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Submarine groundwater springs are characterized by distinct fish communities

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Abstract

The inflow of terrestrial groundwater into the ocean is increasingly recognized as an important local source of nutrients and pollutants to coastal ecosystems. Although there is evidence of a link between fresh submarine groundwater discharge (SGD)-derived nutrients and primary producer and primary consumer abundances, the effects of fresh SGD on the productivity of higher trophic levels such as ichthyofaunal communities remain unclear. To further investigate this relationship, we sampled three sites inside a coral reef lagoon in Mauritius: One site entailing six distinct groundwater springs, a site highly influenced by freshwater influx through the springs, and a strictly marine control site. Using remote underwater video surveys, we found that fish abundances were significantly higher at the groundwater springs than at the other two sampling sites.Principal component analyses showed that the springs and the spring-influenced part of the lagoon were best described by elevated water nutrient loadings, whereas the control site was characterized by higher water salinity and pH. Macroalgae cover was highest at the control site and the springs. Herbivores and invertivores dominated the fish community at the springs, in contrast to generalists at the control site. At the spring-influenced site, we mainly encountered high coral/turf algae cover and high abundances of associated fish feeding groups (territorial farmers, corallivores). Our results provide evidence of a fresh SGD-driven relationship between altered hydrography and distinct fish communities with elevated abundances at groundwater springs in a coral reef lagoon. These findings suggest that the management and assessment of secondary consumer productivity in tropical lagoons should take into account the effects of groundwater springs.

KEYWORDS

biodiversity, coral reef, feeding groups, fish abundance, Mauritius, nutrients, submarine groundwater discharge

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1 | INTRODUCTION

Nutrient input to the coastal ocean is attributed mainly to terrestrial runoff and river discharge (Fabricius, 2005; Jickells, 1998). However, the discharge of fresh terrestrial groundwater into the ocean (fresh submarine groundwater discharge: fresh SGD) was shown at several locations to be a major local source of nutrients to coastal waters (Burnett, Bokuniewicz, Huettel, Moore, & Taniguchi, 2003; Knee & Paytan, 2011; Slomp & Cappellen, 2004). At some locations, fresh SGD can exceed average annual river discharge (Oehler et al., 2018) and nutrient budget (Santos, Burnett, Dittmar, Suryaputra, & Chanton, 2009; Slomp & Van Cappellen, 2004; Sugimoto et al., 2017; Wong et al., 2013). Fresh SGD also bypasses estuary filters, and therefore, its impact on coastal oceans is different compared with river discharge (Burnett et al., 2003). In general, fresh SGD may contain higher nutrient, carbon, and metal concentrations than rivers and thus act as a major nutrient source for various coastal ecosystems, such as coral reefs, estuaries, seagrass beds, and other near coastal communities (Johannes, 1980; Johannes & Hearn, 1985; Moore, 2010; Paytan et al., 2006; Santos et al., 2009).

Despite their high productivity, coral reefs are generally oligotrophic ecosystems (Sammarco, Risk, Schwarcz, & Heikoop, 1999). Concentrations of inorganic nitrogen and phosphorous in reef waters typically do not exceed 1 and 0.3 μM, respectively (Hallock & Schlager, 1986). This suggests that overall productivity in coral reefs is nutrient-limited at large (Harpole et al., 2011). Despite individual studies that show impacts of fresh SGD on coral reefs (Lubarsky, Silbiger, & Donahue, 2018; Richardson, Dulai, Popp, Ruttenberg, & Fackrell, 2017), the implications of fresh SGD-derived nutrient influx to coral reefs are as of yet not fully assessed. Still, multiple studies in temperate lagoons have shown the process' significant ecological impact and provided evidence for a positive relationship between fresh SGD-derived nutrients and primary production (Andrisoa, Stieglitz, Rodellas, & Raimbault, 2019; Gobler & Sañudo-Wilhelmy, 2001; Johannes, 1980; Miller & Ullman, 2004; Sugimoto et al., 2017; Utsunomiya et al., 2017; Waska & Kim, 2011).

Abundances in benthic invertebrates, such as bivalves, polychaetes, and nematodes, also show positive correlations with fresh SGD (Bussmann, Dando, Niven, & Suess, 1999; Dale & Miller, 2008; Encarnação et al., 2015; Hwang, Kim, Lee, & Oh, 2010; Kang & Kim, 2006; Lee, 1993; Miller & Ullman, 2004; Ouisse, Riera, Migné, Leroux, & Davoult, 2011; Piló et al., 2018; Silva et al., 2012; Zipperle & Reise, 2005). Miller and Ullman (2004) therefore hypothesized that polychaetes act as trophic link between fresh SGD-driven nutrient enrichment, elevated benthic microalgae production, and worm-feeding predators such as fish. In accordance, significant higher densities and biomass of mollusks and crustaceans, as well as higher densities of invertivore fishes, have been observed in coastal areas with high SGD (Hata, Sugimoto, Hori, Tomiyama, & Shoji, 2016; Shoji & Tominaga, 2018; Utsunomiya et al., 2017).

Historical ethnographic studies have often suggested that fish seem to thrive around submarine springs (Moosdorf & Oehler, 2017). Past studies also propose that fresh SGD may promote fisheries production in temperate coastal systems (Burnett, Wada, Taniguchi, Sugimoto, & Tahara, 2018; Shoji & Tominaga, 2018) and suggest higher fish abundances near a submarine spring in the tropics (Starke, Ekau, & Moosdorf, 2020). As elevated growth will over time translate into elevated population sizes in marine teleosts (Retzel, Hansen, & Grønkjær, 2007), one might argue that higher food abundance and physiologically beneficial environmental conditions around sources of fresh SGD allow fish to prosper (Bœuf & Payan, 2001; Di Franco et al., 2019; Jarrold & Munday, 2019). Two recent studies showed a positive effect of fresh SGD on fish growth: Fujita et al. (2019) explained a positive relationship between fish growth and fresh SGD-derived nutrient loadings with elevated primary producer and prey abundances, whereas Lilkendey et al. (2019) proposed that a combination of physiological effects caused augmented growth. In any case, all past results imply a link between acidic nutrient-rich fresh SGD and elevated abundances of marine fishes.

The present study aimed to assess the impact of submarine groundwater springs on the productivity of a tropical lagoonal ecosystem, primarily focusing on the abundance and community structure of coral reef-associated fish. To investigate the relationship between groundwater springs and the abundance as well as the diversity of fishes, we used remote underwater video surveys within a coral reef lagoon in Mauritius, Indian Ocean. We also collected baseline data on water salinity, pH, and nutrient concentrations, benthos composition, and total suspended solids to determine the effects of fresh SGD on lagoonal hydrography.

2 | MATERIALS AND METHODS

2.1 | Sampling site

Mauritius is an island (area: 108 km^2) of volcanic origin situated ca. 900 km east of Madagascar and ca. 2,000 km from the east African coast in the southwestern Indian Ocean (Figure 1a). Mauritius is inhabited by a population of 1.2 Mio (2016) and visited by 1.4 Mio tourists yearly (Martial & Boolakey, 2016; Martial & Fatha Mahomed 2019). The sugar industry is still a major agricultural sector in Mauritius, with sugarcane plantations occupying 85% of cultivated area, representing ca. 40% of the country's total area (Kwong, 2005). A high amount of sugar production, increasing tourist numbers, poorly developed wastewater management, and sewer systems are thought to be the major sources of anthropogenic nutrients to coastal waters (Ramessur, 2002). Trou aux Biches is a small town on the northwestern coast of Mauritius, where six distinct groundwater springs discharge in the southern part of the lagoon (Figure 1b,c). The groundwater springs in Trou aux Biches are connected to the aquifer of the Northern Basin, covering an undulating area of 200 km^2 generally below 100 m of elevation (Saddul, 2002). Highly permeable recent lavas underlie the greater part of the basin, and the surface is mainly comprised of sugarcane plantations inland (Proag, 1995) and hotels, resorts, and bungalows in the nearshore area.

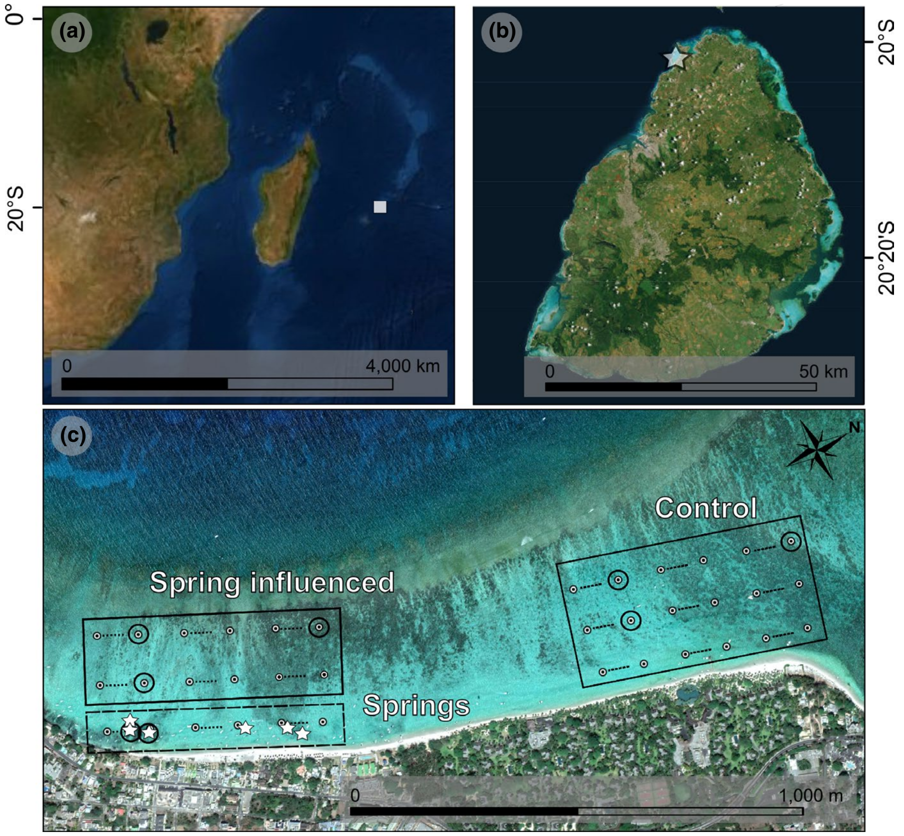

FIGURE 1 Mauritius in the southwestern Indian ocean (a), and the hollow star marks the location of Trou aux Biches lagoon (b). The lagoon was split into the sampling sites "springs," "spring-influenced," and "control" (boxes). White stars indicate the groundwater springs. Nutrient sampling stations are indicated by dotted circles, benthic transects by dashed lines, and camera positions by hollow circles (c)

2.2 | Environmental parameters

The field survey was conducted from October to December 2017, during the early summer months in Mauritius. Salinity was measured in situ using a handheld probe (WTW Cond 3310, TetraCon 325). Water samples were taken directly from the spring area (n = 6), the spring-influenced part in the south (n = 12), and the control (n = 18) in the north part of the lagoon. Additionally, water samples were obtained from two oceanic stations offshore the SGD-influenced and control part of the lagoon (not on map). Water pH was determined in the laboratory using a stationary pH probe (Ohaus Starter 2100). Water samples for nutrient analysis were taken from a depth of 50 cm using a peristaltic pump, filtered, and stored frozen until measurement.

Nutrient analysis of water samples was conducted in the laboratory at the Mauritius Oceanography Institute in Albion, Mauritius. Nitrite, nitrate, phosphate, and silicate were determined using standard methods with a discrete analyzer (SYSTEA Easychem Plus) equipped with a 5 cm absorbance reading unit. The analytical procedures were adapted from Grasshoff, and Koroleff (1983). For nitrite (NO_2^-) determination, sulfanilamide was added to 700 μl of seawater sample to obtain a diazo compound. Under the addition of *N*-(1-naphthyl) ethylenediamine, the compound formed a pink complex. Colorimetric measurements were taken at 543 nm wavelength against a reference of artificial seawater prepared in deionized water (Rider & Mellon, 1946).

For nitrate (NO_3^-) determination, the nitrite content of the sample was determined as described above, followed by a nitrate reduction and a subsequent second determination of nitrites. Starting nitrite concentrations were subsequently subtracted from the NOx concentrations to obtain the nitrate concentration of the sample. Nitrate reduction was done manually on a column filled with copper-coated cadmium pellets activated by a 10 M solution of sodium nitrate prepared in ammonium chloride buffer. The samples were poured into the burette and let pass through the cadmium pellets. The nitrite content of the captured sample was measured in the discrete analyzer. After ca. 5 ml passed through the pellets, 1.5 ml of the sample was captured in 1.5-ml microcentrifuge tubes for subsequent analysis in the discrete analyzer.

For the determination of phosphate (PO_4^{2-}) concentrations, ammonium molybdate and potassium antimony tartrate were added to 700 μl of seawater sample to form an antimony–phospho-molybdate complex. This complex was reduced to an intensely blue-colored molybdenum complex by the addition of freshly prepared ascorbic acid. The absorbance was measured at 880 nm wavelength against a reference of artificial seawater prepared in deionized water.

Silicate (SiO_4^{4-}) was determined by adding ammonium molybdate to 700 μl of seawater sample. Oxalic acid was added to eliminate phosphate interference. The sensitivity of the analysis was increased further by a reduction in the silicomolybdic acid using ascorbic acid to procure "molybdenum blue." The absorbance was measured at wavelengths of 810 and 660 nm against a reference of deionized water.

Benthic coverage was determined using 50-m point intersect transects (Hill & Wilkinson, 2004). All transects were video-recorded (Canon Powershot G16) for subsequent analysis. Transect videos were evaluated in the laboratory, recording benthic makeup every 50 cm ($n = 100$) using classifications by English, Wilkinson, and Baker (1997). Total suspended solids (TSS) were sampled in triplicates along 100 m horizontal transects at the springs, the spring-influenced part of the lagoon, and at the control site using a 20-µm plankton net. Per transect, a total of 4.91 m^3 water (net diameter 25 cm) were filtered. All samples were kept cold in a portable cooling box and frozen at −20°C in the laboratory for subsequent analyses. Frozen TSS samples were defrosted, filtered on a pre-weighted microfiber filter (Whatman GF/F), dried, and weighed again.

2.3 | Fish community

To evaluate fish abundances, Go-Pro Hero 4 video cameras were weighted with 1 kg lead and placed at two stations close to the springs and at three stations at the spring-influenced site as well as at the control site (Figure 1c). We have refrained from placing cameras close to shore at the control site to avoid their theft through tourists. Videos were taken between 9:00 and 16:00 to ensure the capture of diurnally active fishes (English et al., 1997). After each placement, the first 15 min of video was disregarded to allow the fish community to recover to a more natural state after placing the cameras. The first 130 min of video footage was split into three 20-min segments (15 min between segments). Each segment was further divided into 40 single frames (one each 30 s) and evaluated using the MaxN/MIN count method (Cappo et al., 2003; Wells & Cowan, 2007). This method records the maximum number of each species observed at any one time in each of the single frames and yielded nine observations (three stations × three replicates) per sampling site. Videos were used to (a) compose a list of all fish species occurring in the lagoon and (b) determine abundances.

Diversity was assessed using three commonly used metrics: species richness, Shannon's diversity index H', and Pielou evenness J'. Functional groups were used to evaluate changes in the fish community structuring. This method is increasingly used in coral reef studies to understand the effects of disturbances on ecosystem functioning (Graham et al., 2006). Groupings are based on similar ecosystem functioning disregarding taxonomic relationships (Bellwood, Hughes, Folke, & Nyström, 2004). Fish species were classified into feeding groups indicating feeding behavior and dietary composition (Pratchett, Hoey, Wilson, & Messmer, 2011). Herbivores and corallivores were further classified using definitions by Green and Bellwood (2009) and Cole, Pratchett, and Jones (2008), respectively.

2.4 | Statistical analyses

Statistical analyses were carried out using JMP (Pro 14.3, SAS Institute Inc., www.jmp.com). Nutrient concentrations and benthic coverage data were log + 1-transformed and normalized before a principal component analysis (PCA) based on Euclidian distance was performed to test for significant differences between lagoons and sites. To account for pseudoreplication in our dataset, we used one factorial repeated-measures analyses of variances (RM-ANOVAs) to identify differences in TSS, fish abundance, and diversity indices between sampling sites (Millar & Anderson, 2004). Depending on skewness, non-normal data were either log- or square root-transformed (Underwood, 1997). Subsequently, a Bartlett test was applied to test for homogeneity of variances. We tested the response variables against site (springs, spring-influenced, control) as the main effect and replicate as a random effect nested within sampling station. Significant model results were further analysed using Tukey's honest significance difference (HSD) post hoc tests.

To visualize differences among fish communities across sites, non-metric multidimensional scaling (NMDS) was applied based on the rank order of the Bray–Curtis similarities using PRIMER-e v7 (Clarke & Gorley, 2015). Fish abundance data were fourth root-transformed to reduce the values and influence of highly abundant species while also allowing midrange to rare species to influence the analysis (Clarke, 1993; Clarke & Green, 1988; Field, Clarke, & Warwick, 1982). The aptness of the NMDS was determined through the stress factor by which low values express a higher variance (Warwick & Clarke, 1991). Relative grouping of sampling stations was validated using cluster analysis. A similarity percentage (SIMPER) analysis with pooled replicates was used to examine which secondary feeding groups and fish species contributed to similarities within sites. Differences between sites were examined using two-way analysis of similarities (ANOSIM) with station nested within site (Clarke & Warwick, 1994).

3 | RESULTS

Water salinity and pH values were lower at the springs than at the spring-influenced site and again lower at the spring-influenced than at the control site. Average nutrient concentrations were generally higher at the springs than at the spring-influenced and control sites. The offshore station near the spring-influenced part of the lagoon exhibited lower salinity and pH values and higher nutrient concentrations when compared to the station offshore the control site (Table 1).

Principal component analyses were used to investigate spatially resolved differences in hydrography and benthic cover composition. Concerning hydrography, the PCA yielded three distinctive clusters among sampling stations (Figure 2a). The first principal axis (PC1) explained 57.9% of the observed variability and mainly separated the stations by water salinity, nitrate, silicate, and nitrite concentrations. Hydrography at the springs and the spring-influenced part of the lagoon was mainly described by positive PC1 loadings and thus by decreased salinity, elevated nitrate, and silicate concentrations. The second axis (PC2) separated stations according to water pH and

TABLE 1 Mean (±*SD*) salinity, pH, and nutrient concentrations (μM) for all three sites, control, spring-influenced, and springs within the Trou aux Biches lagoon and two offshore stations

Site	Salinity	pH	NO_2^- (μM)	NO_3^- (μM)	PO_4^{2-} (μM)	SiO_4^{4-} (μM)
Control	35.07 ± 0.14	8.45 ± 0.09	0.02 ± 0.00	0.15 ± 0.05	0.82 ± 0.06	1.85 ± 0.61
Spring-influenced	34.65 ± 0.18	8.44 ± 0.05	0.16 ± 0.27	1.09 ± 0.83	1.90 ± 0.12	6.24 ± 3.90
Springs	34.27 ± 0.35	8.30 ± 0.03	0.18 ± 0.06	3.00 ± 0.77	0.92 ± 0.33	12.50 ± 4.53
Offshore						
Control	35.50	8.35	0.02	0.06	0.81	0.95
Spring-influenced	34.80	8.42	0.04	0.69	1.01	3.40

phosphate concentrations and explained 24.5% of the observed variance.

Benthos composition showed only little clustering between sampled transects at the springs, the spring-influenced site, and the control site (Figure 2b). The first principal axis (PC1) explained 37.1% of the observed variability and mainly separated the sampled transects by their percentage cover in sand, coral, rubble, and turf algae. Benthic composition of transects in the spring-influenced part of the lagoon was mainly described by positive PC1 loadings and thus by elevated coral, rubble, and turf algae cover. Mean (±*SD*) coral cover was consequently markedly lower at the springs (0.3 ± 0.6%) and the control site (1.7 ± 2.1%) compared with the spring-influenced part of the lagoon (17.6 ± 15.3%). Mean turf algae cover was lower both at the control site (5.5 ± 4.0%) and the springs (12.0 ± 13.6%) compared with spring-influenced part of the lagoon (20.6 ± 18.1%).

Mean macroalgae cover, on the other hand, was markedly lower throughout transects at the spring-influenced part of the lagoon (2.4 ± 3.7%) when compared to the springs (18.8 ± 19.5) and the control site (14.5 ± 10.2%). The second axis (PC2) separated transects according to their cover in macroalgae, rock, and seagrass cover and explained 24.5% of the observed variances.

Total suspended solids (mean ± *SD*) were significantly higher at the spring-influenced site (0.76 ± 0.47 mg/L) when compared to the springs (0.61 ± 0.27 mg/L) and the control site (0.33 ± 0.25 mg/L; RM-ANOVA, $F_{(2, 14)} = 5.9444$, $p < .05$; Tukey's HSD post hoc test: $p < .05$).

In total, 1,709 individual fishes, representing 95 species from 28 families (Table 2), were recorded in Trou aux Biches lagoon. Out of these, 84 species from 26 families were included in sampled frames. At the spring-influenced site, as well as at the control site, significantly less individual fish were recorded when compared to the springs (RM-ANOVA, $F_{(2, 6)} = 24.8201$, $p < .01$; Tukey's HSD post hoc test: $p < .01$; Figure 3). Although we encountered differences in diversity metrics between sites, none were significant: Shannon's diversity index H' (mean ± *SD*) was highest at the control site (2.40 ± 0.92), followed by the spring-influenced part of the lagoon (2.42 ± 0.76), and lowest at the springs (1.33 ± 0.59; RM-ANOVA, $F_{(2, 6)} = 2.0214$, $p = .2133$). Evenness J' was highest at the control site (0.92 ± 0.11), followed by the spring-influenced site (0.76 ± 0.25) and the springs (0.48 ± 0.18; RM-ANOVA, $F_{(2, 6)} = 4.2714$, $p = .0702$). Most species were observed in the spring-influenced part of the lagoon (23.7 ± 6.82). Here, species richness was, therefore, higher than at the springs directly (15.9 ± 4.54) as well as at the control site (14.3 ± 6.56; RM-ANOVA, $F_{(2, 6)} = 1.7934$, $p = .2452$).

Cluster analysis and NMDS showed apparent clustering of fish community structure composition at the sampling stations for each site. In respect to secondary fish feeding groups, the control site was characterized by generalists, the spring-influenced site by obligate corallivores, territorial farmers, facultative corallivores, omnivores, and scrapers, and the springs by a high abundance of grazer/detritivores, piscivores, planktivores, and invertivores (Figure 4).

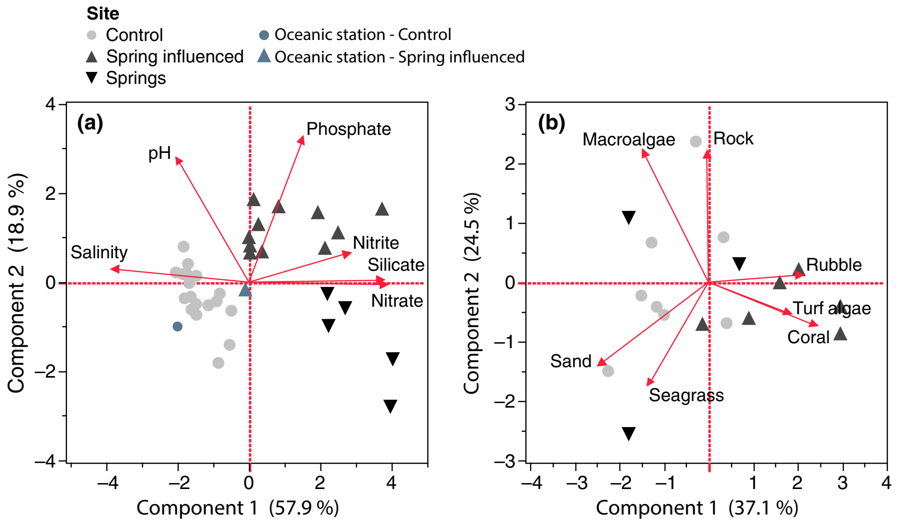

FIGURE 2 Principal component analysis on hydrochemistry (a) and benthic cover (b) at transects and stations located at the groundwater springs, at a site-influenced by fresh submarine groundwater discharge, at a control site, and offshore

TABLE 2 List of all recorded species and relative abundance (%) of families and species occurring in sampled video frames (all samples combined) within the three sites (control, spring-influenced, and springs) of the Trou aux Biches lagoon; § = species present in lagoon but not appearing in sampled video frames, FG = feeding group, H = herbivore, C = carnivore, Co = corallivore, O = omnivore; Gd = grazer/detritivore, Br = browser, Sc = scraper, Tf = territorial farmer, E = ectoparasite feeder, G = generalist, I = invertivore, Pi = piscivore, Fco = facultative corallivore, Oco = obligate corallivore, P = planktivore, x = species not recorded in sampled video frames

					Relative abundance of species		
Family	**%**	**Species**	**1. FG**	**2. FG**	**Control (%)**	**Spring-influenced (%)**	**Springs (%)**
Acanthuridae	10.71	*Acanthuridae* spp.	H	Gd	0.95	x	x
		Acanthurus nigricauda	H	Gd	x	0.46	x
		Acanthurus nigrofuscus	H	Gd	x	0.23	x
		Acanthurus triostegus	H	Gd	2.37	23.34	1.04
		Ctenochaetus binotatus	H	Gd	x	0.46	0.09
		Ctenochaetus striatus	H	Gd	7.11	3.43	1.60
		Naso unicornis	H	Br	0.47	0.69	x
		Zebrasoma desjardinii	H	Gd	1.42	x	0.09
		Zebrasoma scopas	H	Gd	x	0.12	0.00
Apogonidae	7.90	*Cheilodipterus quinquelineatus*	C	Gd	3.32	x	0.19
		Osthorhinchus spp.	O	P	3.79	x	x
		Ostorhinchus cyanosoma	O	P	x	x	10.93
		Ostorhinchus taeniophorus	O	P	x	x	0.19
Aulostomidae	0.94	*Aulostomus chinensis*	C	G	x	0.23	1.41
Balistidae	0.47	*Rhinecantus acuelatus*	O	O	1.90	0.92	x
		Sufflamen sp.§	O	O			
Carangidae	0.70	*Carangidae* sp.	C	Pi	x	x	0.38
		Caranx melagympus	C	Pi	0.47	0.46	0.47
Chaetodontidae	2.05	*Chaetodon auriga*	Co	Fco	x	0.23	x
		Chaetodon interruptus	Co	Fco	x	0.46	x
		Chaetodon lunula	Co	Fco	0.95	1.14	x
		Chaetodon trifascialis	Co	Oco	x	0.69	x
		Chaetodon trifasciatus	Co	Oco	x	0.92	x
		Chaetodon vagabundus	Co	Fco	1.42	1.60	x
		Chaetodon xanthocephalus	Co	Fco	1.42	0.92	0.09
		Heniochus monocerus§	Co	Fco			
Fistulariidae		*Fistularia comersonii*§	C	G			
Gobiidae	0.18	*Gnatholepsis* sp.	H	Gd	1.42	x	x
Holocentridae	0.29	*Sargocentron diadema*	C	I	1.42	x	0.19
Labridae	10.47	*Cheilinus chlorourus*	C	I	4.27	1.14	1.23
		Cheilinus trilobatus	C	I	0.47	0.46	x
		Cheilio inermis	C	I	1.42	0.92	0.75
		Gomphosus caeruleus	C	G	x	1.83	x
		Halichoeres hortulanus	C	I	x	0.23	x
		Halichoeres marginatus	C	I	x	0.46	x
		Halichoeres nebulosus	C	I	x	0.23	1.04
		Halichoeres scapularis	C	I	5.21	2.52	1.60
		Hemigymnus fasciatus	C	I	x	0.92	0.00
		Labroides dimidiatus	C	E	x	x	0.85
		Pseudodax molucanus	C	O	2.37	1.37	0.00

(Continues)

TABLE 2 (Continued)

					Relative abundance of species		
Family	**%**	**Species**	**1. FG**	**2. FG**	**Control (%)**	**Spring-influenced (%)**	**Springs (%)**
		Novaculichthys taeniourus§	C	I			
		Stethojulis albovitatta	C	I	1.90	2.29	0.85
		Stethojulis strigiventer	C	I	x	x	0.57
		Thalassoma genivittatum	C	I	x	0.69	x
		Thalassoma hardwicke	C	G	2.37	2.52	x
Lethrinidae	0.94	*Lethrinus harak*	C	G	1.90	0.92	0.47
		Lethrinus nebulosus	C	G	0.47	0.23	x
		Lethrinus sp.	C	G	0.47	x	x
Lutjanidae	1.46	*Lutjanus kasmira*	C	Pi	x	x	2.36
Monacanthidae	0.59	*Cantherines pardalis*	C	I	x	0.69	x
		Cantherines sp.§	C	I			
		Oxymonacanthus longirostris	Co	Oco	x	1.60	x
		Pervagor aspricaudus§	C	I			
Mugilidae	0.76	*Crenimugil buchanani*	O	P	x	x	1.23
Mullidae	3.10	*Mulloidichthys flavolineatus*	C	I	1.90	1.37	0.66
		Mulloidichthys vanicolensis	C	I	x	x	0.09
		Parupeneus barberinus	C	I	0.95	0.69	0.28
		Parupeneus bifasciatus	C	I	0.47	0.69	x
		Parupeneus ciliatus	C	I	1.90	x	0.38
		Parupeneus indicus§	C	I			
		Parupeneus macronemus	C	I	3.32	1.60	x
Muraenidae	0.06	*Muraenidae* sp.	C	G	x	x	0.09
Myliobatidae		*Myliobatis aquila*§	C	I			
Ostraciidae	0.29	*Ostracion cubicus*	Co	Fco	0.47	x	0.19
		Ostracion meleagris	Co	Fco	x	0.23	x
		Ostracion sp.	Co	Fco	x	0.23	x
Plotosidae	10.30	*Plotosus lineatus*	C	I	x	x	16.59
Pomacentridae	9.36	*Abudefduf sexfasciatus*	O	P	1.90	0.46	x
		Abudefduf sparoides	O	P	x	0.69	x
		Chromis viridis	O	P	0.95	8.70	x
		Chrysiptera unimaculata	H	Gd	x	x	0.19
		Dascyllus abudafur	O	P	2.84	7.78	1.51
		Stegastes limbatus§	H	Tf			
		Stegastes lividus	H	Tf	0.95	x	0.09
		Stegastes nigricans	H	Tf	1.42	8.47	0.94
Scaridae	5.62	*Chlorurus sordidus*	H	Sc	1.90	1.83	0.09
		Hipposcarus harid	H	Gd	3.32	0.23	x
		Scaridae spp. juv.	H	Sc	15.64	4.35	1.23
		Scarus ghobban	H	Sc	x	0.23	x
		Scarus psittacus	H	Sc	x	x	0.09
		Scarus scaber	H	Sc	x	0.69	x
		Scarus spp.	H	Sc	x	0.92	0.09

(Continues)

TABLE 2 (Continued)

Family	%	Species	1. FG	2. FG	Relative abundance of species Control (%)	Spring-influenced (%)	Springs (%)
Serranidae	1.17	*Ephinephelus merra*	C	G	4.27	1.37	0.28
		Grammistes sexlineatus	C	Pi	x	x	0.19
Siganidae	30.95	*Siganus argenteus*	H	Gd	0.95	x	1.13
		Siganus luridus	H	Gd			
		Siganus spp. juv.	H	Gd	3.79	x	47.79
Soleidae	0.06	*Pardachirus marmoratus*	C	I	x	0.23	x
Syngnathidae	0.06	*Corythoichthys schultzi*	O	I	0.47	x	x
Synodontidae	0.18	*Saurida nebulosa*	C	Pi	x	0.46	x
		Synodontidae sp.	C	Pi	x	0.23	x
Tetraodontidae	0.59	*Arothron immaculatus*§	Co	Oco			
		Arothron nigropunctatus	Co	Oco	0.47	1.14	0.28
		Canthigaster benetti	O	O	0.47	x	x
Zanclidae	0.88	*Zanclus cornutus*	Co	Fco	2.37	1.83	0.19

Stations at the control site and at the springs exhibited 75% and 69% similarity, respectively. All stations at the spring-influenced site shared 87% similarity. Based on SIMPER analysis, generalists were showing the highest contribution to the fish community at the control site. The main contributors to the observed patterns at the springs and spring-influenced site were grazer/detritivores and invertivores. At the spring-influenced site, we additionally encountered high contributions of coral-associated fish feeding groups such as territorial farmers and corallivores (Appendix Table A1).

On species level, the average similarity was below 58%. The similarity was mainly driven by honeycomb grouper *Epinephelus merra* (Bloch, 1793;control), Indian Ocean humbug damselfish *Dascyllus abudafur* (Forsskål, 1775; spring-influenced site), and floral wrasse *Cheilinus chlorourus* (Bloch, 1791; springs; Appendix Table A2).

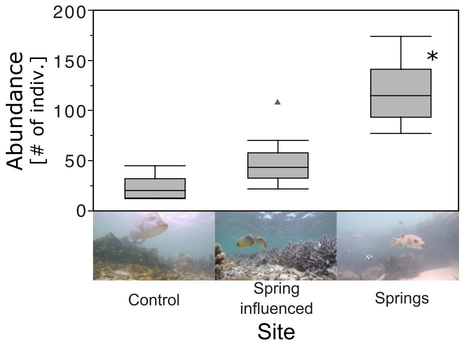

FIGURE 3 Abundance of all recorded individual fish at the three sampling sites. Data for each site are based on three separate video segments at three stations. Box-and-whisker plots display the median (line), interquartile range (box), interdecile range (small whiskers), and the 5th and 95th percentiles (big whiskers). Significant differences between sites are indicated by an asterisk

These between-sites differences in fish community structures were significant with regard to both feeding groups (two-way ANOSIM, global $R = .33$, $p = .029$) and species (two-way ANOSIM, global $R = .34$, $p = .046$).

4 | DISCUSSION

Although globally, fresh SGD amounts to only a small percentage of river discharge (Luijendijk, Gleeson, & Moosdorf, 2020; Taniguchi, Burnett, Cable, & Turner, 2002) tropical coasts export more than 56% of all fresh SGD (Zhou, Sawyer, David, & Famiglietti, 2019). In coastal ecosystems nutrient-rich fresh SGD increases primary production and sustains higher primary and secondary consumer biomass (Dale & Miller, 2008; Encarnação et al., 2015; Hata et al., 2016; Lecher & Mackey, 2018; Piló et al., 2018; Utsunomiya et al., 2017; Waska & Kim, 2011). Further, physiologically beneficial environmental conditions brought about by the submarine influx of terrestrial nutrient-rich cold acidic freshwater elevate the fitness of reef fish, potentially resulting in increased population sizes (Fujita et al., 2019; Lilkendey et al., 2019). The assessment of factors influencing the abundance of consumers, in particular fish, is of ever-growing concern as this information is vital to predicting consequences of anthropogenic actions on ecosystem functioning and productivity (Burnett et al., 2018; Shoji & Tominaga, 2018). Our results suggest a fresh SGD-driven positive relationship between altered hydrography and enhanced secondary consumer abundances around groundwater springs in a coral reef lagoon.

Fresh SGD can be responsible for alternations in benthic communities via local changes in water temperature, salinity, and pH (Amato, Bishop, Glenn, Dulai, & Smith, 2016; Foley, 2018) as well as through relief modifications (Oehler, Bakti, et al., 2019). Because of a time-delayed sampling between the spring-influenced part of the Trou aux Biches lagoon and the control site, we

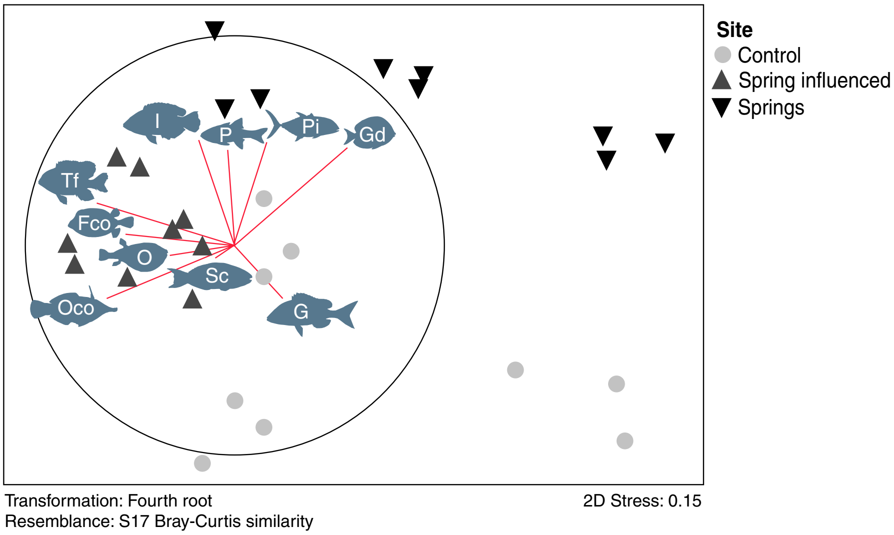

FIGURE 4 Non-metric multidimensional scaling based on fourth root-transformed fish abundance Bray–Curtis similarity comparing all video segments taken within the Trou aux Biches lagoon (control in light gray circles, spring-influenced in gray triangles, and springs in black triangles). Overlaid eigenvectors of secondary feeding classes indicate an association with sites. G: generalists, I: invertivore, Pi: piscivore, Oco: obligate corallivore, Fco: facultative corallivore, Gd: grazer/detritivore, Tf: territorial farmer, S: scraper, O: omnivore, P: planktivore

did not consider water temperature as an environmental indicator for fresh SGD. Recorded values for water salinity and pH, however, were markedly lower at the springs and throughout the spring-influenced part of the lagoon, as was made visually evident via PCA.

The influx of fresh groundwater is a locally important pathway for inland-derived nutrients, especially to tropical coastal marine environments (Luijendijk et al., 2020; Zhou et al., 2019). Recorded nitrate and phosphate concentrations were higher than previously reported for Trou aux Biches lagoon (Hurbungs, Jayabalan, & Chineah, 2002). Higher phosphate levels at the spring-influenced site when compared to the springs may be explained by temporal variability in phosphate influx at differing sampling dates. However, the observed seaward increase in phosphate concentrations may also be facilitated by rapid phosphate uptake of algae found at the springs and stations closest to shore: The spring area was mainly devoid of macroalgae except for large aggregations of *Dictyota* sp. directly at the springs. Members of this genus reportedly prefer waters with high nutrient loadings (den Haan et al., 2016; Lapointe, 1997) and low pH (Cornwall et al., 2017), conditions which were predominant at the springs. As *Dictyota* sp. can rapidly take up large quantities of phosphate, high abundances of these macroalgae at the springs could explain the low phosphate concentrations observed in the surface waters (den Haan et al., 2016). Also, as high silicate concentrations are a tracer for SGD (Oehler, Tamborski, et al., 2019), and because of the lagoonal tidal dynamics and currents (Y. Neehaul personal observation), we do not assume any nutrient enrichment process apart from the influx of groundwater through the springs. Our results, therefore, showed a significant impact of nutrient-rich fresh SGD on lagoonal hydrography well beyond the nearshore spring area. Our control site in the north, on the other hand, clustered with the oceanic sampling stations in the PCA, and therefore, we assumed it to be unaffected by any kind of nutrient enrichment.

The occurrence of fresh SGD in coral reef ecosystems is often associated with adverse effects on coral cover, diversity, and growth (Amato et al., 2016; Crook, Potts, Rebolledo-Vieyra, Hernandez, & Paytan, 2012; Lirman et al., 2003) although positive effects on reef productivity have been proposed (Greenwood, Symonds, Zhong, & Lourey, 2013; Oehler, Bakti, et al., 2019). Markedly higher observed coral cover at the spring-influenced site than at the control site suggests a non-detrimental effect of fresh SGD on the coral cover in Trou aux Biches lagoon. Comparable nitrate and phosphate concentrations were previously shown to decrease calcification rates and increase photosynthesis in corals. The recorded TSS loads, on the other hand, were one order of magnitude lower than values reported to impact coral physiology negatively (Fabricius, 2005). Besides organic matter, TSS encompass all suspended particles such as sand and other inorganic materials. High plankton abundances due to nutrient enrichment processes through groundwater discharge may, therefore, be only one explanation for increased TSS loads among others (Lecher et al., 2015; Sugimoto et al., 2017). Still, elevated planktonic food biomass at the spring-influenced part of the lagoon may sustain high coral cover (Anthony, 1999) and high abundances of the planktivorous damselfish *D. abudafur*.

Our study reports a considerably smaller species richness than previous studies from Mauritius (Adjeroud, Letourneur, Porcher, & Salvat, 1998; Graham, McClanahan, Letourneur, & Galzin, 2007). Besides many advantages, remote underwater video surveys underestimate species richness in comparison to traditional diver-based methods (Caldwell, Zgliczynski, Williams, & Sandin, 2016), mainly because of a smaller survey area. The confined spring area, however, restricted us to a point sampling approach. By choosing unbaited over baited remote underwater video surveys, we avoided a sampling bias toward generalists, carnivores, large predators, and mobile species (Mallet & Pelletier, 2014). Also, ubiquitous coral loss caused by climatic changes may lead to a decrease in reef fish biodiversity (Jones, McCormick, Srinivasan, & Eagle, 2004), and the disappearance of just a single species of coral can already affect overall diversity in fish communities (Komyakova, Jones, & Munday, 2018). Effects of habitat type on fish assemblages on reef flats in the Indian Ocean are consequently regarded as much stronger than temporal factors (e.g., seasonality) (Graham et al., 2007; Letourneur, 1996a). Therefore, we consider the bias on fish assemblage structure introduced by temporal differences in camera deployments as minor. We cannot, however, completely rule out seasonal effects such as spawning migrations and recruitment processes on the recorded fish abundances (Harmelin-Vivien, 1989; Letourneur, 1996b).

Nevertheless, in agreement with past findings (Hata et al., 2016; Shoji & Tominaga, 2018; Starke et al., 2020; Utsunomiya et al., 2017) our observations showed that fish abundances were higher at the groundwater springs when compared to the spring-influenced site and the control. Especially, structural complexity is often positively correlated with the abundance and diversity of fishes in tropical ecosystems (Darling et al., 2017). Groundwater springs also exhibit a certain degree of rugosity, such as crater-like depressions and cone-shaped fissures (Oehler, Bakti, et al., 2019). Pronounced structural complexity may thus serve to explain the elevated fish abundances at the springs when compared to the rest of the lagoon (Brown et al., 2017). Still, diversity, evenness, and species richness were not significantly different between sites, suggesting that the three-dimensional structure of the springs does not drive fish abundances through provision of diverse ecological niches (Rogers, Blanchard, & Mumby, 2014).

Elevated nutrient concentrations increase macroalgae growth in coral reef ecosystems (Amato et al., 2016; Lapointe, 1997; Smith, Tilman, & Nekola, 1999; Szmant, 2002). In this study, however, no positive relationship between the two could be observed. Macroalgae cover was higher at the springs and the control site than throughout the spring-influenced part of the lagoon, where nutrient concentrations were consistently higher when compared to the control site. This suggests either only a small influence of nutrient enrichment on macroalgae growth or robust top-down mechanisms limiting macroalgal proliferation at the spring-influenced site (Burkepile & Hay, 2006; Heck & Valentine, 2007). As in tropical regions fresh SGD has been shown to contribute significantly to reef productivity (Greenwood et al., 2013; Oehler, Bakti, et al., 2019), high macroalgae may point toward increased primary productivity at the springs, potentially supporting the observed higher herbivorous fish abundances. The fish may preferentially graze upon the phosphorus enriched algae directly at the springs (Peterson, Stubler, Wall, & Gobler, 2012). Accordingly, high macroalgal cover at the springs coincides with a high abundance of juvenile Siganidae spp. and high contribution thereof toward community structuring. Some Siganid species are known to recruit in numbers so high that they consume almost all available macroalgae (Paul, Nelson, & Sanger, 1990). The only macroalgae genera that occurs at the springs, *Dictyota* sp., is also a predominant part of the diet of Siganids (Stergiou, 1988) as the family is less repelled by the algae's deterrent metabolites (Paul et al., 1990; Wylie & Paul, 1988). Therefore, the springs may act as a nursery for Siganids while changing from a planktonic to an algal-based diet (Duray, 1998; Kami & Ikehara, 1976).

In contrast to fishes, invertebrates are among the best-studied animal taxa concerning the impact of SGD on marine biota (Encarnação et al., 2013, 2015; Grzelak, Tamborski, Kotwicki, & Bokuniewicz, 2018; Kotwicki et al., 2014; Lecher & Mackey, 2018; Ouisse et al., 2011; Piló et al., 2018; Waska & Kim, 2010; Zipperle & Reise, 2005). Increased invertebrate densities were proposed to lead to elevated invertivorous fish biomass in the vicinity to fresh SGD in temperate coastal regions (Fujita et al., 2019; Hata et al., 2016). Comparably, high contribution of the invertivore species *C. chlororurus* whitesaddle goatfish *Parupeneus ciliatus* (Lacepède, 1802) and three-ribbon wrasse *Stethojulis strigiventer* (Bennett, 1833) to the fish community at the springs suggests a similar causality in Trou aux Biches lagoon.

Observations in temperate systems lead to the hypothesis that fresh SGD contributes to coastal fishery resource biomass through nutrient enrichment as well as via alterations to coastal hydrography (Shoji & Tominaga, 2018; Utsunomiya et al., 2017). This study provides further evidence of a positive relationship between submarine groundwater springs and increased fish abundance in a tropical coral reef ecosystem. Elevated fish abundance, as well as high contributions of herbivore and invertivore fish species to the fish community at the springs, suggests a positive effect of nutrient-rich fresh SGD on food availability and secondary consumer biomass. Especially, the observed elevated fish abundances at the springs could have implications for the management of small-scale fisheries in tropical lagoons: Namely that altered groundwater fluxes on land may cause differences in fish biomass available to fisheries. We acknowledge that this study is just a first step in determining the influence of groundwater springs on tropical lagoonal fisheries. Nonetheless, we recommend that processes such as fresh SGD should be incorporated into management approaches throughout tropical coral reef environments.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study have been deposited in PANGAEA and are accessible at https://doi.org/10.1594/PANGAEA.921340.

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REFERENCES

Adjeroud, M., Letourneur, Y., Porcher, M., & Salvat, B. (1998). Factors influencing spatial distribution of fish communities on a fringing reef at Mauritius, S.W Indian Ocean. *Environmental Biology of Fishes*, *53*, 169–182.

Amato, D., Bishop, J. M., Glenn, C. R., Dulai, H., & Smith, C. M. (2016). Impact of submarine groundwater discharge on marine water quality and reef biota of Maui. *PLoS One*, *11*(11), e0165825. https://doi.org/10.1371/journal.pone.0165825

Andrisoa, A., Stieglitz, T. C., Rodellas, V., & Raimbault, P. (2019). Primary production in coastal lagoons supported by groundwater discharge and porewater fluxes inferred from nitrogen and carbon isotope signatures. *Marine Chemistry*, *210*, 48–60. https://doi.org/10.1016/j.marchem.2019.03.003

Anthony, K. R. N. (1999). Coral suspension feeding on fine particulate matter. *Journal of Experimental Marine Biology and Ecology*, *232*, 85–106. https://doi.org/10.1016/S0022-0981(98)00099-9

Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*, 827–833. https://doi.org/10.1038/nature02691

Bœuf, G., & Payan, P. (2001). How should salinity influence fish growth? *Comparative Biochemistry and Physiology - C Toxicology and Pharmacology*, *130*(4), 411–423. https://doi.org/10.1016/S1532-0456(01)00268-X

Brown, C. J., Jupiter, S. D., Lin, H. Y., Albert, S., Klein, C., Maina, J. M., … Mumby, P. J. (2017). Habitat change mediates the response of coral reef fish populations to terrestrial run-off. *Marine Ecology Progress Series*, *576*, 55–68. https://doi.org/10.3354/meps12221

Burkepile, D. E., & Hay, M. E. (2006). Herbivore vs. nutrient control of marine primary producers: Context-dependent effects. *Ecology*, *87*(12), 3128–3139. https://doi.org/10.1890/0012-9658(2006)87[3128:HVNCOM]2.0.CO;2

Burnett, K. M., Wada, C. A., Taniguchi, M., Sugimoto, R., & Tahara, D. (2018). Evaluating the tradeoffs between groundwater pumping for snow-melting and nearshore fishery productivity in Obama City, Japan. *Water*, *10*, 1556. https://doi.org/10.3390/w10111556

Burnett, W. C., Bokuniewicz, H., Huettel, M., Moore, W. S., & Taniguchi, M. (2003). Groundwater and pore water inputs to the coastal zone. *Biogeochemistry*, *66*, 3–33. https://doi.org/10.1023/B:BIOG.0000006066.21240.53

Bussmann, I., Dando, P. R., Niven, S. J., & Suess, E. (1999). Groundwater seepage in the marine environment: Role for mass flux and bacterial activity. *Marine Ecology Progress Series*, *178*, 169–177. https://doi.org/10.3354/meps178169

Caldwell, Z. R., Zgliczynski, B. J., Williams, G. J., & Sandin, S. A. (2016). Reef fish survey techniques: Assessing the potential for standardizing methodologies. *PLoS One*, *11*(4), 1–14. https://doi.org/10.1371/journal.pone.0153066

Cappo, M., Harvey, E., Malcolm, H., & Speare, P. (2003). Potential of video techniques to monitor diversity, abundance and size of fish in studies of marine protected areas. In J. P. Beumer, A. Grant & D. C. Smith (Eds.). *Aquatic Protected Areas. What works best and how do we know?* (*1*, pp. 455–464). Cairns: University of Queensland.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*(1), 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x

Clarke, K. R., & Gorley, R. N. (2015). *PRIMER v7: User manual/tutorial* (p. 296). Plymouth, UK: PRIMER-E. http://updates.primer-e.com/primer7/manuals/User_manual_v7a.pdf

Clarke, K. R., & Green, R. H. (1988). Statistical design and analysis for a "biological effects" study. *Marine Ecology Progress Series*, *46*, 213–226. https://doi.org/10.3354/meps046213

Clarke, K. R., & Warwick, R. M. (1994). Similarity-based testing for community pattern: The two-way layout with no replication. *Marine Biology*, *118*(1), 167–176. https://doi.org/10.1007/BF00699231

Cole, A. J., Pratchett, M. S., & Jones, G. P. (2008). Diversity and functional importance of coral-feeding fishes on tropical coral reefs. *Fish and Fisheries*, *9*(3), 286–307. https://doi.org/10.1111/j.1467-2979.2008.00290.x

Cornwall, C. E., Revill, A. T., Hall-Spencer, J. M., Milazzo, M., Raven, J. A., & Hurd, C. L. (2017). Inorganic carbon physiology underpins macroalgal responses to elevated CO$_2$. *Scientific Reports*, *7*, 46297. https://doi.org/10.1038/srep46297

Crook, E. D., Potts, D., Rebolledo-Vieyra, M., Hernandez, L., & Paytan, A. (2012). Calcifying coral abundance near low-pH springs: Implications for future ocean acidification. *Coral Reefs*, *31*(1), 239–245. https://doi.org/10.1007/s00338-011-0839-y

Dale, R. K., & Miller, D. C. (2008). Hydrologic interactions of infaunal polychaetes and intertidal groundwater discharge. *Marine Ecology Progress Series*, *363*, 205–215. https://doi.org/10.3354/meps07455

Darling, E. S., Graham, N. A. J., Januchowski-Hartley, F. A., Nash, K. L., Pratchett, M. S., & Wilson, S. K. (2017). Relationships between structural complexity, coral traits, and reef fish assemblages. *Coral Reefs*, *36*(2), 561–575. https://doi.org/10.1007/s00338-017-1539-z

den Haan, J., Huisman, J., Brocke, H. J., Goehlich, H., Latijnhouwers, K. R. W., van Heeringen, S., … Visser, P. M. (2016). Nitrogen and phosphorus uptake rates of different species from a coral reef community after a nutrient pulse. *Scientific Reports*, *6*(28821), 1–13. https://doi.org/10.1038/srep28821

Di Franco, A., Calo, A., Sdiri, K., Cattano, C., Milazzo, M., & Guidetti, P. (2019). Ocean acidification affects somatic and otolith growth relationship in fish: Evidence from an in situ study. *Biology Letters*, *15*(20180662), 1–4. https://doi.org/10.1098/rsbl.2018.0662

Duray, M. N. (1998). *Biology and culture of siganids* (Rev ed.). Tigbauan, Iloilo, Philippines: Aquaculture Department, Southeast Asian Fisheries Development Center.

Encarnação, J., Leitão, F., Range, P., Piló, D., Chícharo, M. A., & Chícharo, L. (2013). The influence of submarine groundwater discharges on subtidal meiofauna assemblages in south Portugal (Algarve). *Estuarine, Coastal and Shelf Science*, *130*, 202–208. https://doi.org/10.1016/j.ecss.2013.04.013

Encarnação, J., Leitão, F., Range, P., Piló, D., Chícharo, M. A., & Chícharo, L. (2015). Local and temporal variations in near-shore macrobenthic communities associated with submarine groundwater discharges. *Marine Ecology*, *36*(4), 926–941. https://doi.org/10.1111/maec.12186

English, S., Wilkinson, C., & Baker, V. (Eds.) (1997). *Survey manual for tropical marine resources*. Townsville, QLD: Australian Institute of Marine Science.

Fabricius, K. E. (2005). Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. *Marine Pollution Bulletin*, *50*(2), 125–146. https://doi.org/10.1016/j.marpolbul.2004.11.028

Field, J. G., Clarke, K. R., & Warwick, R. M. (1982). A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, *8*, 37–52. https://doi.org/10.3354/meps008037

Foley, L. J. (2018). Karst-channelled intertidal submarine groundwater discharge (SGD) conditions the form of the rock pool sessile assemblage. *Estuarine, Coastal and Shelf Science*, *213*, 236–244. https://doi.org/10.1016/j.ecss.2018.08.014

Fujita, K., Shoji, J., Sugimoto, R., Nakajima, T., Honda, H., Takeuchi, M., … Taniguchi, M. (2019). Increase in fish production through bottom-up trophic linkage in coastal waters induced by nutrients supplied via submarine groundwater. *Frontiers in Environmental Science*, *7*(June), 1–10. https://doi.org/10.3389/fenvs.2019.00082

Gobler, C. J., & Sañudo-Wilhelmy, S. A. (2001). Temporal variability of groundwater seepage and brown tide blooms in a Long Island embayment. *Marine Ecology Progress Series*, *217*, 299–309. https://doi.org/10.3354/meps217299

Graham, N. A. J., McClanahan, T. R., Letourneur, Y., & Galzin, R. (2007). Anthropogenic stressors, inter-specific competition and ENSO effects on a Mauritian coral reef. *Environmental Biology of Fishes*, *78*(1), 57–69. https://doi.org/10.1007/s10641-006-9077-5

Graham, N. A. J., Wilson, S. K., Jennings, S., Polunin, N. V. C., Bijoux, J. P., & Robinson, J. (2006). Dynamic fragility of oceanic coral reef ecosystems. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(22), 8425–8429. https://doi.org/10.1073/pnas.0600693103

Grasshoff, K., & Koroleff, F. (1983). Determination of nutrients. In K.Grasshoff K. Kremling & M. Ehrhardt (Eds.), *Methods of seawater analysis* (2nd ed., pp. 125–157). Weinheim/Deerfield Beach, Florida: Verlag Chemie.

Green, A. L., & Bellwood, D. R. (2009). *Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience - A practical guide for coral reef managers in the Asia Pacific Region*. Gland, Switzerland: IUCN working group on Climate Change and Coral Reefs.

Greenwood, J. E., Symonds, G., Zhong, L., & Lourey, M. (2013). Evidence of submarine groundwater nutrient supply to an oligotrophic barrier reef. *Limnology and Oceanography*, *58*(5), 1834–1842. https://doi.org/10.4319/lo.2013.58.5.1834

Grzelak, K., Tamborski, J., Kotwicki, L., & Bokuniewicz, H. (2018). Ecostructuring of marine nematode communities by submarine groundwater discharge. *Marine Environmental Research*, *136*(January), 106–119. https://doi.org/10.1016/j.marenvres.2018.01.013

Hallock, P., & Schlager, W. (1986). Nutrient excess and the demise of coral reefs and carbonate platforms. *Palaios*, *1*(4), 389–398. https://doi.org/10.2307/3514476

Harmelin-Vivien, M. L. (1989). Reef fish community structure: An Indo-Pacific comparison. In M. L. Harmelin-Vivien & F. Bourlière (Eds.), *Vertebrates in Complex Tropical Systems, Ecological Studies* (*69*, pp. 21–60). New York, NY: Springer. https://doi.org/10.1007/978-1-4612-3510-1_2

Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E. S., … Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters*, *14*(9), 852–862. https://doi.org/10.1111/j.1461-0248.2011.01651.x

Hata, M., Sugimoto, R., Hori, M., Tomiyama, T., & Shoji, J. (2016). Occurrence, distribution and prey items of juvenile marbled sole Pseudopleuronectes yokohamae around a submarine groundwater seepage on a tidal flat in southwestern Japan. *Journal of Sea Research*, *111*, 47–53. https://doi.org/10.1016/j.seares.2016.01.009

Heck, K. L., & Valentine, J. F. (2007). The primacy of top-down effects in shallow benthic ecosystems. *Estuaries and Coasts*, *30*(3), 371–381. https://doi.org/10.1007/BF02819384

Hill, J., & Wilkinson, C. (2004). *Methods for ecological monitoring of coral reefs: A resource for managers. Version 1*. (p. 117). Townsville, QLD: Australian Institute of Marine Science.

Hurbungs, M. D., Jayabalan, N., & Chineah, V. (2002). Seasonal distribution of potential toxic benthic dinoflagellates in the lagoon of Trou aux Biches, Mauritius. In J. A. Lalouette & D. Y. Bachraz (Eds.), *Proceedings of the fifth annual meeting of agricultural scientists* (pp. 211–217). Réduit, Mauritius: Food and Agricultural Research Council.

Hwang, D. W., Kim, G., Lee, W. C., & Oh, H. T. (2010). The role of submarine groundwater discharge (SGD) in nutrient budgets of Gamak Bay, a shellfish farming bay. *Korea. Journal of Sea Research*, *64*(3), 224–230. https://doi.org/10.1016/j.seares.2010.02.006

Jarrold, M. D., & Munday, P. L. (2019). Diel CO2 cycles and parental effects have similar benefits to growth of a coral reef fish under ocean acidification. *Biology Letters*, *15*, 20180724. org/10.1098/rsbl.2018.0724

Jickells, T. D. (1998). Nutrient biogeochemistry of the coastal zone. *Science*, *281*, 217–222. https://doi.org/10.1126/science.281.5374.217

Johannes, R. E. (1980). The ecological significance of the submarine discharge of groundwater. *Marine Ecology Progress Series*, *3*, 365–373. https://doi.org/10.3354/meps003365

Johannes, R. E., & Hearn, C. (1985). The effect of submarine groundwater discharge on nutrient and salinity regimes in a coastal lagoon off Perth, Western Australia. *Estuarine, Coastal and Shelf Science*, *21*(6), 789–800. https://doi.org/10.1016/0272-7714(85)90073-3

Jones, G. P., McCormick, M. I., Srinivasan, M., & Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(21), 8251–8253. https://doi.org/10.1073/pnas.0401277101

Kami, H. T., & Ikehara, I. I. (1976). Notes in the Annual Juvenile Siganid Harvest in Guam. *Micronesica*, *12*, 323–325.

Kang, H., & Kim, J.-G. (2006). The estimation of environmental capacity in the Gamak Bay using an eco-hydrodynamic model. *Journal of the Environmental Sciences*, *15*(10), 951–960. https://doi.org/10.5322/JES.2006.15.10.951

Knee, K. L., & Paytan, A. (2011). Submarine groundwater discharge: a source of nutrients, metals, and pollutants to the coastal ocean. In E. Wolanski & D. S. McLusky (Eds.), *Treatise on estuarine and coastal science* (Vol. 4, pp. 205–233). Waltham: Academic Press. https://doi.org/10.1016/B978-0-12-374711-2.00410-1

Komyakova, V., Jones, G. P., & Munday, P. L. (2018). Strong effects of coral species on the diversity and structure of reef fish communities: A multi-scale analysis. *PLoS One*, *13*(8), 1–20. https://doi.org/10.1371/journal.pone.0202206

Kotwicki, L., Grzelak, K., Czub, M., Dellwig, O., Gentz, T., Szymczycha, B., & Böttcher, M. E. (2014). Submarine groundwater discharge to the Baltic coastal zone: Impacts on the meiofaunal community. *Journal of Marine Systems*, *129*, 118–126. https://doi.org/10.1016/j.jmarsys.2013.06.009

Kwong, R. N. G. K. (2005). Status of sugar industry in Mauritius: Constraints and future research strategies. *Sugar Tech*, *7*(1), 5–10. https://doi.org/10.1007/BF02942411

Lapointe, B. E. (1997). Nutrient thresholds for bottom-up control of macroalgal blooms on coral reefs in Jamaica and southeast Florida. *Limnology and Oceanography*, *42*, 1119–1131. https://doi.org/10.4319/lo.1997.42.5_part_2.1119

Lecher, A. L., & Mackey, K. R. M. (2018). Synthesizing the effects of submarine groundwater discharge on marine biota. *Hydrology*, *5*(4), 60. https://doi.org/10.3390/hydrology5040060

Lecher, A. L., Mackey, K., Kudela, R., Ryan, J., Fisher, A., Murray, J., & Paytan, A. (2015). Nutrient loading through submarine groundwater discharge and phytoplankton growth in Monterey bay, CA. *Environmental Science and Technology*, *49*(11), 6665–6673. https://doi.org/10.1021/acs.est.5b00909

Lee, G. H. (1993). *Fisheries oceanographical studies on the production of the farming oyster in Karmak Bay*. Pusan, Korea: Pusan National Fisheries University.

Letourneur, Y. (1996a). Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. I. Patterns of spatial distribution. *Journal of Experimental Marine Biology and Ecology*, *195*(1), 1–30. https://doi.org/10.1016/0022-0981(95)00089-5

Letourneur, Y. (1996b). Dynamics of fish communities on Reunion fringing reefs, Indian Ocean. II. Patterns of temporal fluctuations. *Journal of Experimental Marine Biology and Ecology*, *195*, 31–52. https://doi.org/10.1016/0022-0981(95)00090-9

Lilkendey, J., Pisternick, T., Neumann, S. I., Neelayya, D. D., Bröhl, S., Neehaul, Y., & Moosdorf, N. (2019). Fresh submarine groundwater discharge augments growth in a reef fish. *Frontiers in Marine Science*, *6*, 613. https://doi.org/10.3389/fmars.2019.00613

Lirman, D., Orlando, B., Maciá, S., Manzello, D., Kaufman, L., Biber, P., & Jones, T. (2003). Coral communities of Biscayne Bay, Florida and adjacent offshore areas: Diversity, abundance, distribution, and environmental correlates. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *13*(2), 121–135. https://doi.org/10.1002/aqc.552

Lubarsky, K. A., Silbiger, N. J., & Donahue, M. J. (2018). Effects of submarine groundwater discharge on coral accretion and bioerosion on two shallow reef flats. *Limnology and Oceanography*, *63*(4), 1660–1676. https://doi.org/10.1002/lno.10799

Luijendijk, E., Gleeson, T., & Moosdorf, N. (2020). Fresh groundwater discharge insignificant for the world's oceans but important for coastal ecosystems. *Nature Communications*, *11*(1), 1–12. https://doi.org/10.1038/s41467-020-15064-8

Mallet, D., & Pelletier, D. (2014). Underwater video techniques for observing coastal marine biodiversity: A review of sixty years of publications (1952–2012). *Fisheries Research*, *154*, 44–62. https://doi.org/10.1016/j.fishres.2014.01.019

Martial, C., & Boolakey, R. (2016). *Digest of demographic statistics 2015*. Retrieved from http://statsmauritius.govmu.org/English/StatsbySubj/Documents/Digest/Demography/Digest_Demo_2015.pdf

Martial, C., & Fatha Mahomed, N. (2019). *Population and vital statistics Republic of Mauritius, Year 2018*. Retrieved from http://statsmauritius.govmu.org/English/Publications/Documents/2019/EI1436/Pop_Vital_Yr18.pdf

Millar, R. B., & Anderson, M. J. (2004). Remedies for pseudoreplication. *Fisheries Research*, *70*(2-3), 397–407. https://doi.org/10.1016/j.fishres.2004.08.016

Miller, D. C., & Ullman, W. J. (2004). Ecological consequences of ground water discharge to Delaware Bay, United States. *Ground Water*, *42*(7), 959–970. https://doi.org/10.1111/j.1745-6584.2004.tb02635.x

Moore, W. S. (2010). The effect of submarine groundwater discharge on the ocean. *Annual Review of Marine Science*, *2*(1), 59–88. https://doi.org/10.1146/annurev-marine-120308-081019

Moosdorf, N., & Oehler, T. (2017). Societal use of fresh submarine groundwater discharge: An overlooked water resource. *Earth-Science Reviews*, *171*, 338–348. https://doi.org/10.1016/j.earscirev.2017.06.006

Oehler, T., Bakti, H., Lubis, R. F., Purwoarminta, A., Delinom, R., & Moosdorf, N. (2019). Nutrient dynamics in submarine groundwater discharge through a coral reef (western Lombok, Indonesia). *Limnology and Oceanography*, *64*(6), 2646–2661. https://doi.org/10.1002/lno.11240

Oehler, T., Eiche, E., Putra, D., Adyasari, D., Hennig, H., Mallast, U., & Moosdorf, N. (2018). Timing of land-ocean groundwater nutrient fluxes from a tropical karstic region (southern Java, Indonesia). *Journal of Hydrology*, *565*, 662–671. https://doi.org/10.5194/hess-2017-621

Oehler, T., Tamborski, J., Rahman, S., Moosdorf, N., Ahrens, J., Mori, C., … Beck, M. (2019). DSi as a tracer for submarine groundwater discharge. *Frontiers in Marine Science*, *6*(September), 1–13. https://doi.org/10.3389/fmars.2019.00563

Ouisse, V., Riera, P., Migné, A., Leroux, C., & Davoult, D. (2011). Freshwater seepages and ephemeral macroalgae proliferation in an intertidal bay: II. Effect on benthic biomass and metabolism. *Estuarine, Coastal and Shelf Science*, *91*(1), 272–281. https://doi.org/10.1016/j.ecss.2010.10.034

Paul, V. J., Nelson, S. G., & Sanger, H. R. (1990). Feeding preferences of adult and juvenile rabbitfish signus-argenteus in relation to chemical defenses of tropical seaweeds. *Marine Ecology*, *60*(1), 23–34. https://doi.org/10.3354/meps060023

Paytan, A., Shellenbarger, G. G., Street, J. H., Gonneea, M. E., Davis, K., Young, M. B., & Moore, W. S. (2006). Submarine groundwater discharge: An important source of new inorganic nitrogen to coral reef ecosystems. *Limnology and Oceanography*, *51*(1), 343–348. https://doi.org/10.4319/lo.2006.51.1.0343

Peterson, B. J., Stubler, A. D., Wall, C. C., & Gobler, C. J. (2012). Nitrogen-rich groundwater intrusion affects productivity, but not herbivory, of the tropical seagrass thalassia testudinum. *Aquatic Biology*, *15*(1), 1–9. https://doi.org/10.3354/ab00413

Piló, D., Barbosa, A. B., Teodósio, M. A., Encarnação, J., Leitão, F., Range, P., … Chícharo, L. (2018). Are submarine groundwater discharges affecting the structure and physiological status of rocky intertidal communities? *Marine Environmental Research*, *136*(January), 158–173. https://doi.org/10.1016/j.marenvres.2018.02.013

Pratchett, M. S., Hoey, A. S., Wilson, S. K., Messmer, V., & Graham, N. A. J. (2011). Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity*, *3*(3), 424–452. https://doi.org/10.3390/d3030424

Proag, V. (1995). *The Geology and Water Resources of Mauritius*, Geography of Mauritius series, Moka, Mauritius: Mahatma Gandhi Institute.

Ramessur, R. T. (2002). Anthropogenic-driven changes with focus on the coastal zone of Mauritius, south-western Indian Ocean. *Journal of Material Cycles and Waste Management*, *3*(1–3), 99–106. https://doi.org/10.1007/s10113-002-0045-0

Retzel, A., Hansen, A. D., & Grønkjær, P. (2007). Otolith growth of Springer's demoiselle, Chrysiptera springeri (Pomacentridae, Allen & Lubbock), on a protected and non-protected coral reef. *Journal of Applied Ichthyology*, *23*(5), 568–572. https://doi.org/10.1111/j.1439-0426.2007.00865.x

Richardson, C. M., Dulai, H., Popp, B. N., Ruttenberg, K., & Fackrell, J. K. (2017). Submarine groundwater discharge drives biogeochemistry in two Hawaiian reefs. *Limnology and Oceanography*, *62*, 348–363. https://doi.org/10.1002/lno.10654

Rider, B. F., & Mellon, M. G. (1946). Colorimetric determination of nitrites. *Industrial and Engineering Chemistry - Analytical Edition*, *18*(2), 96–99. https://doi.org/10.1021/i560150a003

Rogers, A., Blanchard, J. L., & Mumby, P. J. (2014). Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, *24*(9), 1000–1005. https://doi.org/10.1016/j.cub.2014.03.026

Saddul, P. (2002). *Mauritius A Geomorphological Analysis*. Moka, Mauritius: Mahatma Gandhi Institute.

Sammarco, P. W., Risk, M. J., Schwarcz, H. P., & Heikoop, J. M. (1999). Cross-continental shelf trends in coral δ15N on the Great Barrier Reef: Further consideration of the reef nutrient paradox. *Marine Ecology Progress Series*, *180*, 131–138. https://doi.org/10.3354/meps180131

Santos, I. R., Burnett, W. C., Dittmar, T., Suryaputra, I. G. N. A., & Chanton, J. (2009). Tidal pumping drives nutrient and dissolved organic matter dynamics in a Gulf of Mexico subterranean estuary. *Geochimica et Cosmochimica Acta*, *73*(5), 1325–1339. https://doi.org/10.1016/j.gca.2008.11.029

Shoji, J., & Tominaga, O. (2018). Relationships between submarine groundwater discharge and coastal fisheries as a water-food nexus. In A. Endo & T. Oh (Eds.), *The water-energy-food nexus* (pp. 117–131). Singapore: Springer. https://doi.org/10.1007/978-981-10-7383-0_9

Silva, A., Tavares, P., Shapouri, M., Stigter, T. Y., Monteiro, J. P., Machado, M., … Ribeiro, L. (2012). Estuarine biodiversity as an indicator of groundwater discharge. *Estuarine, Coastal and Shelf Science*, *97*, 38–43. https://doi.org/10.1016/j.ecss.2011.11.006

Slomp, C. P., & Van Cappellen, P. (2004). Nutrient inputs to the coastal ocean through submarine groundwater discharge: Controls and potential impact. *Journal of Hydrology*, *295*(1–4), 64–86. https://doi.org/10.1016/j.jhydrol.2004.02.018

Smith, V. H., Tilman, G. D., & Nekola, J. C. (1999). Eutrophication: Impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environmental Pollution*, *100*, 179–196. https://doi.org/10.1016/S0269-7491(99)00091-3

Starke, C., Ekau, W., & Moosdorf, N. (2020). Enhanced productivity and fish abundance at a submarine spring in a coastal lagoon on Tahiti, French Polynesia. *Frontiers in Marine Science*, *6*(January), 1–12. https://doi.org/10.3389/fmars.2019.00809

Stergiou, K. I. (1988). Feeding habits of the Lessepsian migrant *Siganus luridus* in the eastern Mediterranean, its new environment. *Journal of Fish Biology*, *33*(4), 531–543. https://doi.org/10.1111/j.1095-8649.1988.tb05497.x

Sugimoto, R., Kitagawa, K., Nishi, S., Honda, H., Yamada, M., Kobayashi, S., … Tominaga, O. (2017). Phytoplankton primary productivity around submarine groundwater discharge in nearshore coasts. *Marine Ecology Progress Series*, *563*, 25–33. https://doi.org/10.3354/meps11980

Szmant, A. M. (2002). Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? *Estuaries*, *25*(4), 743–766. https://doi.org/10.1007/BF02804903

Taniguchi, M., Burnett, W. C., Cable, J. E., & Turner, J. V. (2002). Investigation of submarine groundwater discharge. *Hydrological Processes*, *16*, 2115–2129. https://doi.org/10.1002/hyp.1145

Underwood, A. J. (1997). *Experiments in Ecology: Their logical design and interpretation using analysis of variance*. (pp. 1–522). New York, NY: University of Cambridge Press.

Utsunomiya, T., Hata, M., Sugimoto, R., Honda, H., Kobayashi, S., Miyata, Y., … Taniguchi, M. (2017). Higher species richness and abundance of fish and benthic invertebrates around submarine groundwater discharge in Obama Bay, Japan. *Journal of Hydrology: Regional Studies*, *11*, 139–146. https://doi.org/10.1016/j.ejrh.2015.11.012

Warwick, R. M., & Clarke, K. R. (1991). A comparison of some methods for analysing changes in benthic community structure. *Journal of the Marine Biological Association of the United Kingdom*, *71*(1), 225–244. https://doi.org/10.1017/S0025315400037528

Waska, H., & Kim, G. (2010). Differences in microphytobenthos and macrofaunal abundances associated with groundwater discharge in the intertidal zone. *Marine Ecology Progress Series*, *407*, 159–172. https://doi.org/10.3354/meps08568

Waska, H., & Kim, G. (2011). Submarine groundwater discharge (SGD) as a main nutrient source for benthic and water-column primary production in a large intertidal environment of the Yellow Sea. *Journal of Sea Research*, *65*(1), 103–113. https://doi.org/10.1016/j.seares.2010.08.001

Wells, R. J. D., & Cowan, J. H. Jr (2007). Video estimates of red snapper and associated fish assemblages on sand, shell, and natural reef habitats in the North-Central Gulf of Mexico. *American Fisheries Society Symposium*, *60*, 39–57.

Wong, W. W., Grace, M. R., Cartwright, I., Cardenas, M. B., Zamora, P. B., & Cook, P. L. M. (2013). Dynamics of groundwater-derived nitrate and nitrous oxide in a tidal estuary from radon mass balance modeling. *Limnology and Oceanography*, *58*(5), 1689–1706. https://doi.org/10.4319/lo.2013.58.5.1689

Wylie, C. R., & Paul, V. J. (1988). Feeding preferences of the surgeonfish Zebrasoma flavescens in relation to chemical defenses of tropical algae. *Marine Ecology Progress Series*, *45*, 23–32. https://doi.org/10.3354/meps045023

Zhou, Y., Sawyer, A. H., David, C. H., & Famiglietti, J. S. (2019). Fresh submarine groundwater discharge to the near-global coast. *Geophysical Research Letters*, *46*(11), 5855–5863. https://doi.org/10.1029/2019GL082749

Zipperle, A., & Reise, K. (2005). Freshwater springs on intertidal sand flats cause a switch in dominance among polychaete worms. *Journal of Sea Research*, *54*(2), 143–150. https://doi.org/10.1016/j.seares.2005.01.003

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APPENDIX

TABLE A1 Similarity percentage (SIMPER) analysis results for secondary feeding groups at three sites in Trou aux Biches lagoon, Mauritius

	Average similarity	Average abundance	Average similitude	Contribution (%)	Accumulative (%)
Springs					
Grazer/detritivore	69.07	2.57	18.03	26.11	26.11
Invertivores		2.08	14.84	21.49	47.60
Generalists		1.27	10.06	14.57	62.17
Territorial farmers		1.03	8.26	11.95	74.12
Spring-influenced					
Invertivores	86.84	1.63	11.57	13.32	13.32
Grazer/detritivores		1.80	11.45	13.19	26.51
Planktivores		1.66	11.20	12.89	39.40
Territorial farmers		1.41	9.79	11.27	50.68
Generalists		1.35	9.45	10.88	61.56
Obligate corallivores		1.31	8.78	10.11	71.67
Control					
Generalists	74.88	1.31	14.26	19.05	19.05
Grazer/detritivores		1.45	14.19	18.95	38.00
Invertivores		1.46	13.80	18.43	56.43
Planktivores		1.18	11.69	15.61	72.04

TABLE A2 Similarity percentage (SIMPER) analysis results for fish species at three sites in Trou aux Biches lagoon, Mauritius

	Average similarity	Average abundance	Average similitude	Contribution (%)	Accumulative (%)
Springs					
Cheilinus chlorourus	39.94	1.08	3.91	9.80	9.80
Juvenile *Siganus* spp.		2.00	3.81	9.53	19.33
Stegastes nigricans		0.98	3.25	8.13	27.46
Caranx melagympus		0.84	2.97	7.45	34.91
Parupeneus ciliatus		0.81	2.97	7.45	42.35
Stethojulis strigiventer		0.86	2.97	7.45	49.80
Siganus argenteus		0.79	1.59	3.98	53.78
Aulostomus chinensis		0.32	1.50	3.77	57.55
Cheilio inermis		0.72	1.50	3.77	61.31
Ctenochaetus striatus		0.86	1.46	3.66	64.97
Halichoeres scapularis		0.86	1.41	3.54	68.51
Mulloidichthys flavolineatus		0.69	1.37	3.43	71.94
Spring-influenced					
Dascyllus abudafur	57.63	1.39	3.93	6.82	6.82
Stegastes nigricans		1.41	3.83	6.65	13.47
Acanthurus triostegus		1.60	3.51	6.09	19.56
Ctenochaetus striatus		1.14	3.35	5.80	25.36
Stethojulis albovitatta		1.02	2.94	5.11	30.47
Thalassoma hardwicke		1.03	2.76	4.80	35.27
Chlorurus sordidus		0.97	2.74	4.76	40.03
Gomphosus caeruleus		0.97	2.74	4.76	44.78
Halichoeres scapularis		1.01	2.62	4.54	49.33
Zanclus cornutus		0.94	2.44	4.24	53.56
Parupeneus macronemus		0.91	2.38	4.13	57.70
Arothron nigropunctatus		0.84	2.24	3.88	61.58
Chaetodon lunula		0.84	2.24	3.88	65.46
Chaetodon xanthocephalus		0.84	2.24	3.88	69.34
Juvenile *Scaridae* spp.		1.02	2.24	3.88	73.22
Control					
Ephinephelus merra	37.09	1.00	4.89	13.18	13.18
Juvenile *Scaridae* spp.		1.27	4.77	12.86	26.05
Cheilinus chlorourus		0.98	4.42	11.91	37.96
Halichoeres scapularis		1.01	4.13	11.15	49.10
Lethrinus harak		0.81	3.72	10.02	59.12
Osthorchinus spp.		0.71	2.12	5.73	64.85
Chaetodon xanthocephalus		0.55	1.61	4.35	69.20
Ctenochaetus striatus		0.83	1.51	4.08	73.27