (300 m offshore by 300 m alongshore) for Wailupe (Fig. 3). A grid was superimposed on the site from groundwater seep to reef crest and the grid was refined in order to have comparable sampling effort along the

gradient of SGD. Benthic algal surveys were done at the grid intersection points ($n = 97$ for Wailupe and $n = 115$ for Black Point). The survey consisted of 25 cm by 25 cm quadrats, where species-specific percent algal cover, species-specific invertebrate percent cover and counts, and substrate type were measured. All taxa were identified to lowest taxonomic level. Surveys were completed between May–August 2016. Although salinity time series were not taken synchronously with the benthic surveys, the data was taken during the same season and 1 year apart and therefore include data with similar mixing and swell trends. The most abundant biological communities at these sites are composed of perennials and their presence and absence does not change significantly during the year, but the species-specific biomass can change with season (La Valle et al. 2019). The tidal ranges that occurred during the period of time the salinity time series were taken were equivalent to the tidal ranges that occurred during the benthic surveys. Tide is the main driver for SGD delivery; the month-long time series of salinity encompassed spring and neap tides and all the tidal heights experienced by this reef flat from May to August 2016. Thus, the SGD flux and variability will be comparable to the time these surveys were taken.

The relative abundance data by taxa ranged from zero to one; it was square root transformed to down-weight ubiquitous taxa and to account for patchiness of reef species. Nonmetric multidimensional scaling (NMDS) was used to visualize community dissimilarity matrices (bray–curtis dissimilarity) using the `metaMDS` function in the R package `vegan` (Oksanen et al. 2017) in R.

We ran distance-based linear models (DistLM) on the distance matrix of community data by site using EOF1 and EOF2 as fixed effects (predictors) and substrate type as a random

Table 1. Benthic species (response variable) at the two sites used for logistic regressions.

	Wailupe	Both sites	Black Point
Benthic taxa	* <i>Gracilaria salicornia</i>	* <i>Acanthophora spicifera</i>	<i>Bryopsis pennata</i>
	* <i>Avrainvillea amadelpha</i>	* <i>Halimeda discoidea</i>	<i>Pterocladia</i> sp.
	CCA	* <i>Liagora</i> sp.	* <i>Jania</i> sp.
	* <i>Galaxaura</i> sp.	†Calcifying macroalgae	
	<i>Spyridia</i> sp.		
	Turf		
	Zoanthids		

*Calcifying macroalgal taxa included in the.

†Calcifying macroalgae group.

‡Invasive species.

effect was used to explore species composition to quantify variance in benthic community structure explained by EOFs (Zelditch et al. 2012). The DistLM enables us to quantify whether either or both EOF1s contribute significantly to patterns observed in the multivariate community structure while taking in account the variability in the substrate type (Zelditch et al. 2012). The function `adonis` in the R package `vegan` was used to create these models (Oksanen et al. 2017).

Species-specific relationships with variability in SGD

In order to characterize how presence or absence of each benthic taxon was related to SGD, logistic regression models were run at each site using the `glm` function in the `stats` package (R Core Team) with EOF1 as the predictors. Only species that appeared in at least three benthic samples were analyzed for univariate relationships to SGD. Table 1 shows a list of the benthic taxa and a list of substrate type used in the logistic regressions at Wailupe, Black Point, and both sites. All logistic regression p -values were controlled for false discovery rate ($\alpha = 0.05$) using the function `p.adjust` with the Benjamini Hochberg method in the R package `stats` (Benjamini and Hochberg 1995).

Results

Salinity time series and spatiotemporal analyses

EOFs were applied on the salinity time series datasets at both Wailupe and Black Point, resulting in EOF loading maps (Fig. 4A,C,E,G) and complementary normalized principal components (nPC) time series (Fig. 4B,D,F,H). EOF analyses yield as many EOF loading maps and nPC time series as the amount of time series inputted in the analysis. For our analyses, we inputted 23 time series for each site and therefore were given 23 EOF loading maps and corresponding nPC time series for each site. These are ordered by the amount of variability each EOF explains in the spatiotemporal data, with EOF1 explaining the most amount of variability. The first and second EOFs at Black Point explained 35.3% and 16.0% of the spatiotemporal variance, respectively. Similarly, at Wailupe

EOFs 1 and 2 explained 36.8% and 18.9% of the spatiotemporal variance, respectively. Beyond EOFs 1 and 2, the variability explained by the successive EOFs (i.e., EOFs 3–23) was <6% for each one and were not useful for physical interpretations in patterns of variability as described by a rule of thumb that states EOFs are considered to be significant if the 95% confidence intervals of the neighboring eigenvalues are not overlapping with another (North et al. 1982).

EOF1 shows the main source of variation as a 12.0–12.5 h period, indicating that tidal variation drives the majority of the salinity variability. The EOF1 loading maps for Wailupe and Black Point (Fig. 4A,E) show higher loadings close to the SGD seeps at both sites. As expected, SGD seeps and surrounding areas are the most variable with tide in terms of salinity, with high freshwater SGD fluxes at low tide at both sites. EOF2 time series show that an average 17.5% of the spatiotemporal variability occurs at a 24-h period (Fig. 4D,H). The EOF2 loading map shows higher variability on the middle of the reef (roughly equidistant from the SGD seeps and the reef crest).

Benthic surveys and community structure analyses

Benthic surveys showed that the main taxa found at Wailupe were *A. spicifera* (present in $n = 32/40$ samples, which were quadrats in this case, average relative cover $\mu = 9.85\%$), *Gracilaria salicornia* (present in $n = 29/40$ samples, $\mu = 13.1\%$), *Halimeda discoidea* (present in $n = 20/40$ samples, $\mu = 3.86\%$), and *Lyngbya* sp. (present in $n = 18/40$ samples, $\mu = 3.05\%$). Black Point had less macroalgal cover with the most abundant species being *Pterocladia* sp. (present in $n = 51/98$ samples, $\mu = 8.54\%$), turf (present in $n = 35/98$ samples, $\mu = 5.94\%$), and *Bryopsis pennata* (present in $n = 13/98$ samples, $\mu = 2.83\%$). Distance-based linear modeling showed that multivariate benthic algal community structure was significantly related to both EOF1 and EOF2 at Black Point and significantly related only to EOF2 at Wailupe (Table 2). These results indicate that community structure was related to both tidal and daily SGD (salinity) variability at Black Point and only related to daily

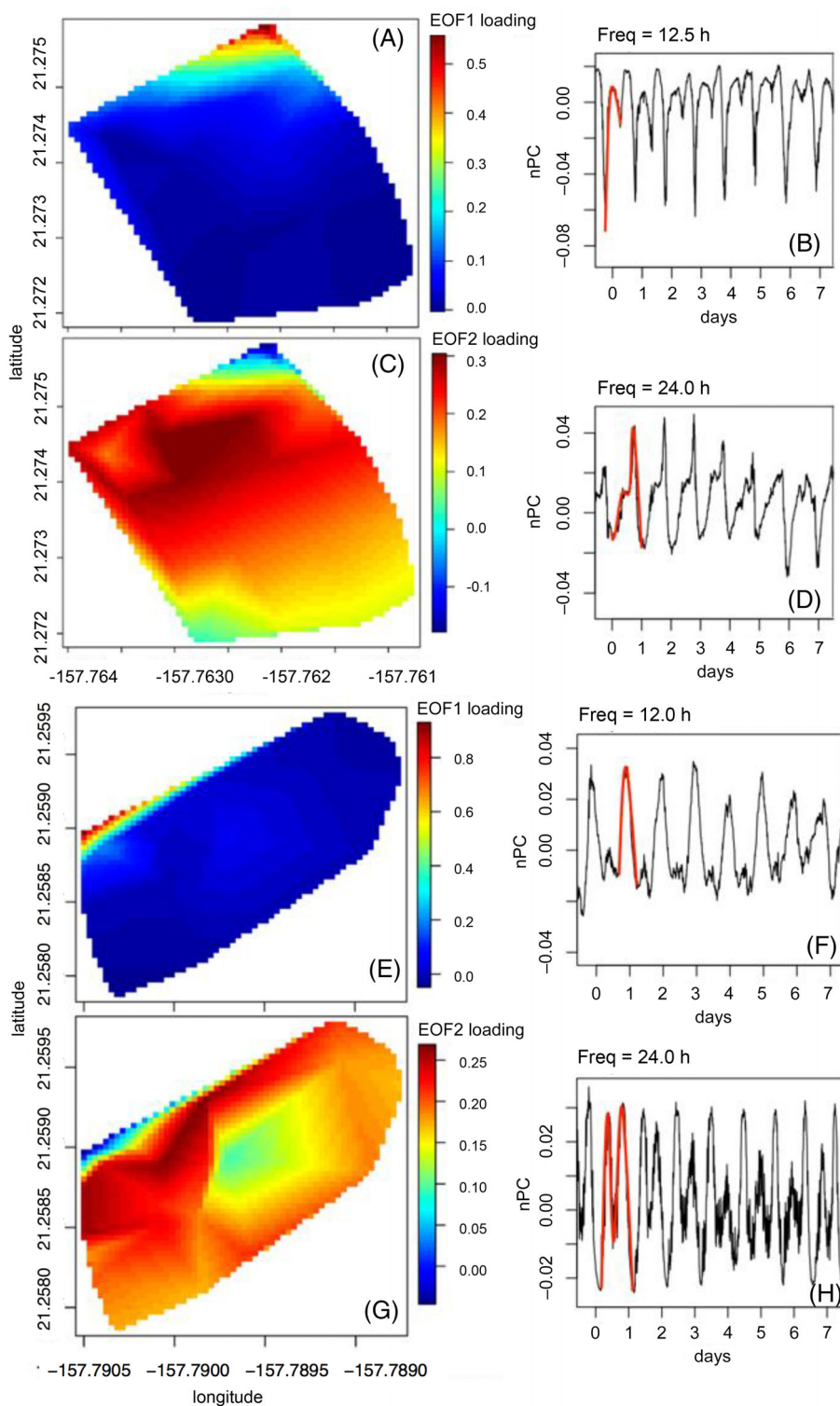


Fig. 4. EOF1 and EOF2 loading maps and associated time series showing important patterns of variance in SGD. **(A)** EOF1 loading map for Wailupe, **(B)** normalized principal components (nPC) time series for the first 7 d for EOF1 at Wailupe, **(C)** EOF2 loading map for Wailupe, **(D)** nPC time series for the first 7 d for EOF2 at Wailupe, **(E,F)** EOF1 loading map and nPC time series for Black Point and **(G-H)** EOF2 loading map and nPC time series for Black Point. The highest peak in the periodogram from each nPC (Fig. S1) was back calculated to the frequencies that were responsible for most of the variation in the time series. These frequencies are shown on top of the time series and a sample cycle of the time period is highlight in red on the time series plot.

Table 2. Model output and R syntax for DistLM.

Model and R syntax	Model output	EOF1	EOF2
Distance-based linear model for Wailupe	<i>F</i> stat	2.25	4.83
Adonis (distance matrix of community data at Wailupe ~ EOF1 + EOF2 + [1 substrate], distance = "bray", data = benthic community Wailupe)	<i>R</i> ²	0.0256	0.0556
	<i>p</i>	0.0790	0.00390*
Distance-based linear model for Black Point	<i>F</i> stat	3.10	5.15
Adonis (distance matrix of community data at Black Point ~ EOF1 + EOF2 + [1 substrate], distance = "bray", data = benthic community Black Point)	<i>R</i> ²	0.0252	0.0419
	<i>p</i>	0.0113 *	0.0001*

*To a *p* value < 0.05.

SGD variability at Wailupe. NMDS plots of community structure at the two sites are shown in Fig. S3 shaded by EOF1 and EOF2. NMDS1 is driven by the abundance of *G. salicornia* and NMDS2 is driven by *A. spicifera* and at Wailupe. At Black Point, NMDS1 and NMDS2 are driven by *Pterocliadiella* sp. and

turf, respectively. NMDS1 and NMDS2 were both significantly correlated with EOF2 (Fig. S3,D and Table S4) at Black Point. At Wailupe, NMDS1 was not correlated with EOFs but NMDS2 was significantly correlated with both EOF1 (Fig. S3A and Table S3) and EOF2 (Fig. S3,C and Table S3).

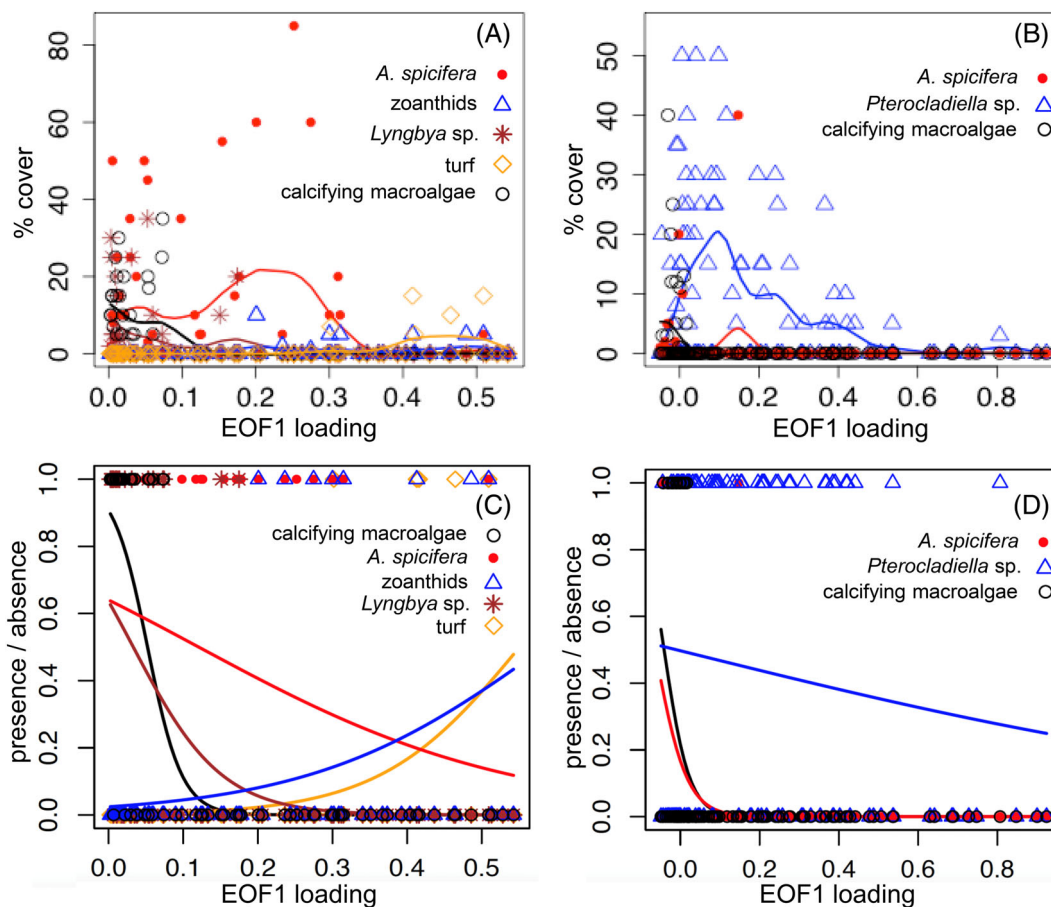


Fig. 5. Taxa specific visualizations of % cover with tidal variability (EOF1) and logistic regression plots. Only taxa with significant relationships to logistic regression models shown. Percent cover plots for Wailupe (A) and Black Point (B). Lines in a and B are smoothers color coded by taxa. Logistic regression plots for Wailupe (C) and Black Point (D).

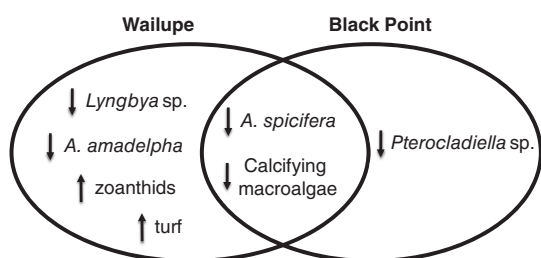


Fig. 6. Visualizations of taxa-specific significant relationships with EOF1 (a measure of SGD variability). Arrows refer to the direction of the relationship. The overlap of the two ellipses shows taxa with the same significant relationships at both sites.

Species-specific relationships with variability in SGD

Note that all logistic regressions that were significant for EOF1 were also significant for EOF2, therefore through all further discussion of significant relationships, note that all inverse relationships with EOF2 also stand. Calcifying algae and *A. spicifera* showed the same relationship with SGD at both sites; they were significantly more likely to be present in areas with low SGD tidal variability (EOF1) (Figs. 5 and 6 and Tables S2 and S3). Most species, with the exception of turf and zoanthids at Wailupe, were absent (0% cover) close to the SGD (Figs. 5A,C, 6, and Table S3). Turf and zoanthids at Wailupe were significantly more likely to be present in areas with high SGD tidal variability, while *A. amadelpha* and *Lyngbya* sp. were significantly more likely to be present in areas with low SGD tidal variability (Figs. 5A,C, 6, and Table S3). At Black Point, *Pterocliadiella* sp. was significantly more present in areas with low SGD tidal variability (Figs. 5B, D, 6, and Table S4).

Discussion

Characterizing the spatial and temporal variation in SGD using EOFs

Several studies have looked at the biogeochemistry associated with SGD in coral reef systems. These studies often look at multiple parameters of importance for a biological response such as coral growth, microbial, and phytoplankton community composition and abundance. To evaluate the variability of the biogeochemistry associated with SGD, these parameters are often measured during neap and spring tides within a day and across seasons. This is a sensible approach to give a sense of the range of variability experienced on a reef with SGD. Although most of the biogeochemical and physical variability on a reef with SGD is likely to be connected to tidal processes, this study looked at whether this was true and whether community composition could be related to SGD-variability at other temporal scales. Preliminary correlation analyses between EOF1, EOF2, salinity range, and distance from the SGD seep showed that for Wailupe, EOF1 is highly correlated with salinity range ($r = 0.94$, Fig. S4) and distance from the seep ($r = -0.76$, Fig. S4) though this is not the case for Black

Point ($r = -0.48$ for salinity range and $r = 0.42$ for distance from the SGD seep, Fig. S4). An NMDS plot of community composition at both sites shaded by distance from the seep also shows no obvious patterns or gradients in the community composition data (Fig. S5). This goes to show that even though these two reefs are only about 4 km apart and are similar in depth and daily breezes, there are nuanced complexities in the reefs' hydrodynamic processes that affect SGD delivery across each reef. For example, Black Point has several large lava rocks near shore which can affect current patterns, while Wailupe is a much more topographically homogenous reef without large boulders nearshore. Hence, the EOF analyses can more accurately reflect in-situ SGD-derived salinity variability experienced on these reefs using high frequency time series data that are able to collapse this variability into quantifiable periods that could have otherwise been missed by simple summary statistics.

In this study, we quantified the importance in the frequency of variation of salinity—inherently coupled with inorganic nutrients, lower temperatures, and lower pH—in structuring benthic communities on a reef in a spatially explicit way. This is important from a biological perspective because the taxa most abundant at these sites include macroalgae and sessile invertebrates whose presence and abundance depends on processes, which occur over timescales of weeks, months, and years. Therefore, it is important to quantify variation in the fluctuations in SGD-derived biogeochemistry on longer timescales than a day and to look at these effects with respect to the spatial delivery of SGD.

We used EOFs to characterize the spatial and temporal variability in SGD with the first two EOFs explaining more than 50% of the total variability of SGD-derived salinity at the two sites. In a highly dynamic coastal system, 50% accounts for a major contributor to the variability on this reef's salinity and nutrient regime. EOF1 is the tidal (~12 h period) signal of SGD flux resulting from the mixed semi-diurnal tide. EOF1 can be considered a measure of SGD influence at the site. This EOF1 map of variability (loading map, see Fig. 4A and E for examples) is usually what other studies try to represent with low tide measurements of conservative SGD proxies in a system with tidally modulated SGD. In a mixed semi-diurnal tidal regime, SGD gradients are mainly driven by one tidal cycle, low tide to next low tide (Fig. 4A–B,E–F). EOF2 shows that the daily, 24 h period, of variability is important on a large portion of the middle of the backreef (Fig. 4C–D,G–H).

At Wailupe and Black Point, waves breaking at the reef crest are the predominant flushing mechanism for oceanic waters. Wolanski et al. (2009) found that these reef flats have a residence time of about a day. Thus, EOF2 could show this coastal hydrodynamic effect of SGD staying on the reef flat over the course of a day due to daily water residence time. A time series with snapshots taken every 10 min shows that areas of low salinity are found on the reef flat during high tides (Fig. S6). Not all high tides show this pattern, which points to the

importance of running an EOF analysis to get quantitative values for the important periods of variability experienced by the reef flat in terms of biogeochemistry associated with SGD. Without EOFs, we would not have identified this important periodicity and would have not had the spatial information to look for patterns in community structure. Without this statistical analysis, we would not have been able to observe a correlation between daily variability in salinity and the spatial pattern in community structure. This approach is often used with ocean observing systems data to understand regional variability in a given parameter. We explored EOFs as a dimension-reducing tool used to account for the spatial and temporal complexity of the delivery of SGD and found that EOFs provided an effective and potentially very powerful way of summarizing the variability of SGD in space and time.

SGD and multivariate community structure

Multivariate community structure was significantly related to both tidal and daily signals (both EOFs) at Black Point and daily signals (EOF2) at Wailupe. Generally, we found that SGD lowers diversity in areas close (tens of meters) to the area of discharge; we recorded a higher number of taxa away from the SGD, while near the SGD source only 1–2 species were present. These patterns agree with past research in this same system (La Valle et al. 2019) and in seagrass communities (Kantún-Manzano et al. 2018). The literature and our findings suggest that SGD can shape the local species composition, diversity, and richness of biological communities. The direction of these changes may have to do with biological and physical processes such as turnover time, species initial presence or absence, and mobility. In terms of the biogeochemistry associated with SGD in high tropical islands, the main factors driving community composition can be (1) salinity, which is usually lower than surrounding coastal water, (2) nutrient concentrations, which can be orders of magnitude higher than background concentrations depending on land use, and (3) carbonate chemistry parameters such as pH values usually closer to 7 and variable DIC concentrations. Other parameters such as temperature (usually lower than surrounding coastal water) and the presence of trace metals and pollutants (e.g., pharmaceuticals, household chemicals) can have localized effects on coral health (Lecher and Mackey 2018) and microbial communities (Knee et al. 2008).

SGD and calcifying communities

At both sites, calcifying macroalgae were not found close to the groundwater seep, possibly due to the groundwater creating an inhospitable environment for the calcification of macroalgae. Groundwater enters the bay at pH values close to 7.36–7.62 (Richardson et al. 2017a, La Valle et al. in prep). At this pH, DIC concentrations are low in carbonate and bicarbonate ions. These ions are the building blocks for calcification and their low availability can inhibit calcification.

However, low salinity and limited hard substrate may also prevent colonization close to the groundwater seep.

Previous work by Lubarsky et al. (2018), at the same sites (salinity sensors for this experiment were placed in the same spatial grid as this coral growth experiment) where our study was done, shows that maps of *Porites lobata's* mean % change in buoyant weight correlates with EOF1 ($r = 0.50$, Fig. S7) and EOF2 at Wailupe ($r = 0.48$, Fig. S7). EOF1 was highly correlated to pH ($r = 0.70$, Fig. S7) at Black Point and to total alkalinity (TA) at both Wailupe ($r = -0.74$, Fig. S7) and Black Point ($r = -0.76$, Fig. S7). Groundwater at Black Point has higher TA values than surrounding seawater, while Wailupe groundwater has lower TA values than coastal seawater (Nelson et al. 2015; Lubarsky et al. 2018). The high correlation between EOF1 and TA at both sites is further evidence that EOF1 from the time series of SGD-derived salinity is a good proxy for the biogeochemistry of SGD.

The relationship between nutrients, temperature, and aragonite has been studied (Silverman et al. 2007) and measured for this site and related to community productivity (Richardson et al. 2017a) but has not been related to different benthic calcifying functional groups. The relationship between the associated temperature, salinity, nutrients, and pH of SGD and the calcification of benthic organisms is multifaceted. Interestingly, although it has been hypothesized that inputs of TA from SGD to coral reefs may assist calcification and drive increased coral cover by buffering against the negative effects of ocean acidification (Cyronak et al. 2014; Davis 2019), Lubarsky et al. (2018) found it unlikely that TA affected coral growth because growth patterns were similar across sites, despite opposite patterns in TA. Crook et al. (2012) also found lower abundances of reef building coral near low pH SGD springs. However, scleractinian corals can withstand low pH waters but experience lower tissue density and higher bioerosion rates (Crook et al. 2012; Lubarsky et al. 2018).

Future work should focus on the groundwater-based “calcification boundaries” of different calcifying functional groups such as crustose coralline algae, branching calcifying algae, and coral. This would require mapping carbonate chemistry at a fine resolution grid in a reef flat with groundwater, mapping the calcifying organisms at a fine scale, and then trying to resolve the parameters where the functional groups occur. A more direct approach would involve testing the limits for calcification experimentally with set concentrations of known SGD water chemistry. It would be interesting to pursue both coral growth experiments and the spatiotemporal analysis of variability with salinity in other reefs with SGD input to see whether there is a relationship between coral growth and variability of SGD-derived salinity and temperature.

SGD and benthic species distribution

Zoanths and turf were abundant close to the SGD (Fig. 5C). Phase shifts from coral to zoanths have been documented in Brazil (Cruz et al. 2015) as well as Hawai'i (Smith

et al. 1981; Amato et al. 2016). Additionally, phase shifts from coral to corallimorph-dominated reefs have also been documented on Palmyra Atoll (Work et al. 2008). Amato and colleagues (2016) found that coastal areas in Maui with SGD contaminated by wastewater was barren of corals and almost entirely dominated by colonial zoanthids. This study supports this positive relationship between zoanthids and SGD. In the same study, Amato and colleagues (2016) found an inverse relationship between fleshy macroalgae and turf. It may be possible that SGD supports turf indirectly by creating environments where only few macroalgae, mainly *G. salicornia* at Wailupe, are able to grow and live.

A. spicifera, the most ubiquitous macroalgal invader in Hawai'i's nearshore environments (Russell 1992), was found away from the SGD (Fig. 5C-D). Our past research presented consistent data on the distribution of *A. spicifera* with respect to SGD (La Valle et al. 2019). Interestingly, *A. spicifera* has increased photosynthetic capacity in nutrient enriched waters (Dailer et al., 2012) but its distribution is limited by temperature (positive growth at 25–27°C) and salinity (positive growth between 19 and 36) (Russell 1992). Past research at this site from the authors has found *A. spicifera* in areas with salinities above 27 and temperatures above 27°C (La Valle, unpublished). Both salinity and nutrient levels control major physiological functions—salinity drives osmotic and solute regulation (Wiencke and Bischof 2012), while nutrient concentrations drive uptake rates and productivity (Valiela et al. 1997; Thomas and Cornelisen 2003). Our results suggest that the salinity and low temperature associated with the SGD may override the nutrient effect on *A. spicifera* in this context, pointing to a physiological tradeoff between salinity and temperature tolerance and nutrient availability. The multiple chemical characteristics of SGD in tropical regions (i.e., low temperature, low salinity, high nutrients) may have differential effects on macroalgal species' distribution.

Among the other species that were most abundant with increasing distance from the SGD source were *A. amadelpha* and *Lyngbya* sp. (Fig. 5C). *A. amadelpha* is another main invasive macroalgae in Hawai'i (Smith et al. 2002; Cox et al. 2013) and a known ecosystem engineer (Littler et al. 2004). *A. amadelpha* is present in high abundance in Paiko Lagoon, on the eastern end of Maunalua Bay. The cover of *A. amadelpha* at Wailupe is much lower than at Paiko Lagoon currently and has maintained this low cover at this site for the past 15 years (McGowan 2004). It is possible that *A. amadelpha*'s cover is higher than the data suggests as it can be overgrown by native epiphytic algae and epifauna (Smith et al. 2002). *Lyngbya* sp. is a cyanobacteria that forms coarse filamentous tufts with toxins, lyngbyatoxin-a and debromoaplysiatoxin, that can cause swimmer's itch on contact (Capper et al. 2005). This finding contradicts past work, which has found increased cyanobacterial abundance close to SGD (Blanco et al. 2011). It is worth mentioning that this site has high *Lyngbya* sp. cover, not found on nearby reef flats. This may mean that although

Lyngbya sp. does not grow adjacent to the SGD, the SGD is still able to support the cyanobacteria's growth at a certain distance away from the SGD source, reflected in the covariation of its presence/absence with both EOF1 and EOF2. Future studies could identify the nitrogen sources to *Lyngbya* sp. using isotopic techniques in order to ascertain that the SGD is the main source of N and P to this alga.

At Black Point, *Pterocliadiella* sp. was mainly found away from SGD (Fig. 5D). *Pterocliadiella* sp. used to be uncommon in Hawai'i (Cox et al. 2013), and therefore it is surprising that it was found in such high abundance at this site. Like *Lyngbya* sp., it may be that *Pterocliadiella* sp.'s abundance could be supported by SGD in areas that experience more brackish and saline water masses due to the mixing of SGD and coastal water. A few studies have looked at the combined effects of different Cadmium concentrations and salinity treatments (Schmidt et al. 2015) on this genus but more experimental studies need to be done on this alga and its physiological tolerance to freshwater, high nutrient levels, and lower temperatures.

Future work, limitations, implications

The biogeochemical composition of SGD is highly variable and depends on the composition of the aquifer, residence time of groundwater, microbial community composition, and most importantly land use (agricultural, industrial, urban). The terrestrial portion of the coastal zone is an area with high human activity and can therefore have high gradients of contaminants that can have a large impact on the chemistry of SGD especially when it comes to pollutant, nutrient, and organic content (Burnett et al. 2006). Discharging groundwater interacts with this zone picking up dissolved constituents and continuously depositing them into aquatic systems. Although SGD biogeochemistry varies by watershed, it may be possible to generalize the effects of high inorganic nutrient loading and low salinity due to SGD for particular systems at the functional group or genus level in coral reefs. In our study, we saw SGD decreasing the diversity of benthic communities, creating different spatial distributions in calcifying communities, and supporting the presence and abundance of zoanthids and turf—changing the structure of these reef communities in a significant way.

At these two sites, we know SGD is the main source of freshwater. Autonomous salinity sensors are a cost-effective way to gather high-resolution spatial and temporal information across areas with groundwater discharge. This method has the potential to be useful in several types of nearshore or shallow environments and can easily be implemented along with biological surveys to look at spatial relationships between SGD and both individual taxa as well as multivariate community structure. Considering the ubiquity of SGD especially in high volcanic islands with associated reef systems, it is important for future work to focus on the groundwater-based “calcification boundaries” of different calcifying organisms such as

crustose coralline algae, branching calcifying algae, and coral. It is imperative for coral reef health and management that the effects of SGD on macroalgal communities at these sites is known, particularly given that the macroalgal blooms are often composed of opportunistic invasive species, which can cover and outcompete coral. As any ecological endeavor, these research questions should be pursued at various spatial and temporal scales that are relevant to the biological communities of interest.

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Conflict of Interest

None declared.

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