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Natural Variability in Caribbean Coral Physiology and Implications for Coral Bleaching Resilience

Leila Chapron[1], Verena Schoepf[1,2], Stephen J. Levas[1,3], Matthew D. Aschaffenburg[4], Mark E. Warner[4] and Andréa G. Grottoli[1]**

[1] School of Earth Sciences, The Ohio State University, Columbus, OH, United States, [2] Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, Amsterdam, Netherlands, [3] Geography, Geology and Environmental Science, University of Wisconsin, Whitewater, WI, United States, [4] School of Marine Science and Policy, University of Delaware, Lewes, DE, United States

Coral reefs are among the most diverse and complex ecosystems in the world that provide important ecological and economical services. Increases in sea surface temperature linked to global climate change threatens these ecosystems by inducing coral bleaching. However, it is not fully known if natural intra- or inter-annual physiological variability is linked to bleaching resilience or recovery capacity of corals. Here, we monitored the coral physiology of three common Caribbean species (*Porites divaricata, Porites astreoides, Orbicella faveolata*) at six time points over 2 years by measuring the following traits: calcification, biomass, lipids, proteins, carbohydrates, chlorophyll *a*, algal endosymbiont density, stable carbon isotopes of the host and endosymbiotic algae, and the stable carbon and oxygen isotopes of the skeleton. The overall physiological profile of all three species varied over time and that of *P. divaricata* was consistently different from the two other coral species. *Porites divaricata* had higher energy reserves coupled with higher contributions of heterotrophically derived carbon to host tissues than both *P. astreoides* and *O. faveolata*. Consistently higher overall energy reserves and heterotrophic contributions to tissues appear to buffer against environmental stress, including bleaching events. Thus, natural physiological variability among coral species appears to be a stronger predictor of coral bleaching resilience than intra- or inter-annual physiological variability within a coral species.

Keywords: *Porites divaricata*, *Porites astreoides*, *Orbicella faveolata*, coral physiology, natural variability, coral bleaching, energy reserves, heterotrophy

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****Correspondence:***
Leila Chapron
chapron@obs-banyuls.fr
Andréa G. Grottoli
grottoli.1@osu.edu

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INTRODUCTION

Coral reef ecosystems have important ecological and economic value, as they provide critical habitat for associated species and support billions of dollars each year to the global economy (e.g., Costanza et al., 2014; Hoegh-Guldberg, 2015; Spalding et al., 2017). Unfortunately, coral reef ecosystems are threatened by increasing seawater temperatures associated with global climate change, leading to rising frequency and intensity of coral bleaching events (e.g., Teneva et al., 2012; Frieler et al., 2013; Cziesielski et al., 2019). Specifically, coral bleaching is the loss of endosymbiotic algae (family Symbiodiniaceae) and/or their photosynthetic pigments, giving corals a pale or white appearance,

altering their energy budget, and eventually leading to their death (e.g., Hoegh-Guldberg and Smith, 1989; Glynn, 1996; Downs et al., 2002; Grottoli et al., 2014; Suggett and Smith, 2020). While coral vulnerability to heat-induced bleaching is well documented, the underlying natural variability in physiology could contribute to coral susceptibility and/or resilience to heat waves.

Several physiological traits associated with resistance to, and recovery from, coral bleaching fluctuate on a seasonal basis (e.g., Fitt et al., 2000; Rodrigues and Grottoli, 2007; Hagedorn and Carter, 2015) and include tissue thickness (e.g., Loya et al., 2001; Thornhill et al., 2011; Levas et al., 2013), energy reserves (i.e., lipids, proteins, carbohydrates) (e.g., Rodrigues and Grottoli, 2007; Anthony et al., 2009; Grottoli et al., 2014; Schoepf et al., 2015), Symbiodiniaceae species switching or shuffling (e.g., Abrego et al., 2008; Grottoli et al., 2014; Cunning et al., 2015), and heterotrophic plasticity (e.g., Grottoli et al., 2006; Levas et al., 2013). However, the link between natural temporal variability in physiology and bleaching remains poorly understood.

Temporal variability of coral physiological traits *in situ* has been reported for Hawaiian, Florida, western Pacific and Australian corals. Differences among species and location are typically based on a limited number of physiological traits such as skeletal $\delta^{13}C$, tissue bleaching, algal density, biomass or calcification (e.g., Fairbanks and Dodge, 1979; Grottoli and Wellington, 1999; Marshall and Baird, 2000; Stimson et al., 2002; Thornhill et al., 2011; Ross et al., 2015, 2018). Markers of energy reserves such as tissue biomass, protein, and carbohydrates are typically lowest in the summer or fall (e.g., Fitt et al., 2000; Rodrigues and Grottoli, 2007; Thornhill et al., 2011; Levas et al., 2013), while lipids are typically highest in the summer (e.g., Ben-David-Zaslow and Benayahu, 1999; Oku et al., 2003; Towle et al., 2015). In addition, all of these energy reserves often vary among species and sites (e.g., Fitt et al., 2000; Thornhill et al., 2011; Hinrichs et al., 2013; Towle et al., 2015). However, natural intra- and inter-annual variability in Caribbean coral energy reserves has not been investigated. In addition, Symbioniaceae and chlorophyll *a* concentrations are often at their lowest in mid-to-late summer when temperature and irradiance are at their peak values, and vice versa in the winter (e.g., Fagoonee, 1999; Fitt et al., 2000; Thornhill et al., 2011). Most coral bleaching events occur in late summer or early fall (e.g., Hoegh-Guldberg, 1999; Baker et al., 2008; Courtney et al., 2018) when protein and carbohydrate energy reserves, Symbiodiniaceae, and chlorophyll *a* are naturally low (e.g., Fitt et al., 2000; Oku et al., 2003; Rodrigues and Grottoli, 2007; Thornhill et al., 2011). Experimental bleaching studies have revealed that some corals with high energy reserves and photosynthetic pigments tend to be more resistant to bleaching when exposed to heat stress (e.g., Grottoli et al., 2006, 2014; Schoepf et al., 2015). Thus, coral species with relatively higher concentrations of energy reserves and photosynthetic pigments overall, or with higher concentrations in late summer, may be more resistant to natural *in situ* bleaching as well.

Heterotrophy is a critical source of fixed carbon for corals, especially when bleached (e.g., Carriquiry et al., 1994; Grottoli et al., 2006, 2014; Hughes et al., 2010; Connolly et al., 2012). Isotopic and feeding studies indicate that the proportionate contribution of heterotrophically acquired carbon varies seasonally but not for all species (e.g., Porter, 1976; Carriquiry et al., 1994; Felis et al., 1998; Grottoli and Wellington, 1999; Rodrigues and Grottoli, 2006; Levas et al., 2013, 2016; Schoepf et al., 2015). Yet, natural intra- and inter-annual variability in Caribbean coral heterotrophy has not yet been investigated. Lower heterotrophy before, during, and/or after bleaching has been linked to slower bleaching recovery (e.g., Grottoli et al., 2006, 2014; Rodrigues and Grottoli, 2006). Thus, corals with higher heterotrophic capacity and/or plasticity during the late summer, should be less susceptible to bleaching and likely to recover more quickly from thermal stress.

Finally, high coral calcification rates are often viewed as an indicator of coral health (e.g., Cortés and Risk, 1985; Guzmán et al., 1994), as this is an energetically costly process (e.g., Cohen and McConnaughey, 2002; Allemand et al., 2011). Calcification rates are typically higher in summer than in winter (e.g., Crossland, 1984; Lough and Barnes, 2000; Ross et al., 2018). Calcification increases with increasing temperatures up to an optimum (e.g., Jokiel et al., 1978; Marshall and Clode, 2004) and then decreases or stops when temperatures rise above a certain threshold (e.g., Leder et al., 1991; Reynaud et al., 2003; Rodrigues and Grottoli, 2006; Jokiel, 2011). Further, calcification is typically enhanced due to higher light availability in summer months (see Gattuso et al., 1999; Allemand et al., 2011 for review). When bleached, coral calcification dramatically decreases or stops (e.g., Carilli et al., 2009; Grottoli et al., 2014; Hagedorn et al., 2016; D'Olivo and McCulloch, 2017; Fisch et al., 2019), as stressed corals prioritize energy allocation toward maintaining metabolic demand and minimizing energy reserve losses (e.g., Edmunds and Davies, 1989; Cabral-Tena et al., 2013). Thus, corals that grow more slowly overall, or slower during the summer and early fall, may be less susceptible to bleaching and/or recover more quickly as they may already be prioritizing energy reserves or other metabolic processes over calcification.

Overall, the intra- and inter-annual variability in coral physiology could underlie coral bleaching susceptibility, severity, and persistence during recovery. To the best of our knowledge, only one study to date has assessed several physiological traits (i.e., chlorophyll *a*, Symbiodiniaceae density, colony brightness, and skeletal density) over a 2-year survey in *Pocillopora damicornis* on the Great Barrier Reef (Cooper et al., 2008). However, more studies are needed that comprehensively assess multiple physiological and isotopic traits of corals *in situ* over multiple years, particularly for Caribbean corals. Here, we measured seven physiological traits (e.g., calcification, biomass, lipid, protein, carbohydrate, chlorophyll *a*, Symbiodinaceae density, and tissue and skeletal isotopes) in the three Caribbean coral species *Porites divaricata* (branching morphology), *Porites astreoides* (mounding/encrusting morphology), and *Orbicella faveolata* (mounding, formerly *Montastraea faveolata* (Budd et al., 2012) from a common garden from July 2009 to June 2011. Using a multivariate approach, we quantified coral overall physiological variability over time and among species and identified the trait (s) that underly variability. Understanding how key physiological traits of coral health vary among species and over time can help us assess how natural variability in

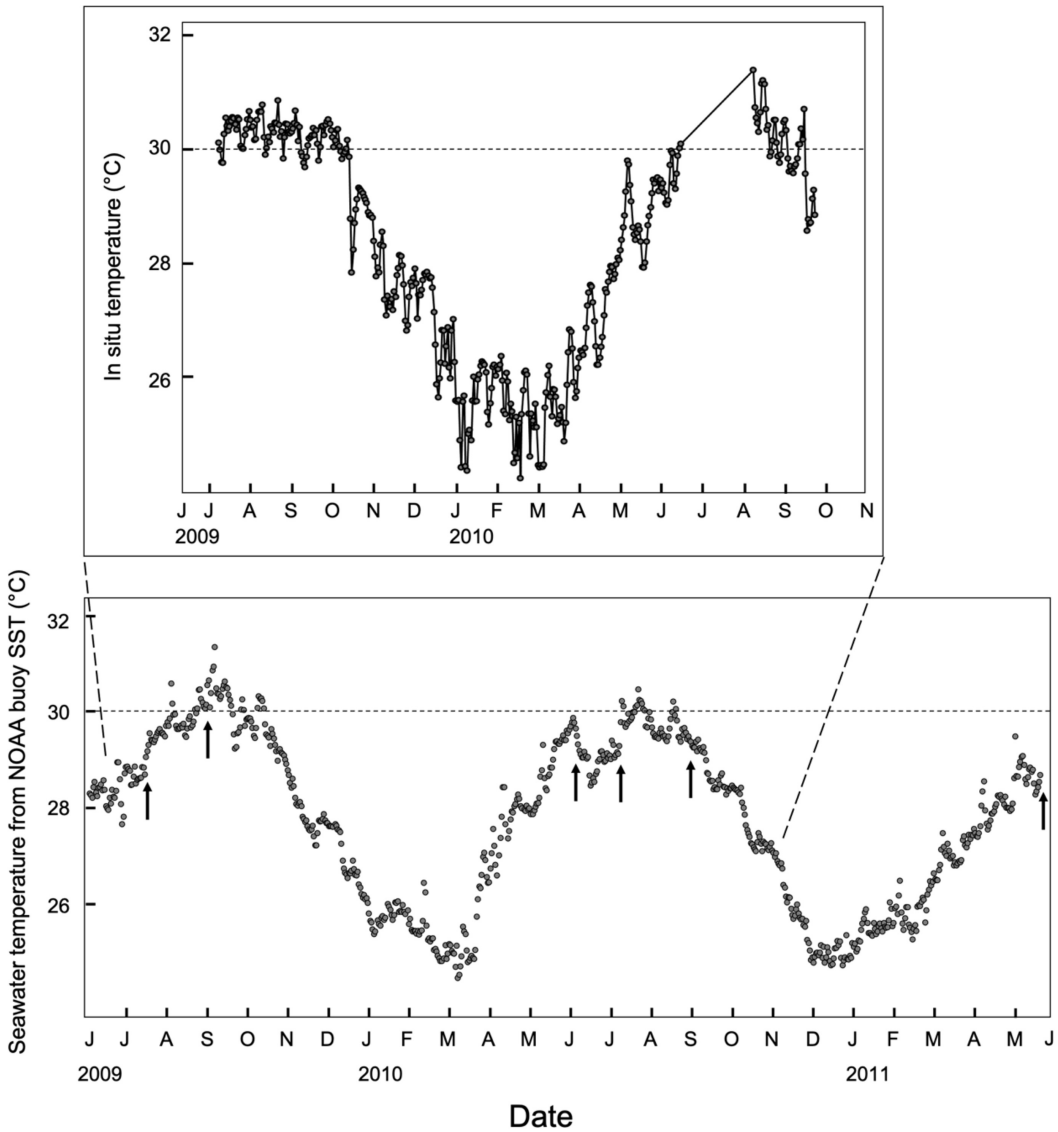

FIGURE 1 | Average daily seawater temperature records between June 2009 and June 2011 from the NOAA buoy station 42058 central caribbean at 2 m depth (14°23′20″ N 74°48′10″ W) and inset with *in situ* temperature from temperature loggers deployed on the reef at the common garden beside the corals between June 2009 and November 2010 (20°52.8150N, 86°50.9890W). The local bleaching threshold (∼30°C) is represented by the dotted line. Months are indicated by their first letter and the year is indicated at the first listed month for that year. The sampling times are represented by the arrows.

coral physiology potentially modulates resistance and resilience of corals to bleaching.

MATERIALS AND METHODS

Coral Collection and Experimental Design

Coral collection methods were previously described in Grottoli et al. (2014). Briefly, six ramets from nine healthy (no bleaching visible) genets of *Porites divaricata*, *Porites astreoides*, and *Orbicella faveolata* were collected from 2.4 to 7.9 m depth from a reef near Puerto Morelos, Mexico. They were mounted on labeled PVC tiles, buoyantly weighed (Jokiel et al., 1978), and redeployed in a common garden at 4.9 m depth on the back reef (20°52.8150N, 86°50.9890W) on July 2009 where submersible loggers recorded the seawater temperature every hour. One ramet per genet was pre-assigned to a collection time of July 2009 (0 month), September 2009 (1.5 months), June 2010 (11 months), July 2010 (12 months), September 2010 (13.5 months), and June 2011 (23 months). At each time interval, all surviving ramets per species assigned to that time point were collected and missing or dead ramets were recorded. Ramets were buoyantly weighed and daily calcification rates were calculated as the difference between weights at the start of the study and collection time, divided by the respective number of days elapsed

since the last measurement, and standardized to surface area. Coral fragments were then frozen at −80°C and shipped to The Ohio State University on dry ice and stored at −80°C for further analysis.

Tissue Biomass, Symbiont Density, Chlorophyll *a*, and Energy Reserves

Tissue biomass was quantified using methods described by McLachlan et al. (2020) from ground corals. Symbiont density was measured according to methods described in Warner et al. (2006) using 6 replicate counts on a hemocytometer. Chlorophyll *a* pigments were extracted using a double extraction and quantified spectrophotometrically with the equations of Jeffrey and Humphrey (1975). Symbiont density, chlorophyll *a*, and tissue biomass were all standardized to colony surface area using the aluminum foil method (Marsh, 1970).

Total soluble lipids (henceforth referred as lipids) were chloroform extracted from a whole, ground coral (∼1 cm^2) sub-sample from each fragment according to established methods (e.g., Grottoli et al., 2004; Rodrigues and Grottoli, 2007). Animal soluble protein and carbohydrate (henceforth referred as protein and carbohydrate, respectively) were extracted from a second whole, ground coral sub-sample according to established methods (DuBois et al., 1956; Smith et al., 1985). The energetic value of lipid, protein, and carbohydrate concentrations were calculated and reported in Joules (Gnaiger and Bitterlich, 1984) and standardized to the ash-free dry weight (Grottoli et al., 2014).

Stable Isotopic Analysis

Tissue C isotopic analyses were performed on separated animal host and endosymbiont fractions using established methods (e.g., Rodrigues and Grottoli, 2006; Hughes et al., 2010). In brief, coral tissue was removed using an airbrush and the algal and animal fractions were separated by centrifugation. Each sample was individually combusted in a Costech Elemental Analyzer coupled to a Finnigan Delta Plus Advantage stable isotope ratio mass spectrometer (SIRMS) via a Conflo III open split interface at The Ohio State University. The carbon isotopic composition of the animal host ($\delta^{13}C_h$) and algal endosymbiont ($\delta^{13}C_e$) were reported as the per mil deviation of the stable isotopes ^{13}C:^{12}C relative to Vienna-Peedee Belemnite Limestone standard (v-PDB). The difference between $\delta^{13}C_h$ and $\delta^{13}C_e$ ($\delta^{13}C_{h-e}$) was calculated to determine the relative contribution of photoautotrophic vs. heterotrophic carbon to the internal DIC pool (e.g., Muscatine, 1989; Rodrigues and Grottoli, 2006; Price et al., 2021). Repeated measurements of the commercial standard USGS-24 had a standard deviation of ± 0.04‰.

Skeletal C and O isotopic analyses were performed following the established method by Grottoli et al. (2017). Briefly, the coral fragments were cleaned of tissue with high-pressure tap water and dried at room temperature. No additional cleaning was performed as it can lead to uncorrectable isotopic fractionation of the sample (Grottoli et al., 2005). Using a Dremel tool with a diamond-tipped drill bit, the top 100–200 μm of skeletal material was shaved off the tip of each coral fragment at the point of maximum linear extension. Each coral skeletal sample was finely ground and a 80–100 μg subsample was analyzed for $\delta^{13}C$ and $\delta^{18}O$ using an automated Carbonate Kiel device coupled to a Finnigan Delta IV SIRMS at The Ohio State University. Samples were acidified under vacuum with 100% ortho-phosphoric acid, and the resulting CO_2 was cryogenically purified and delivered to the mass spectrometer. The standard deviation of repeated measurements of an internal carbonate standard (n = 40) was ± 0.03‰ for $\delta^{13}C$ and ± 0.05‰ for $\delta^{18}O$. All $\delta^{13}C$ and $\delta^{18}O$ values were reported as the per mil deviation relative to the Vienna Peedee Belemnite Limestone Standard (v-PDB). In general, increases in coral skeletal $\delta^{13}C$ ($\delta^{13}C_s$) are linked to greater carbon contribution via photosynthesis and/or decreased heterotrophic carbon incorporated in the tissues, as the pool of inorganic carbon available for calcification through respiration is enriched (e.g., Grottoli and Wellington, 1999; Grottoli, 2002). $\delta^{18}O$ variability results from temperature-induced kinetic fractionation (e.g., Weber and Woodhead, 1972; Kim and O'Neil, 1997) relative to seawater $\delta^{18}O$ changes and salinity (Epstein et al., 1953). In corals, skeletal $\delta^{18}O$ ($\delta^{18}O_s$) increases as temperature decreases and seawater $\delta^{18}O$ increases (e.g., McConnaughey, 1989; Leder et al., 1996). However, when corals are bleached, dramatic decreases in calcification can lead to reduced fractionation, enhance equilibration with seawater, and increases in $\delta^{13}C_s$ and $\delta^{18}O_s$ (e.g., Rodrigues and Grottoli, 2006; Grottoli et al., 2017).

Statistical Analysis

The number of alive, dead, and missing coral ramets of each species was recorded at each time point. Differences in mortality among species at each time point were evaluated by a Fisher's exact test (**Supplementary Table 1**).

All multivariate statistics were performed using Primer software V6. Coral physiological profiles (i.e., calcification, biomass, lipids, proteins, carbohydrates, chlorophyll *a*, Symbiodiniaceae density, and $\delta^{13}C_{h-e}$) were compared among species with a multivariate one-way analysis of similarity (ANOSIMs; Clarke, 1993; 9999 permutations). Temporal differences in intraspecific and interspecific coral physiological profiles were compared by two separate multi-variate one-way PERMANOVAs (9999 permutations). Similarity percentage analysis (SIMPER) were performed to identify which of the physiological traits contributed the most to the differences among species. The data were visualized using non-metric multidimensional scaling (NMDS) plots.

Univariate statistics were performed with R software (v3.4.3) to evaluate how each individual physiological trait differed among species, genets, and over time. Assumptions of normality were evaluated by the Shapiro-Wilk test, and homoscedasticity was assessed by the Bartlett test. The $\delta^{18}O_s$ and $\delta^{13}C_e$ were normally distributed. None of the other physiological traits were normally distributed but did meet assumptions of homoscedasticity. Since no genet effects were found for any physiological trait, it was removed from the models. Physiological trait differences among species and time points were compared by non-parametric Kruskal-Wallis tests, except for $\delta^{18}O_s$ and $\delta^{13}C_e$ where two-ways ANOVAs were performed. Differences among

TABLE 1 | Results of pair-wise tests of the one-way analysis of similarity (ANOSIM) of the physiological profiles of *Porites divaricata, Porites astreoides,* and *Orbicella faveolata* (global $R = 0.33$, $p = 0.001$).

	R statistic	*P*-value	Possible # of permutations	Actual # of permutations	Average dissimilarity	Main biological traits	% Contribution
P. divaricata vs. *P. astreoides*	0.394	**0.0009**	Very large	999	19.78	Lipid	16.06
						Biomass	14.81
						Carbohydrate	14.41
						Protein	13.09
						Chl *a*	11.93
P. divaricata vs. *O. faveolata*	0.571	**0.0011**	Very large	999	21.08	Biomass	20.34
						Carbohydrate	16.41
						Symb. density	12.41
						$\delta^{13}C_{h-e}$	12.36
						Lipid	12.10
P. astreoides vs. *O. faveolata*	0.102	0.2724	Very large	999			

Physiological profiles included the following traits, calcification, biomass, lipids, proteins, carbohydrates, chlorophyll a, Symbiodinaceae density (Symb. density), and $\delta^{13}C_{h-e}$. *Significant differences are in bold. For species that significantly differ from each other, similarity percentages (SIMPER) of the contribution of each physiological trait to the dissimilarities were computed.*

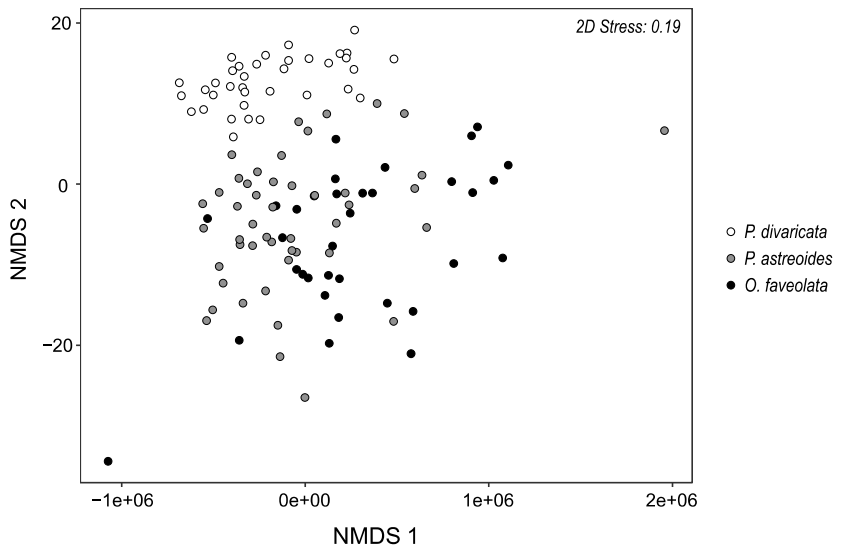

FIGURE 2 | Multivariate NMDS plot ($R = 0.33$) for *Porites divaricata* (white), *Porites astreoides* (gray), and *Orbicella faveolata* (black) across all time points. Variables included in the analyses were calcification, lipids, proteins, carbohydrates, chlorophyll *a*, Symbiodiniaceae density, and $\delta^{13}C_{h-e}$. Corresponding ANOSIMs in **Table 1**.

groups for each physiological trait were compared by Tukey *Post hoc* tests.

RESULTS

Daily average seawater temperature on the reef ranged from 24.2 to 31.4°C with the lowest temperatures in January–March and the warmest temperatures in July–September (**Figure 1**). No severe heat stress events (Bleaching threshold SST 29.8°C, MMM + 1°C) were recorded by Coral Reef Watch in this region during our 2-year survey (Quintana Roo station (5 km), NOAA Coral Reef Watch, 2019). Nevertheless, seawater temperature exceeded 29.8°C for 63 days in 2009 and 42 days in 2010 (National Data Buoy Center, 2021). The same pattern was observed for seawater recorded on the reef with $\geq$ 29.8°C temperatures for 80 days in 2009 and more than 27 days in 2010 (temperature logger failed during July and August 2010, **Figure 1**). This induced mild paling of some *O. faveolata* ramets in September of 2009 but no paling for the two *Porites* species (**Supplementary Table 1**). Mild paling was also observed for some *O. faveolata* ramets in June 2010 (11 months), September 2010 (13.5 months) and June 2011 (23 months), and in *P. divaricata* ramets in September 2010 (13.5 months) and June 2011 (23 months) (**Supplementary Table 1**).

While no mortality was observed for *Porites* coral fragments over time (**Supplementary Figure 1** and **Supplementary Table 1**), two fragments of *O. faveolata* ramets died at 23 months (**Supplementary Figure 1**). Unfortunately, all the *O. faveolata* ramets from the 0-month timepoint were lost. In addition, the

TABLE 2 | Results of the pair-wise tests from the one-way PERMANOVAs testing the effect of time on coral physiological profiles of *Porites divaricata*, *Porites astreoides, and Orbicella faveolata.*

Species	Groups	Den. df	t	*P*-value	Unique perms
P. divaricata	0 vs. 1.5	10	2.24	**0.003**	495
	0 vs. 11	14	4.32	**0.001**	5,058
	0 vs. 12	14	3.43	**<0.001**	5,027
	0 vs. 13.5	10	3.32	**0.002**	495
	0 vs. 23	10	3.32	**0.002**	495
	1.5 vs. 11	10	2.69	**0.003**	495
	1.5 vs. 12	10	1.88	**0.006**	495
	1.5 vs. 13.5	6	2.53	**0.030**	35
	1.5 vs. 23	6	2.13	**0.031**	35
	11 vs. 12	14	3.84	**<0.001**	5,054
	11 vs. 13.5	10	2.66	**0.005**	495
	11 vs. 23	10	2.38	**0.004**	494
	12 vs. 13.5	10	2.82	**0.003**	495
	12 vs. 23	10	2.23	**0.002**	495
	13.5 vs. 23	6	1.15	0.279	35
P. astreoides	0 vs. 1.5	9	2.09	**0.007**	462
	0 vs. 11	12	3.86	**<0.001**	1,987
	0 vs. 12	12	3.68	**<0.001**	1,981
	0 vs. 13.5	12	3.30	**<0.001**	1,983
	0 vs. 23	12	3.03	**<0.001**	1,990
	1.5 vs. 11	13	1.79	**0.004**	4,339
	1.5 vs. 12	13	1.70	**0.041**	4,341
	1.5 vs. 13.5	13	1.69	**0.023**	4,284
	1.5 vs. 23	13	1.37	0.087	4,295
	11 vs. 12	16	2.30	**0.001**	8,199
	11 vs. 13.5	16	1.69	**0.028**	8,167
	11 vs. 23	16	1.41	0.055	8,152
	12 vs. 13.5	16	3.20	**<0.001**	8,165
	12 vs. 23	16	2.67	**<0.001**	8,152
	13.5 vs. 23	16	1.08	0.322	8,198
O. faveolata	1.5 vs. 11	9	1.19	0.234	165
	1.5 vs. 12	8	1.44	**0.048**	120
	1.5 vs. 13.5	10	1.89	**0.009**	220
	1.5 vs. 23	8	1.33	0.080	120
	11 vs. 12	13	1.54	**0.046**	5,060
	11 vs. 13.5	15	2.19	**0.002**	8,144
	11 vs. 23	13	1.39	0.089	5,073
	12 vs. 13.5	14	1.67	**0.026**	6,682
	12 vs. 23	12	1.54	**0.018**	1,710
	13.5 vs. 23	14	1.97	**0.003**	6,669

Physiological profiles included the following physiological traits: calcification, biomass, lipids, proteins, carbohydrates, chlorophyll a, Symbiodinaceae density, and $\delta^{13}C_{h-e}$. *Significant differences are in bold. Group comparisons are between sampling months where 0 = July 2009, 1.5 = September 2009, 11 = June 2010, 12 = July 2010, 13.5 = September 2010, and 23 = June 2011.*

thin branches of *P. divaricata* ramets dislodged from the epoxy base over time resulting in one *P. divaricata* ramet being lost after 11 months, as well as four ramets after 12 months and five ramets after 13.5 months.

Variation in Physiological Profiles Among Species and Over Time

The physiological profile of *P. divaricata* differed significantly from that of *P. astreoides* and *O. faveolata,* though the latter two did not differ significantly from one other (**Figure 2** and **Table 1A**). At least a third of the dissimilarity between species was due to total lipids and biomass, or biomass and carbohydrates (**Table 1**).

The physiological profiles of each species also varied over time within and between years, with 93, 80, and 70% of time points significantly differing from each other within *P. divaricata, P. astreoides*, and *O. faveolata*, respectively (**Table 2**). The physiological profile of *P. divaricata* changed on intra- and interannual timescales and did not fluctuate on a predictable

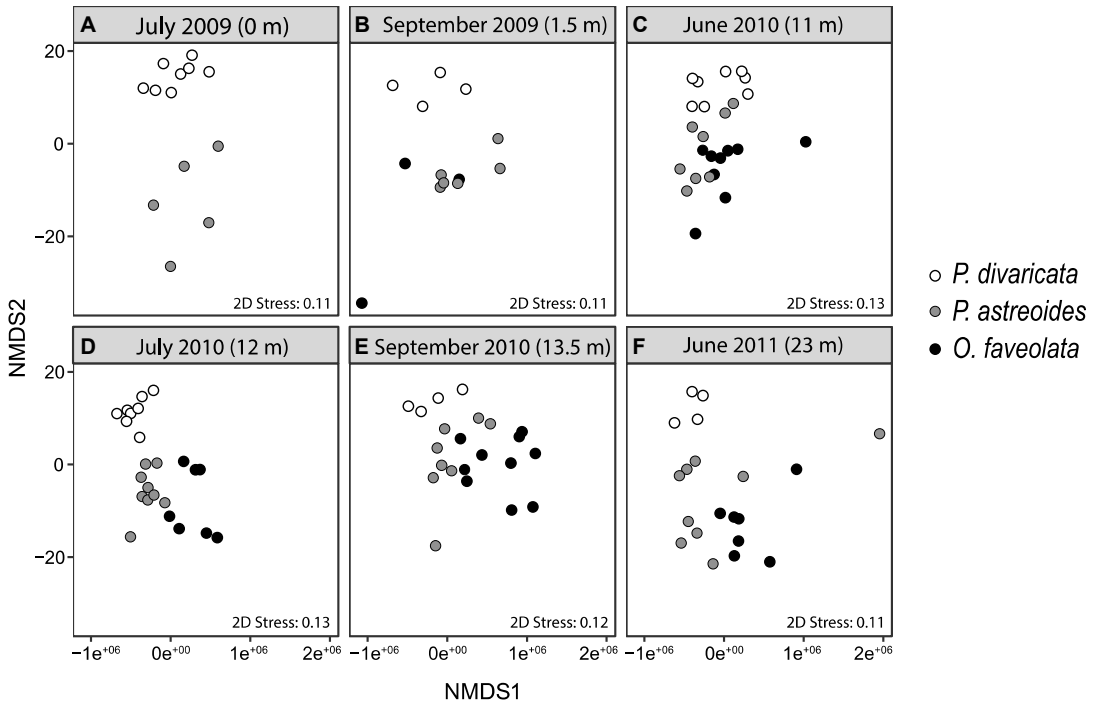

FIGURE 3 | Multivariate NMDS plots for *Porites divaricata* (white), *Porites astreoides* (gray), and *Orbicella faveolata* (black) at **(A–F)** each time point (*m* = months). Variables included in the analyses were calcification, biomass, lipids, proteins, carbohydrates, chlorophyll *a*, Symbiodiniaceae density, and $\delta^{13}C_{h-e}$. Corresponding PERMANOVAs in **Tables 2**, **3**.

TABLE 3 | Results of the pair-wises tests of the one-way PERMANOVAs testing differences among physiological profiles of coral species (*Porites divaricata, Porites astreoides, Orbicella faveolata*) within each time point.

Time	Groups	df	T	*P*-value	Unique perms
0	*P. divaricata* vs. *P. astreoides*	11	3.06	**<0.001**	1,287
1.5	*P. divaricata* vs. *P. astreoides*	8	1.68	0.076	210
	P. divaricata vs. *O. faveolata*	5	1.88	**0.032**	35
	P. astreoides vs. *O. faveolata*	7	0.96	0.379	74
11	*P. divaricata* vs. *P. astreoides*	15	2.19	**<0.001**	8,133
	P. divaricata vs. *O. faveolata*	14	2.49	**<0.001**	5,034
	P. astreoides vs. *O. faveolata*	15	1.42	0.071	8,211
12	*P. divaricata* vs. *P. astreoides*	15	4.68	**<0.001**	8,183
	P. divaricata vs. *O. faveolata*	13	4.85	**<0.001**	5,044
	P. astreoides vs. *O. faveolata*	14	3.27	**<0.001**	6,646
13.5	*P. divaricata* vs. *P. astreoides*	11	3.43	**<0.001**	715
	P. divaricata vs. *O. faveolata*	11	3.89	**<0.001**	715
	P. astreoides vs. *O. faveolata*	16	2.27	**0.003**	8,206
23	*P. divaricata* vs. *P. astreoides*	11	2.51	**<0.001**	715
	P. divaricata vs. *O. faveolata*	9	3.13	**<0.001**	330
	P. astreoides vs. *O. faveolata*	14	1.66	**0.025**	6,658

Physiological profiles included the following traits: calcification, biomass, lipids, proteins, carbohydrates, chlorophyll a, Symbiodiniaceae density, and $\delta^{13}C_{h-e}$. *Significant effects are in bold. Time is in months over the duration of the study where 0 = July 2009, 1.5 = September 2009, 11 = June 2010, 12 = July 2010, 13.5 = September 2010, and 23 = June 2011.*

seasonal basis as the variability patterns differed between the observation years (**Table 2**). The physiological profiles of *P. astreoides* and *O. faveolata* also varied on intra- and interannual timescales, but their profiles returned to a common state in June of each years (i.e., no difference in their profiles at 11 and 23 months) (**Table 2**). Within each sampling month, the overall physiological profiles differed among two or more of the species during the first 11 months of the study (**Figures 3A–C** and

Table 3). However, the physiological profiles of all three species always differed from each other throughout the entire second year of the study (**Figures 3D–F** and **Table 3**).

Variation in Individual Physiological Traits Among Species and Over Time

For all species combined, there was a significant species by time interaction effect for the physiological traits of calcification, biomass, lipids, proteins, carbohydrates, chlorophyll *a,* Symbiodiniaceae density, and $\delta^{13}C_{h-e}$ (**Supplementary Table 2**). Closer investigation revealed that carbohydrates was the only trait that differed between *P. astreoides* and *O. faveolata* (**Supplementary Table 3**) while *P. divaricata* differed from the other two species all traits except calcification and chlorophyll *a* (**Supplementary Table 3**).

Over time, calcification, biomass, Symbiodiniaceae density, and $\delta^{13}C_{h-e}$ did not differ for *P. divaricata* (**Figures 4A,B,G,H** and **Supplementary Table 4**). In contrast, lipids, proteins, carbohydrates and chlorophyll *a* showed significant variability over time within and between year (**Figures 4C–F** and **Supplementary Table 4**). Lipid concentrations were generally higher the second year and proteins were higher at 13.5 months compared to 1.5 months (**Figures 4C,D** and **Supplementary Table 4**). Carbohydrates were higher at 0, 1.5, and 12 months compared to the rest of time points (**Figure 4E** and **Supplementary Table 4**) while chlorophyll *a* was highest at 0 months (late summer) and lowest at 11 months (early summer) (**Figures 4E,F** and **Supplementary Table 4**).

In *P. astreoides,* calcification, lipids, proteins, and symbiont density did not differ over time (**Figures 4I,K,L,O** and **Supplementary Table 4**). In contrast, biomass, carbohydrates, chlorophyll *a* and $\delta^{13}C_{h-e}$ showed a significant temporal variability within and between years (**Figures 4J,M,N,P** and **Supplementary Table 4**). Biomass was higher at 0 months and lower at 11, 12, and 13.5 months (**Figure 4J** and **Supplementary Table 4**), and carbohydrate concentrations were higher at 0, 1.5, and 12 months (**Figure 4M** and **Supplementary Table 4**). Chlorophyll *a* was higher at 0 months (**Figure 4N** and **Supplementary Table 4**) and $\delta^{13}C_{h-e}$ significantly declined over the course of the second year (**Figure 4P** and **Supplementary Table 4**).

Finally for *O. faveolata,* calcification, biomass, total lipids, proteins and $\delta^{13}C_{h-e}$ did not differ over time (**Figures 4Q–T,X** and **Supplementary Table 4**). Carbohydrates were significantly higher and chlorophyll *a* significantly lower at the end of the study (**Figures 4U,V** and **Supplementary Table 4**), while Symbiodiniaceae density was the lowest at 1.5 months and highest at 13.5 months (**Figure 4W**).

Variation in Individual Isotopic Traits Among Species and Over Time

For all species combined, there was a significant species by time interaction effect for $\delta^{13}C_e$ and $\delta^{18}O_s$ as well as significant species and time effects in $\delta^{13}C_h$ and $\delta^{13}C_s$ (**Supplementary Table 5**). Closer investigations revealed that *P. divaricata* differed isotopically from the other two species by having the lowest

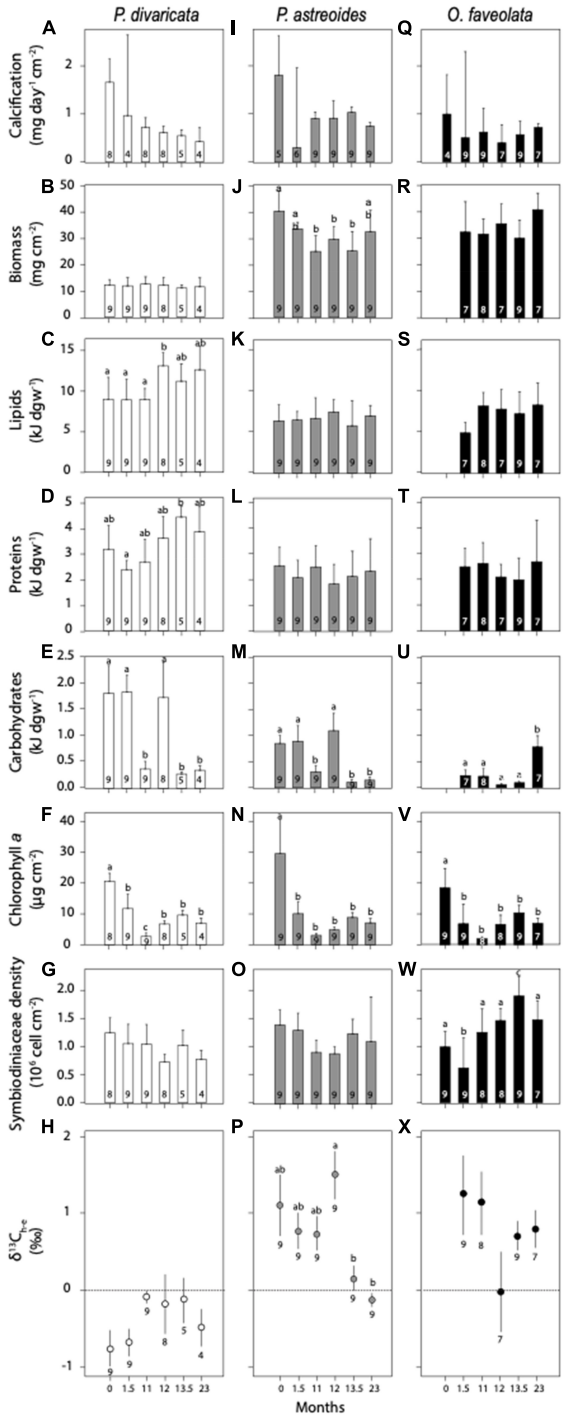

FIGURE 4 | Average (± 1 SE) calcification, biomass, lipids, proteins, carbohydrates, chlorophyll *a* (Chl *a*), Symbiodiniaceae density, and $\delta^{13}C_{h-e}$ of **(A–H)** *Porites divaricata* (white), **(I–P)** *Porites astreoides* (gray), **(Q–X)** *Orbicella faveolata* (black) at each time point (0 month = July 2009, 1.5 months = September 2009, 11 months = June 2010, 12 months = July 2010, 13.5 months = September 2010, and 23 months = June 2010). Averages that do not significantly differ from each other share similar letters or no letters. All Kruskal-Wallis, ANOVA, and Tukey *post hoc* results in **Supplementary Tables 3**, **4**. Sample sizes are represented within each bar and below $\delta^{13}C_{h-e}$ averages.

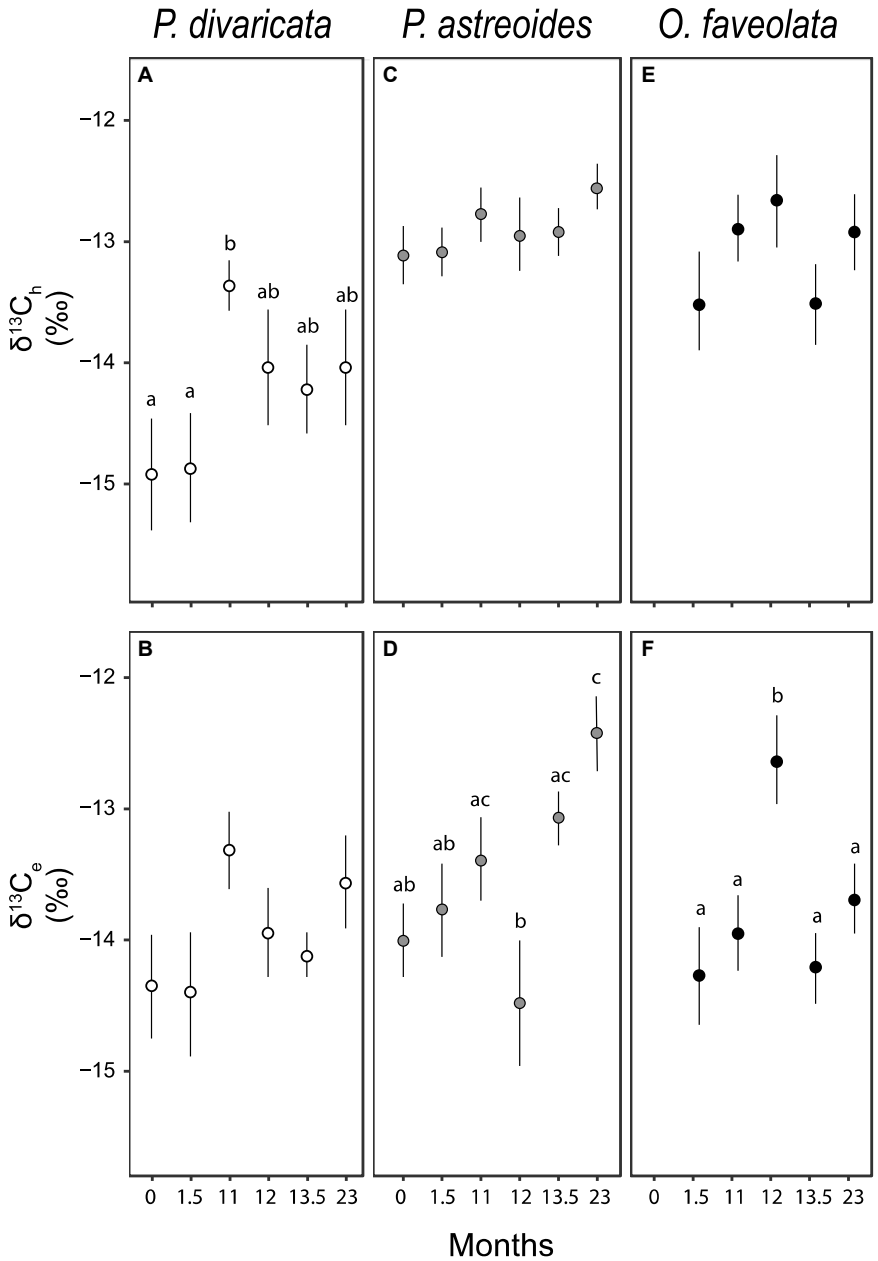

FIGURE 5 | Average (± 1 SE) stable carbon isotopic values of **(A,C,E)** the animal host ($\delta^{13}C_h$) and **(B,D,F)** endosymbiont ($\delta^{13}C_e$) fractions of *Porites divaricata* (white), *Porites astreoides* (gray), and *Orbicella faveolata* (black) at each time point (0 month = July 2009, 1.5 months = September 2009, 11 months = June 2010, 12 months = July 2010, 13.5 months = September 2010, and 23 months = June 2010). Sample sizes range from 5 to 9 for each average. All Kruskal-Wallis, ANOVA and Tukey *post hoc* results in **Supplementary Table 6**.

$\delta^{13}C_h$, $\delta^{13}C_s$, and $\delta^{13}O_s$ averages while *P. astreoides* had isotopically more depleted $\delta^{13}C_s$ and $\delta^{13}O_s$ than *O. faveolata* (**Figures 5**, **6** and **Supplementary Table 6**). To investigate further, changes in each isotopic trait over time were evaluated within each species.

While the $\delta^{13}C_h$ of *P. divaricata* differed over time with generally higher values in the second year, $\delta^{13}C_e$ did not (**Figures 5A,B** and **Supplementary Table 7**). In contrast, $\delta^{13}C_h$ in *P. astreoides* and *O. faveolata* did not change over time while their $\delta^{13}C_e$ values did (**Figures 5C–F** and **Supplementary Table 7**). For *P. astreoides*,$\delta^{13}C_e$ increased over the course of each year though only significantly so in the second year while $\delta^{13}C_e$ was highest at 12 months in *O. faveolata.*

Porites divaricata $\delta^{13}C_s$ exhibited a gradually declining trend over the course of the study, though significant differences were only detected between 11 and 13.5 months (**Figure 6A** and **Supplementary Table 7**). $\delta^{18}O_s$ also showed a gradually decreasing trend over the course of the study, though significant

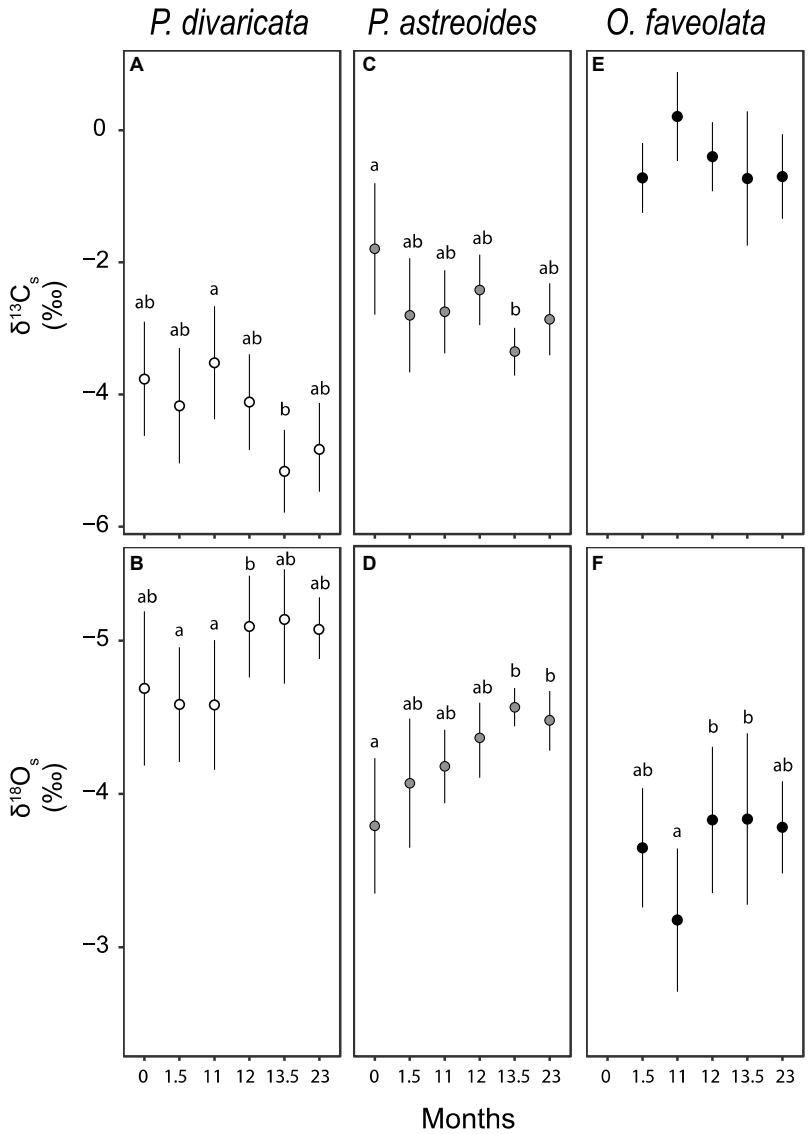

FIGURE 6 | Average (± 1 SE) skeletal stable **(A,C,E)** carbon ($\delta^{13}C_s$) and **(B,D,F)** oxygen ($\delta^{18}O_s$) isotopic values of *Porites divaricata* (white), *Porites astreoides* (gray) and *Orbicella faveolata (black)* at each time points (0 = July 2009, 1.5 = September 2009, 11 = June 2010, 12 = July 2010, 13.5 = September 2010, and 23 = June 2010). Sample sizes range from 5 to 9. Note that the y-axis values for $\delta^{18}O_s$ are inverted. All Kruskal-Wallis, ANOVA and Tukey *post hoc* results in **Supplementary Table 6**.

differences were only detected between 12 and 1.5 and 11 months (**Figure 6B** and **Supplementary Table 7**). In *P. astreoides*, $\delta^{13}C_s$ and $\delta^{18}O_s$ generally decreased over time while in *O. faveolata*$\delta^{13}C_s$ did not change over time and $\delta^{18}O_s$ was lowest at 11 months and highest at 12 and 13.5 months (**Figures 6C–F** and **Supplementary Table 7**).

DISCUSSION

While variations in coral physiological profiles over time were observed within and among all three species, calcification rate was the only trait that did not fluctuate over the 2-year period nor among species. This suggested that these species were stable in their habitat during this 2-year survey despite natural environmental and other physiological fluctuations.

Porites divaricata Differed From Both *Porites astreoides* and *Orbicella faveolata*

Porites divaricata exhibited strong temporal variability and was distinctly different from the other two species at the physiology profile and individual trait levels throughout most of the study (**Figures 2–4**). This species contained the highest relative concentrations of lipid, protein and carbohydrate despite having

the lowest biomass compared to *P. astreoides* and *O. faveolata* (**Figures 4B–D,J–L,R–T**), which is consistent with previous experimental studies using the same genets (e.g., Schoepf et al., 2015; Levas et al., 2018). *Porites divaricata* was the only species to exhibit temporal variability in all three of its energy reserves (i.e., lipids, protein, and carbohydrates) predominantly on an inter-annual basis (**Figures 4C–E**), suggesting that this species modulates these biomolecules in response to inter-annual variability in environmental conditions (e.g., heat wave events). The dynamic nature of lipids in *Porites* corals is well documented with post-bleaching catabolism of lipids *in P. divaricata* (e.g., Schoepf et al., 2015; Levas et al., 2018), seasonal variability in *P. compressa* lipids in Hawaii (Stimson, 1987), and intra and inter-annual variability in *Porites* sp. triacylglycerol (Carilli et al., 2012).

There was also noticeable temporal variability in chlorophyll *a* concentration with higher values the first year coupled with higher late summer concentrations compared to other time points (**Figure 4F**). This intra and inter- annual variability coupled with stable Symbiodiniaceae density indicates that *P. divaricata* modulates its chlorophyll *a* concentration per cell throughout the year most likely in response to seasonal temperature and light fluctuations (e.g., Brown et al., 1999; Hoogenboom et al., 2012). This suggests that *P. divaricata* is able to maintain their endosymbionts density across the range of temperatures experienced during the study. The trend in chlorophyll *a* was the same across all coral species, as they all show a cyclical pattern that most likely is driven by seasonal photoacclimation. In fact, all species appear to have photoacclimatized to the common garden location as suggested with the decrease in chlorophyll *a* after 1.5 months at the site (**Figures 4F,N,V**). Unfortunately, algal symbiont type was not monitored in our corals over time in our field study. However, algal symbiont type was quantified in ramets of the same coral genets in an accompanying bleaching experiment that showed that *P. divaricata* and *O. faveolata* shuffle their algal symbiont to favor more thermally tolerant ones following heat stress while *P. astreoides* cannot (Grottoli et al., 2014). Thus, photoacclimation in this field study occurred in all three species while algal symbiont types were probably shifting in two of the three species.

Porites divaricata $\delta^{13}C_{h-e}$ and $\delta^{13}C_h$ values were lower than in the other species (**Figures 4H,P,X**, 5A,C,E), suggesting that this coral incorporates a higher proportion of heterotrophically derived carbon that could be due to its higher uptake and/or lower release of dissolved organic carbon than the other two species (Levas et al., 2016). This is consistent with previous experimental studies showing the lowest $\delta^{13}C_h$ values in non-bleached control *P. divaricata* compared to the other two coral species (Schoepf et al., 2015; Levas et al., 2018). *Porites divaricata* was also the only species with natural intra- and interannual variability in $\delta^{13}C_h$ values (**Figure 5A**), suggesting that it has a greater capacity to modulate the proportion of heterotrophic derived carbon into its tissues on these time scales. Heterotrophic plasticity can lead to higher resilience in corals to global change (e.g., Grottoli et al., 2006; Hughes and Grottoli, 2013; Baumann et al., 2014; Conti-Jerpe et al., 2020), suggesting that *P. divaricata* may overcome thermal stress by increasing their heterotrophic acquisition of carbon. $\delta^{13}C_s$ values of *P. divaricata* were the lowest compared to the other species (**Figures 6A,C,E**), which is also consistent with higher heterotrophic incorporation (e.g., Carriquiry et al., 1994; Grottoli and Wellington, 1999). While decreased light can also result in lower $\delta^{13}C_s$ (e.g., Fairbanks and Dodge, 1979; Falkowski et al., 1984; Carriquiry et al., 1994; Grottoli and Wellington, 1999; Grottoli, 2002), all three species were exposed to the same light environment in the common garden, leaving only differences in heterotrophy as the most likely driver for the offset in $\delta^{13}C_s$ in *P. divaricata* compared to the other two species (**Figures 5**, **6**).

Porites astreoides and *Orbicella faveolata*

While the overall physiological profiles of *P. astreoides* and *O. faveolata* exhibited significant temporal variability, they typically did not differ from each other (**Figures 2–5**). This temporal variability was mostly driven by biomass, carbohydrates, chlorophyll *a*, and $\delta^{13}C_{h-e}$ in *P. astreoides* and the same variables plus Symbiodiniaceae density in *O. faveolata* (**Figure 4**). In addition to photoacclimation to the common garden site (**Figure 4N,V**), *P. astreoides* exhibited stable Symbiodiniaceae density through the survey suggesting a potential capacity to maintain their endosymbiont density across the range of temperatures experienced during the study (**Figure 4O**). *Orbicella faveolata* was the only species to show intra- and interannual variability in both chlorophyll *a* and Symbiodiniaceae density (**Figure 4W**). This is consistent with Fitt et al. (2000) observations on *O. faveolata*, showing a seasonality in both chlorophyll *a* and Symbiodiniaceae density with lower values in late summer/early fall compared to spring/winter. Thus, *O. faveolata* photoacclimated its pigments to the common garden conditions but additional modulation of Symbiodinaceae may be a compensating response to the range of temperatures experienced during the study. However, at heat stress temperatures that induce severe bleaching, Symbiodinaceaea density and chlorophyll *a* dramatically decrease in both species thought *O. faveolata* recovers faster than *P. astreoides* following repeat bleaching (Grottoli et al., 2014; Schoepf et al., 2015; Levas et al., 2018). The field observations presented here confirm that *O. faveolata* was able to increase their Symbiodiniaceae density in response to two consecutive years of warm summers whereas *P. astreoides* cannot.

Carbohydrates were the only energy reserve that varied over time and among all three species with the lowest values observed for *O. faveolata* (**Figures 4E,M,U**). Interestingly, both *Porites* species displayed the same temporal pattern with lower values in early summer (June) which then increased during summer (July) and decreased again for fall (for September 2010). It seems that the carbohydrate values mostly followed temperature fluctuations in 2010. Previous experimental studies demonstrated that all three coral species catabolized carbohydrates in responses to bleaching inducing heat stress, though *P. divaricata* consistently had the highest concentrations compared to the other two species

(e.g., Schoepf et al., 2015; Levas et al., 2018). The observed stable lipid and protein concentrations (**Figures 4C–D,K–L,S–T**) are consistent with other *in situ* and experimental data from *P. astreoides* and *O. faveolata* over time (e.g., Teece et al., 2011; Schoepf et al., 2015; Levas et al., 2018), but need to be considered with caution as we do not have results from *O. faveolata* at time 0 (July 2009).

P. astreoides and *O. faveolata* had higher $\delta^{13}C_{h-e}$ values than *P. divaricata* (**Figures 4H,P,X**), suggesting that the two former species incorporated a lower proportion of heterotrophically derived carbon into its tissues. This is not consistent with observations from manipulative tank experiments where $\delta^{13}C_{h-e}$ values were not always lowest for *P. divaricata* compared to *P. astreoides* and *O. faveolata* (e.g., Schoepf et al., 2015; Levas et al., 2018). This suggests that coral carbon budgets may change under experimental conditions or under more extreme heat stress conditions, and highlights the importance of field observations. Variation in $\delta^{13}C_{h-e}$ was driven by temporal variability in $\delta^{13}C_e$ values as $\delta^{13}C_h$ did not vary over time (**Figures 5C–F**), suggesting a stronger influence of photosynthetically derived carbon to the pool of carbon in tissues relative to heterotrophically derived carbon in both species. This is very interesting since *P. astreoides* and *O. faveolata* host very different dominant species of Symbiodiniaceae (Grottoli et al., 2014).

Implications for Coral Bleaching and Resilience

This long-term *in situ* study highlights the significant natural variability in coral physiological profiles among coral species and over time. The physiological profile and isotopic signatures of *P. divaricata* were distinct from *P. astreoides* and *O. faveolata* throughout the study. *Porites divaricata* had the highest energy reserve stores (i.e., lipids, protein, carbohydrates) and the highest heterotrophic tissue contributions of all three species—two traits that are associated with lower susceptibility and higher resilience against bleaching (e.g., Grottoli et al., 2006; Anthony et al., 2009; Conti-Jerpe et al., 2020). While these traits varied on an intra-annual basis, they were not necessarily higher in late summer or early fall as would be predicted if corals modulated energy reserves and heterotrophy on a seasonal basis as a strategic mechanism to buffer themselves seasonally warm waters in late summer and possible thermal stress. However, the timing of spawning in these species may play a large role in the temporal variations in lipid levels. In fact, *P. divaricata* spawning peaks in spring while *P. astreoides*' spawning season can last from January to September and *O. faveolata* from August to September (e.g., Szmant, 1986; McDermond, 2014). Thus, *P. divaricata* has a greater period of time to rebuild lipid levels lost during spawning before seawater temperatures reach maximum values in late summer. This may allow *P. divaricata* to be more competitive than *P. astreoides* and *O. faveolata* in a warming ocean where bleaching events can occur annually.

With comparable calcification rates among all species, there was also no apparent trade-off between skeletal growth and energy reserves or the relative contributions of photoautotrophic and heterotrophic carbon. Instead, consistently higher overall energy reserves and heterotrophic contributions to tissues in *P. divaricata* appear to buffer against intra- and interannual variability in environmental conditions, including bleaching events. However, the high variability in calcification among genets at 1.5 months when seawater temperature was the highest indicates that some individuals of all three species were stressed from the longer than usual warm period in 2009. Interestingly, despite a loss in symbiont density at 1.5 months, *O. faveolata* maintained calcification suggesting a high capacity to translocate carbon from the remaining Symbiodiniaceae or catabolism of lipid stores though additional research is needed to test this. Experimental evidence supports the buffering hypothesis (i.e., high energy reserves and heterotrophic capacity and/or plasticity) as *P. divaricata* was the most tolerant of the three species to repeated experimental bleaching stress with some capacity for shuffling to heat tolerant Symbiodiniaceae species as well (e.g., Grottoli et al., 2014; Schoepf et al., 2015; Levas et al., 2016). These strategies were also observed in manipulative experiments of bleached Hawaiian and Red Sea corals, where species with high energy reserves and/or heterotrophic carbon contributions are more tolerant to heat stress and/or recover more quickly (e.g., Grottoli et al., 2006; Rodrigues and Grottoli, 2007; Grottoli et al., 2017). Thus, variability in physiological profiles among coral species appears to be a better predictor for coral bleaching resilience than temporal, intra- and/or interannual physiological variability within a coral species.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: www.bco-dmo.org at www.bco-dmo.org/project/516103.

AUTHOR CONTRIBUTIONS

AG and MW designed the study. LC did the statistical approach, analyzed the data, and draft the manuscript. AG, VS, SL, and MA participated in the fieldwork. VS and MA carried out laboratory analyses. All authors contributed to revising the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.811055/full#supplementary-material

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