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Differences in Fatty Acids and Lipids of Massive and Branching Reef-Building Corals and Response to Environmental Changes

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Reef-building corals present various colony morphologies that may greatly influence their nutritional ecology. Fatty acids (FAs) and lipids are important components of corals and have been increasingly used to research the nutritional ecology of corals. In this study, we examined the symbiodiniaceae density, corallite area, total lipid content, and FAs composition of 14 species of corals with different colony morphologies. The results showed that the different colony morphology of coral was significantly correlated with the corallite area but not with the symbiodiniaceae density. Massive corals, with a large corallite area (7.16 ± 6.29 mm^2), could ingest a high quantity of food, leading to high levels of total lipid content and unsaturated FAs [particularly n-6 polyunsaturated FAs (PUFAs) and monounsaturated FAs]. For branching corals, the total lipid content and saturated FAs (SFAs, 16:0 and 18:0) were significantly positively correlated with the Symbiodiniaceae density, indicating that branching corals are predominantly autotrophic. Moreover, compared with healthy corals, bleached corals consume larger amounts of stored energy (such as lipids and SFAs) to maintain their normal physiological functions. Although bleached corals may obtain PUFAs from heterotrophic assimilation or biosynthesize, the efficiency is too low to sufficiently replenish essential PUFAs in a short time. Overall, massive corals with more initial total lipid content and PUFAs exhibit an advantage under adverse environmental conditions.

Keywords: colony morphology, reef-building coral, fatty acids, nutritional ecology, total lipid content

1 INTRODUCTION

Reef ecosystems are among the world's most productive and biodiverse marine ecosystems (Hughes et al., 2017; Conti-Jerpe et al., 2020). Reef-building corals, or scleractinians, are distinct organisms in reef ecosystems and play fundamental roles as ecosystem engineers (Jones and Ray, 2011; Martínez-Castillo et al., 2020). Scleractinian skeletons are mainly composed of calcium carbonate (aragonite), which maintains the shape of their polyps. They also exhibit various colony morphologies, such as massive, branching, columnar, laminar, corymbose, and digitate (Veron, 2000). The different colony morphologies of scleractinians often show diverse symbiodiniaceae density (Thornhill et al., 2011), corallite width (Loya et al., 2001), and tissue thickness (Edmunds et al., 2014). Importantly, these differences may strongly influence coral nutritional ecology parameters, such as energy storage (Pupier et al., 2021), trophic strategies (Radice et al., 2019; Conti-Jerpe et al., 2020), and even response mechanisms to environmental changes (Loya et al., 2001; Hughes et al., 2017), which can affect the evolution of coral communities.

Lipid reserves serve as a universal proxy for the health status of corals (Conlan et al., 2017; Bhojoo et al., 2018). Fatty acids (FAs), the primary components of lipids, play important roles in energy storage, cell membrane structure, and overall fitness (Berge and Barnathan, 2005; Farre et al., 2010). Therefore, lipid content and FAs composition have been investigated as tools for understanding the resistance and resilience of corals under environmental stress (Baumann et al., 2014; Grottoli et al., 2014; Schoepf et al., 2015; Chapron et al., 2022). For instance, numerous studies demonstrated that corals depend on initial lipid stores to survive during bleaching events (Rodrigues et al., 2008; Baumann et al., 2014; Tagliafico et al., 2017). Chapron et al. (2022) also found that corals with higher overall energy reserves and heterotrophic contributions to tissues can better buffer against environmental stress. Moreover, Teece et al. (2011) demonstrated that the supplement of n-3 polyunsaturated FAs (PUFAs) and saturated FAs (SFAs) is important for coral to sustain growth under turbid conditions. As such, analyses of lipid content and FAs are important aspects of understanding coral nutritional ecology.

Because of the influence of climate change and intensified anthropogenic factors, numerous coral bleaching events and the resultant mortality have been reported in various geographical areas (Loya et al., 2001; Grottoli et al., 2006; Hughes et al., 2017). Notably, changes in the community structure and species diversity of corals before and after a bleaching event are morphology specific. Kayanne et al. (2010) found that massive Porites had higher bleaching resilience or recovery capacity than branching Acropora and Porites in the 1998 bleaching event on Ishigaki Island. Moreover, Loya et al. (2001) suggested that colony morphology affected bleaching vulnerability and subsequent coral mortality; massive corals are the "winners," and branching corals are the "losers" in coral bleaching. Although colony morphology of coral affects bleaching vulnerability and subsequent mortality, few studies have focused on these effects from the perspective of nutritional ecology (Baker et al., 2015; Conti-Jerpe et al., 2020).

Therefore, in the present study, we assessed Symbiodiniaceae density, corallite area, total lipid content, and FAs composition of corals with different colony morphology, including healthy and bleached samples. This study aimed to determine the differences in total lipid content and FAs composition between massive and branching corals, and between healthy and bleached samples, to understand the morphology specificity of coral nutritional ecology. These findings could provide a theoretical basis for evaluating and predicting the changes in the community structure and species diversity of corals.

2 MATERIALS AND METHODS

2.1 Corals Sampling

On November 2–3, 2018, 14 specimens of reef-building corals (**Table 1**) belonging to nine genera (seven families) were collected by SCUBA in the Luhuitou fringing reef (3 m depth) at the Tropical Marine Biological Research Station in Hainan, Chinese Academy of Sciences (18°14′N, 109°28′E). Moreover, three bleached Acropora spp. (A. florida, A. nana, and A. intermedia) were also sampled after a tropical cyclone on December 28, 2018. Images were collected using a camera

TABLE 1 | Families, genera, species, and colony morphology of the collected samples.

No.	Families	Genera	Species	Colony morphology
ACR1	Acroporidae	*Acropora*	*Acropora hyacinthus*	Branching
ACR2	Acroporidae	*Acropora*	*Acropora nana*	Branching
ACR3	Acroporidae	*Acropora*	*Acropora digitifera*	Branching
ACR4	Acroporidae	*Acropora*	*Acropora florida*	Branching
ACR5	Acroporidae	*Acropora*	*Acropora muricata*	Branching
ACR6	Acroporidae	*Acropora*	*Acropora intermedia*	Branching
POC	Pocilloporidae	*Pocillopora*	*Pocillopora damicornis*	Branching
PAV	Agariciidae	*Pavona*	*Pavona decussata*	Branching
POR1	Poritidae	*Porites*	*Porites lutea*	Massive
POR2	Poritidae	*Porites*	*Porites lobata*	Massive
PLA	Merulinidae	*Platygyra*	*Platygyra acuta*	Massive
GAL	Euphylliidae	*Galaxea*	*Galaxea fascicularis*	Massive
COE	Merulinidae	*Coelastrea*	*Coelastrea aspera*	Massive
HYD	Merulinidae	*Hydnophora*	*Hydnophora exesa*	Massive

(TG-6, Tokyo, Olympus, Japan) before sampling. All coral specimens were identified by taxonomists at the South China Sea Institute of Oceanology, Chinese Academy of Sciences. From October 2018 to January 2019, the temperature (°C) and light intensity (lux) of the sampling area were monitored continuously at 2-h intervals using a HOBO logger (UA-002-64, Onset Computer, Bourne, MA, USA) (**Figure 1**). The HOBO logger was cleaned weekly to reduce the interference of algae, sediment, and other fouling organisms as much as possible.

Healthy (n = 8) and bleached (n = 3) samples from different colonies (3–5 cm fragments) of each coral species were collected and immediately transported to the laboratory, where they were divided into two subsamples. One subsample (healthy, n = 5; bleached, n = 3) was freeze-dried in a vacuum freezing dryer (Biosafer-21A, Duhong Biological Technology Co., Ltd., Guangzhou, China), crushed into 0.1–0.3-mm pieces, and then frozen at −80°C until analyses of the total lipid content and FA composition. The other subsample (healthy, n = 3) was stored at −20°C until analyses of the Symbiodiniaceae density and corallite area.

2.2 Symbiodiniaceae Density

The Symbiodiniaceae density in the coral tissues was evaluated as described by Martínez-Castillo et al. (2020) with some modifications. Coral tissues were removed from the coral fragment using jets of pressurized air in filtered seawater (~1 ml) until only the white coral skeleton was visible. The tissue slurry was homogenized using a hand-held blender (MY-10, Jingxin Technology, Jiangsu, China) for 45 s and centrifuged (3,000×g, 5 min; Microfuge 20, Beckman Coulter, Brea, CA, USA); the supernatant was then removed. The process was repeated three times. The number of Symbiodiniaceae per slurry volume was counted using hemocytometer plates with four replicate counts. The total number of Symbiodiniaceae per area was calculated based on the volume of the homogenate and coral surface area ($\times 10^6$ cells cm^{-2}). The coral surface area was measured using a structured light 3D scanner (JTscan-MS, Guangzhou Jeatech Electronics Technology Co., Ltd., Guangdong, China).

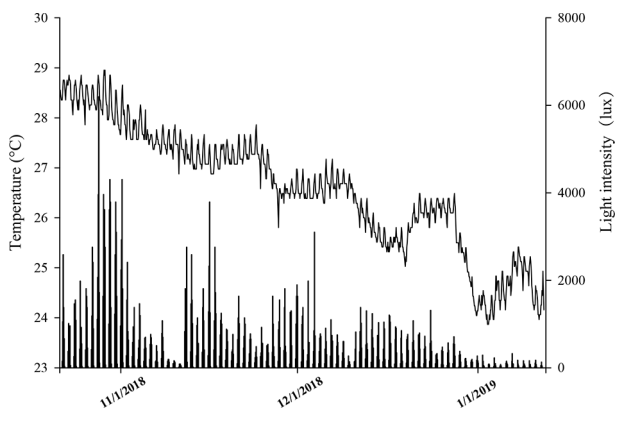

FIGURE 1 | The temperature (°C) and light intensity (lux) of Luhuitou fringing reef (3m) from October 2018 to January 2019.

2.3 Corallite Area

Given that the shape of coral corallite is irregular, the area of the corallite (mm^2) was measured as described by Conti-Jerpe et al. (2020). Images of the skeleton of each sample were captured under a microscope (CX31, Olympus, Japan) after determining the Symbiodiniaceae density, and ImageJ software (version 1.8.0; NIH, Bethesda, MD, USA) was used to calculate the area of the coral corallite (mm^2) for 10 replicates.

2.4 Total Lipid Content

To ensure the accuracy of the measurement of the total lipid content and prevent the oxidation of FAs, total lipid content and FA composition were assessed separately. The crushed samples (approximately 0.5 g) were packed in a filter paper, and lipids were extracted using a Soxhlet extractor (AG-SXT-06, Shanghai Ouge Electronics Co., Ltd., Shanghai, China). Petroleum ether (boiling point, 60°C–90°C) was used as the solvent, and a thermostat-heating mantle was used to maintain 90°C for 5 h. The total lipid content was considered as the difference in sample weight between before and after the extraction.

Total lipid content was measured in crushed whole coral samples (skeleton, animal tissue, and Symbiodiniaceae), normalized to the dry weight, and expressed as a percentage (g lipid/g dry weight).

2.5 Fatty Acid Methyl Esters Obtention and Analysis

Approximately 1-g sample (dry weight) from each sample was analyzed. The samples were homogenized, and each lipid fraction was extracted using chloroform/methanol (2:1, v/v) containing 0.01% butylated hydroxytoluene as an antioxidant, as previously described by Liu et al. (2019). The chloroform layer was separated from the methanol layer and dried to a constant weight under a stream of nitrogen to obtain the total lipid content.

Fatty acid methyl esters (FAMEs) were obtained by esterification with 2 ml methyl esterification reagent (hydrochloric acid/methanol, 1:5, v/v) at 90°C for 3 h, as described by Liu et al. (2018). The upper phase was dried under nitrogen and resuspended in hexane.

FAMEs were quantified by injecting 1 μl of sample into a gas chromatograph instrument (GC-2010 Plus; Shimadzu, Kyoto, Japan) equipped with a flame-ionization detector (GC-2010; Shimadzu, Kyoto, Japan) and an RTX-WAX fused-silica capillary column (length, 30 m; internal diameter, 0.25 mm; thickness, 0.25 μm; Phenomenex, Torrance, CA, USA). The gradient temperature program was set as follows: (i) initial temperature of 60°C for 1.0 min; (ii) increase at a rate of 10°C min^{-1} to 190°C; (iii) increase at 2.0°C min^{-1} to 260°C; and (iv) hold at 260°C for 0.6 min. The FAMEs were identified and quantified by comparing the retention times (identification) and peak areas (quantification) with the 37-FAME Mix calibration solution (Supelco, Bellefonte, PA, USA).

2.6 Statistical Analyses

R software version 3.5.2 (The R Project for Statistical Computing, Vienna, Austria) was used for statistical analyses. The distribution of the data was evaluated for normality using the Kolmogorov–Smirnov test ($p > 0.05$). Levene's test ($p > 0.05$) was

used to assess the homogeneity of variance. Data of massive and branching samples were then evaluated by t-test analysis to identify significant differences ($p < 0.05$). The correlation of total lipid content between the Symbiodiniaceae density and corallite area was determined using Pearson's product-moment correlation with the package "corrplot," and the FA composition of corals between massive and branching corals was characterized using multivariate principal component analyses with the package "vegan" (Oksanen et al., 2010). Graphs were prepared using the ggplot2 package (Wickham, 2016).

To facilitate a comparison of FA compositions, we calculated the unsaturation index (UI) and the unsaturated-to-saturated fatty acid ratio (U/S) as reported by Snyder et al. (2012) and Wallaert and Babin (1994). The UI and U/S algorithms were as follows:

$$UI = \sum(\%\ \text{monoenes} + 2 \times \%\ \text{dienes} + 3 \times \%\ \text{trienes} \ldots)/100$$

$$U/S = \sum(\%\ UFA)/\sum(\%\ SFA)$$

where monoenes, dienes, and trienes … are FAs containing 1, 2, 3…double bonds, respectively; % is the weight percentage; UFA indicates unsaturated FA; and SFA indicates saturated FA.

3 RESULTS

3.1 Symbiodiniaceae Density and Corallite Area

The Symbiodiniaceae density and corallite area are shown in **Tables 2**, **3**. The Symbiodiniaceae density ranged from 1.96×10^6 (A. nana) to 1.02×10^6 cells cm^{-2} (Platygyra acuta). The average Symbiodiniaceae density of the massive and branching corals were $1.50 \pm 0.26 \times 10^6$ and $1.55 \pm 0.36 \times 10^6$ cells cm^{-2}, respectively. There was no significant difference ($p > 0.05$) in the Symbiodiniaceae density between the massive and branching corals.

The corallite area of massive corals (7.19 ± 6.24 mm^2) was significantly larger ($p < 0.05$) than that of the branching corals (0.69 ± 0.25 mm^2). P*latygyra* acuta showed the largest corallite area (17.35 ± 5.11 mm^2), followed by Coelastrea aspera (10.33 ± 2.02 mm^2), and *Pocillopora* damicornis showed the smallest area (0.44 ± 0.12 mm^2).

TABLE 3 | Correlations of total lipid content (TL) of massive and branching corals with corallite area (CA) and Symbiodiniaceae density (SD).

	Branching corals		Massive corals	
	r	*p*	*R*	*p*
TL × CW	0.107	0.801	0.941	0.005
TL × ZD	0.875	0.004	–0.586	0.222

3.2 Total Lipid Content

The total lipid content of the 14 species of scleractinians are shown in **Table 2**. Among all species, the highest total lipid content was observed in P. acuta ($10.81 \pm 0.96\%$), followed by Galaxea fascicularis ($9.61 \pm 1.16\%$), whereas P. damicornis showed the lowest total lipid content ($2.90 \pm 0.20\%$). The total lipid content varied with the colony morphology. Overall, the branching corals ($3.60 \pm 0.36\%$) showed lower lipid content than massive corals ($7.45 \pm 2.87\%$) (**Table 2**). Moreover, the total lipid

TABLE 2 | Levels of TL (%), CA (mm^2), SD ($\times 10^6$cells cm^{-2}), SFAs (%), MUFAs (%), PUFAs (%), n-3 PUFAs (%), n-6 PUFAs (%), U/S, and UI of massive and branching corals.

	Branching corals									Massive corals					*p*-value
	ACR1	ACR2	ACR3	ACR4	ACR5	ACR6	POC	PAV	POR1	POR2	PLA	GAL	COE	HYD	
TL	3.86 ± 0.46	4.34 ± 0.31	3.67 ± 0.15	3.76 ± 0.41	3.56 ± 0.15	3.43 ± 0.26	2.90 ± 0.35	3.52 ± 0.21	4.93 ± 0.21	4.09 ± 0.26	10.81 ± 1.32	9.61 ± 1.05	9.56 ± 0.77	5.69 ± 0.51	0.0024
CA	0.86 ± 0.10	0.72 ± 0.06	0.61 ± 0.04	0.62 ± 0.03	0.79 ± 0.07	1.16 ± 0.07	0.44 ± 0.03	1.33 ± 0.06	1.35 ± 0.05	1.09 ± 0.07	17.35 ± 2.56	8.71 ± 1.70	10.33 ± 2.96	4.34 ± 0.52	0.0128
SD	1.81 ± 0.06	1.96 ± 0.05	1.43 ± 0.03	1.36 ± 0.03	1.41 ± 0.04	1.13 ± 0.04	1.44 ± 0.04	1.45 ± 0.02	1.83 ± 0.05	1.77 ± 0.05	1.02 ± 0.06	1.84 ± 0.03	1.22 ± 0.04	1.54 ± 0.05	0.8359
SFAs	63.90 ± 0.51	62.56 ± 0.89	60.62 ± 0.89	60.54 ± 1.70	62.33 ± 1.20	64.20 ± 0.66	59.68 ± 1.01	63.61 ± 1.28	55.71 ± 1.07	55.49 ± 1.05	54.82 ± 1.46	55.82 ± 1.99	56.39 ± 1.00	53.70 ± 1.18	<0.0001
MUFAs	7.59 ± 0.39	7.58 ± 0.20	9.51 ± 0.55	9.96 ± 0.98	8.91 ± 0.20	7.40 ± 0.20	10.41 ± 0.14	8.31 ± 0.05	7.37 ± 0.26	6.31 ± 0.51	15.495 ± 0.56	18.00 ± 0.86	8.35 ± 0.69	9.90 ± 0.26	0.2149
PUFAs	28.21 ± 0.60	28.58 ± 1.08	29.64 ± 0.33	29.50 ± 0.88	28.76 ± 0.12	28.15 ± 0.68	29.91 ± 0.38	28.08 ± 1.25	36.89 ± 0.91	37.24 ± 0.54	29.70 ± 0.91	26.18 ± 1.14	35.26 ± 1.38	36.39 ± 1.43	0.0439
n-3PUFAs	21.05 ± 0.44	22.61 ± 0.19	22.35 ± 0.40	21.33 ± 0.75	21.84 ± 0.37	20.68 ± 0.46	23.82 ± 0.38	17.83 ± 0.87	22.50 ± 0.30	24.15 ± 0.83	15.14 ± 0.41	13.61 ± 1.8	21.57 ± 0.90	21.48 ± 0.35	0.1866
n-6PUFAs	7.46 ± 0.32	7.25 ± 0.90	7.52 ± 0.39	8.17 ± 0.36	6.92 ± 0.47	7.72 ± 0.22	9.10 ± 0.26	10.58 ± 0.45	14.39 ± 0.63	14.05 ± 0.33	14.56 ± 0.55	12.57 ± 0.66	13.69 ± 0.54	14.91 ± 1.15	0.0005
U/S	0.56 ± 0.01	0.58 ± 0.02	0.64 ± 0.02	0.65 ± 0.05	0.60± 0.01	0.55 ± 0.02	0.68 ± 0.01	0.57± 0.03	0.79 ± 0.03	0.80 ± 0.03	0.82 ± 0.05	0.79 ± 0.07	0.77 ± 0.03	0.86 ± 0.04	<0.0001
UI	1.27 ± 0.01	1.27 ± 0.04	1.39 ± 0.02	1.31 ± 0.04	1.31± 0.01	1.27 ± 0.03	1.33± 0.01	1.19 ± 0.06	1.51 ± 0.03	1.55 ± 0.03	1.298± 0.03	1.25 ± 0.07	1.47 ± 0.05	1.46 ± 0.02	0.0257

Values are presented as mean ± SD.

TL, total lipid content; CA, corallite area; SD, symbiodiniaceae density; SFAs, saturated fatty acids; MUFAs, monounsaturated fatty acids; PUFAs, polyunsaturated fatty acids; n-3 PUFAs, Omega-3 series polyunsaturated fatty acids; n-6 PUFAs, Omega-6 series polyunsaturated fatty acids; U/S, the unsaturated-to-saturated fatty acid ratio; UI, the unsaturation index.

content of branching corals was positively correlated with the Symbiodiniaceae density but unrelated to the corallite area. In contrast, the total lipid content of massive corals was positively correlated with the corallite area but not with the symbiodiniaceae density (**Table 3**).

Compared to healthy corals, a significant decrease in total lipid content was found in the bleached coral samples (**Figure 2**), which accounted for only approximately 25% of the total lipid content of the healthy group. The average total lipid content was 3.84 ± 0.49% for healthy corals and 1.01 ± 0.16% for bleached corals.

3.3 FA Composition

3.3.1 FA Composition of Branching and Massive Corals

A total of 18–25 FAs were found in all corals, including 6–9 SFAs, 3–6 monounsaturated fatty acids (MUFAs), and 8–10 PUFAs. For all corals, the proportion of SFAs, MUFAs, and PUFAs were 55.49%–64.20%, 6.31%–17.84%, and 25.11%–38.21%, respectively. Moreover, 16:0 and 18:1n9 were predominant in SFAs and MUFAs, respectively. However, the largest proportion of PUFAs is significantly different among the varieties of coral species.

Most specimens studied belonged to two colony morphologies (branching and massive), making them suitable for examining the relationship between the coral FA composition and colony morphology. Therefore, all FA compositions were used for principal coordinate analysis (PCA), and the results are shown in **Figure 3**. The first two components explained 81.15% of the total data variance. Branching corals showed great clustering, mainly because of differences in the levels of SFAs (such as 16:0 and 14:0) and n-3 PUFAs (such as 20:5n3). However, massive corals were subdivided into two parts; G. fascicularis, C. aspera, and P. acuta have high proportions of MUFAs (such as 16:1n7 and 18:1n9), whereas Hydnophora exesa, Porites lutea, and *Porites* lobata showed high levels of PUFAs, (18:3n3, 18:2n6, and 22:6n3). Hence, both U/S and UI of massive corals (except for G. fascicularis) were higher than those of branching corals. Generally, the colony morphology of coral was significantly correlated with SFAs, n-6PUFAs, and PUFAs (**Table 2**). Compared with branching corals, massive corals showed higher levels of PUFAs (particularly n-6 PUFAs) and lower levels of SFAs.

3.3.2 FA Composition of Healthy and Bleached Corals

The differences in the FA composition between healthy and bleached corals are shown in **Table 4** and **Figure 4**. The three species of bleached corals exhibited the same trends in the changes in FAs. The concentrations of both SFAs (such as 14:0, 16:0, and 18:0) and UFAs (such as 16:1n7, 18:1n9, 20:3n3, 20:5n3, and 22:6n3) of the bleached corals were significantly lower than those of healthy corals, especially SFAs, showing reductions of nearly 50% (average value: healthy, 1,743.23 μg g^{-1}; bleached, 865.13 μg g^{-1}). Changes in the PUFAs of bleached corals were even greater. In bleached corals, the levels of C_{20-22} PUFAs (such as 20:3n3, 20:5n3, and 22:6n3) were significantly lower (average value: healthy, 549.41 μg g^{-1}; bleached, 223.50 μg g^{-1}), whereas those of C_{18} PUFAs (such as 18:2n6, 18:3n3, and 18:3n6) (average value: healthy, 263.27 μg g^{-1}; bleached, 273.53 μg g^{-1}) were significantly higher than in healthy corals.

4 DISCUSSION

4.1 Total Lipid Content and FAs Composition in Branching and Massive Corals

4.1.1 Total Lipid Content

The total lipid content of massive corals was higher than that of the branching corals. Corroborating the present research, Rotmann and Thomas (2012) and Yost et al. (2013) demonstrated that

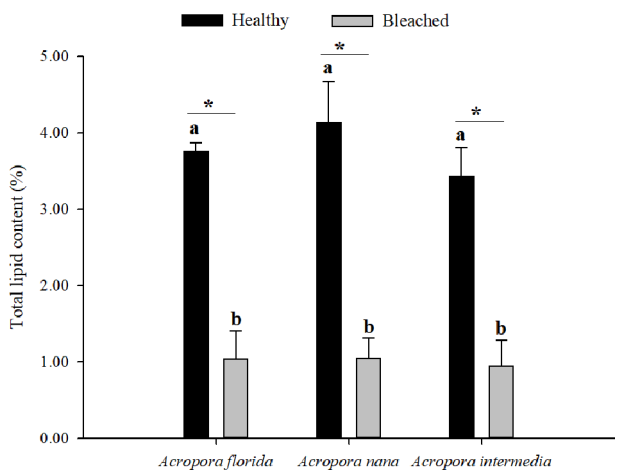

FIGURE 2 | Total lipid content (%) of healthy (n = 5) and bleaching (n = 3) corals. Note: Values are mean ± SD. The different letters mean a significant difference between healthy and bleaching coral for all samples ($p < 0.05$); the "*" means a significant difference between healthy and bleaching samples for each species ($p < 0.05$).

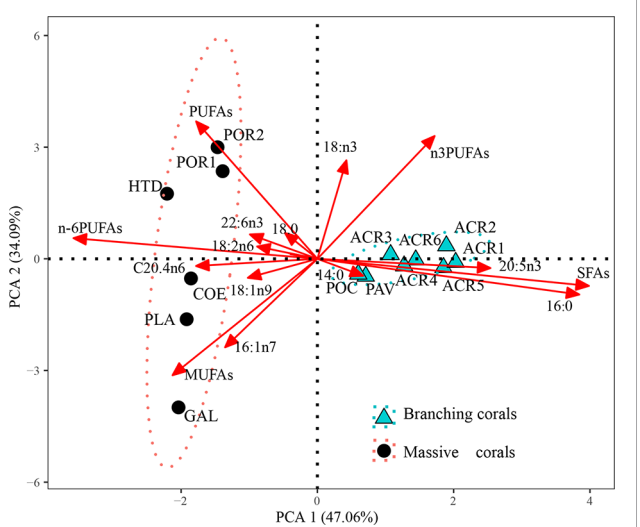

FIGURE 3 | Principal component analysis (PCA) of fatty acids (% of total fatty acids) of massive (black round) and branching (green triangle) corals (only healthy corals).

TABLE 4 | Concentration of FAs (μg g^{-1}) of bleached (n = 3) and healthy corals (n = 5).

	Acropora nana (ACR2)			*Acropora florida* (ACR4)			*Acropora intermedia* (ACR6)		
	Healthy	**Bleached**	***p-value***	**Healthy**	**Bleached**	***p-value***	**Healthy**	**Bleached**	***p-value***
10:0	–	–	–	–	–	–	8.033 ± 3.36	–	0.0144
12:0	2.70 ± 0.36	–	0.0002	–	–	–	–	–	–
14:0	114.43 ± 9.36	16.72 ± 1.11	0.0001	124.02 ± 8.11	39.63 ± 3.49	0.0001	102.42 ± 7.56	49.06 ± 4.36	0.0004
15:0	2.95 ± 0.33	–	0.0001	–	–	–	–	–	–
16:0	966.25 ± 34.69	444.59 ± 40.21	0.0001	1153.73 ± 45.66	435.90 ± 31.22	0.0000	1117.19 ± 89.23	453.88 ± 50.11	0.0004
17:0	2.95 ± 0.15	–	0.0000	–	–	–	–	–	–
18:0	383.60 ± 19.13	272.70 ± 21.22	0.0026	467.36 ± 11.32	330.94 ± 13.65	0.0002	496.91 ± 8.98	342.85 ± 30.54	0.0011
20:0	15.49 ± 2.33	–	0.0003	23.29 ± 4.65	–	0.0010	31.559 ± 3.32	–	0.0001
22:0	5.41 ± 0.23	–	0.0000	9.68 ± 3.36	–	0.0075	10.90 ± 1.36	–	0.0002
23:0	44.51 ± 5.87	24.59 ± 4.44	0.0095	71.39 ± 6.32	49.005 ± 6.15	0.0118	74.88 ± 10.21	50.21 ± 10.47	0.0432
SFAs	1538.31	843.93	0.0002	1849.49	855.47	0.0001	1841.9	895.99	0.0005
14:1n5	3.18 ± 1.13	–	0.0086	–	–	–	–	–	–
16:1n7	55.32 ± 6.63	36.39 ± 4.44	0.0148	72.6 ± 7.52	39.93 ± 3.57	0.0025	56.81 ± 8.11	23.24 ± 3.11	0.0026
17:1n7	5.16 ± 0.51	–	0.0001	–	–	–	–	–	–
18:1n9	85.33 ± 4.12	62.46 ± 8.15	0.0123	159.12 ± 6.61	143.09 ± 12.37	0.1191	103.00 ± 5.21	107.87 ± 15.11	0.6256
20:1n9	29.51 ± 2.21	10.57 ± 1.24	0.0002	40.23 ± 4.08	7.26 ± 1.58	0.0002	34.71 ± 3.31	9.47 ± 2.23	0.0004
22:1n9	6.64 ± 0.94	–	0.0003	13.31 ± 1.17	–	0.0000	17.79 ± 2.21	–	0.0002
MUFAs	186.15	109.43	0.0033	285.26	190.27	0.0033	212.31	140.58	0.0111
18:2n6	29.02 ± 3.32	76.72 ± 9.21	0.0011	87.42 ± 5.12	99.52 ± 4.32	0.0354	43.61 ± 4.11	108.45 ± 15.17	0.0020
18:3n3	230.41 ± 15.98	265.24 ± 7.71	0.0273	186.04 ± 11.13	222.94 ± 13.57	0.0220	174.43 ± 13.34	218.33 ± 20.12	0.0345
18:3n6	31.72 ± 2.15	66.15 ± 6.67	0.0010	–	40.54 ± 3.91	0.0001	7.17 ± 1.12	32.71 ± 4.22	0.0005
20:2n6	4.92 ± 0.12	–	0.0000	14.22 ± 2.11	–	0.0003	12.62 ± 1.88	–	0.0003
20:3n3	37.62 ± 2.31	15.74 ± 3.11	0.0006	35.70 ± 5.12	8.17 ± 1.19	0.0008	31.27 ± 4.36	26.97 ± 3.54	0.2554
20:3n6	52.13 ± 3.37	30.98 ± 6.62	0.0079	52.33 ± 7.31	26.62 ± 5.88	0.0090	59.39 ± 5.51	46.76 ± 7.21	0.0735
20:4n6	57.54 ± 4.19	31.23 ± 2.21	0.0007	87.12 ± 6.33	35.09 ± 5.12	0.0004	98.69 ± 3.89	61.11 ± 11.32	0.0056
20:5n3	148.77 ± 7.71	52.38 ± 6.15	0.0001	242.00 ± 11.02	91.66 ± 7.56	0.0000	205.13 ± 13.57	85.50 ± 6.67	0.0002
22:2n6	1.97 ± 0.07	–	0.0000	–	–	–	–	–	–
22:6n3	139.18 ± 13.31	40.82 ± 4.41	0.0003	185.43 ± 10.04	58.08 ± 7.64	0.0001	182.18 ± 8.84	59.39 ± 8.14	0.0001
PUFAs	733.27	569.26	0.0188	890.26	582.62	0.0022	814.51	639.21	0.0225

Values are mean ± SD.

MUFAs, monounsaturated fatty acids; PUFAs, polyunsaturated fatty acids; SFAs, saturated fatty acids; "–", not detected.

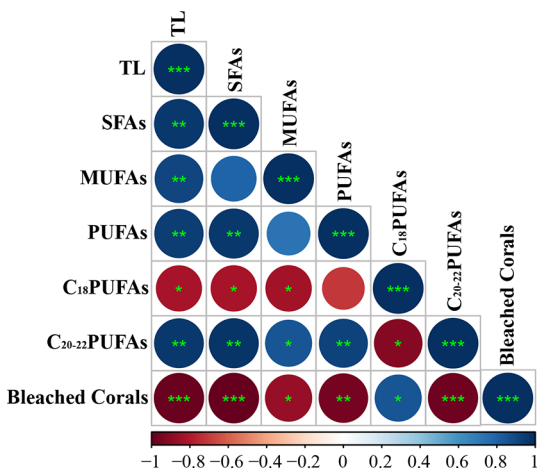

FIGURE 4 | Heatmap of the correlation relationship between bleached corals and FAs composition (SFA, PUFAs, MUFAs, C_{18} PUFAs, and $C_{20–22}$ PUFAs, %) and total lipid content (TL, %). Note: MUFA, monounsaturated fatty acid; PUFA, polyunsaturated fatty acid; SFA, saturated fatty acid; C_{18}PUFA, 18-carbon chain PUFA; $C_{20–22}$PUFA, 20–22-carbon chain PUFA. The symbols "*","**," and "****" represent statistically significant results "$p < 0.05$," "$p < 0.01$," and "$p < 0.001$," respectively. Heatmap color is presented as Pearson correlation coefficients whereby 1 (blue) is a total positive linear correlation, 0 (white) is no linear correlation, and −1 (red) is total negative linear correlation.

massive corals stored more energy-source molecules, such as lipids, than branching corals did. This may be because of the morphology specificity of the trophic pattern. Although autotrophy is the main lipid source of corals, there is also a non-negligible lipid input through heterotrophy (Rossi et al., 2020; Pupier et al., 2021). Corals can take up plankton, suspended particles, and dissolved organic material, particularly poor-swimming and mid-sized (200–400 μm) zooplankton organisms, which are important sources of lipid supplementation for corals (Palardy et al., 2005; Palardy et al., 2008; Houlbrèque and Ferrier-Pagès, 2009). Furthermore, the corallite area of massive corals was larger than that of branching corals (**Table 2**) and was positive with total lipid content (**Table 3**). Corallites are cup-like skeletal structures containing individual coral polyps, and thus, the corallite area is a good proxy for polyp size—a key functional trait linked to nutrient acquisition (Todd et al., 2004; Conti-Jerpe et al., 2020). Palardy et al. (2005) found that the feeding rates in the mounding (or massive) coral Pavona clavus were higher than in the branching coral P. damicornis. Therefore, massive corals, with large corallite area, present a high heterotrophic capacity, which may lead to higher total lipid content than that of branching corals.

4.1.2 FA Composition

Colony morphology was significantly correlated with SFAs and PUFAs (mainly in n-6 PUFAs). The composition of SFAs (such as 14:0, 16:0, and 18:0) were more than 50% for all samples,

particularly in branching corals (>60%), which is consistent with previous studies (Iluz and Dubinsky, 2015; Conlan et al., 2017). Photosynthesis of Symbiodiniaceae is the most important SFA source (Yamashiro et al., 1999). Bishop and Kenrick (1980) demonstrated that approximately 20%–40% of SFAs (such as 10:0, 16:0, and 18:0) in corals are obtained from Symbiodiniaceae. Moreover, in our study, the total lipid content was positively correlated with the Symbiodiniaceae density in branching corals, indicating that branching corals are predominantly autotrophic.

Branching corals contained a high level of 20:5n3, whereas 18:3n3, 20:4n6, and 22:6n3 were abundant in massive corals (**Figure 3**). The PUFAs profile of coral was significantly affected by Symbiodiniaceae (Teece et al., 2011; Pupier et al., 2021). Zhukova and Titlyanov (2003) demonstrated that Symbiodiniaceae isolated from P. damicornis had higher 20:5n3 (11.2%) and 22:6n3 (10.7%), whereas those isolated from Millepora intricata had higher 18:4n3 (26.2%). Furthermore, biosynthesis of PUFAs by Symbiodiniaceae is a complex and variable process (Neuringer et al., 1988; Chen et al., 2015), and it can also be regulated by the coral hosts (Imbs et al., 2007). Overall, the specific UFAs in coral hosts and Symbiodiniaceae lead to the differences in UFAs in different corals.

FAs composition of corals has not only different biosynthetic origins but also different biological sources. Various foods consumed by corals have different characteristics FAs (Kattner and Hagen, 2009; Imbs et al., 2010). The diversity in quantity and quality of food and randomness of food uptake result in uncertainty in the FAs composition of coral. Therefore, massive corals have a large corallite area, which takes up a wide range of foods, leading to FA composition more discrete than that of branching corals. Furthermore, three large corallite massive corals (G. fascicularis, C. aspera, and P. acuta) showed higher proportions of MUFAs (16:1n7 and 18:1n9) compared to other corals. MUFAs have been confirmed as the trophic marker of herbivorous microzooplankton (Dalsgaard et al., 2003; Imbs et al., 2010). A similar result for this species was reported by Radice et al. (2019), who showed that G. fascicularis contains a high proportion of MUFAs derived from copepods.

4.2 Total Lipid Content and FAs Composition in Bleached and Healthy Corals

Most corals maintain an endosymbiotic association with algae of the family Symbiodiniaceae (Radice et al., 2019). However, the symbiotic relationship is fragile and may collapse because of adverse environmental changes, provoking coral bleaching (whitening of corals caused by the loss of symbiotic dinoflagellates) and even mortality (Hughes et al., 2017; Tagliafico et al., 2017).

Lipids are involved in most biochemical and physiological processes in corals; thus, these may reflect the health status of corals. We found that bleached corals lost more than 50% and 75% of their original SFAs and total lipid content, respectively, which is common following bleaching events (Yamashiro et al., 1999; Imbs and Yakovleva, 2012). Symbiodiniaceae inherently contain considerable amounts of lipids and SFAs (Chen et al., 2015; Conlan et al., 2017). Therefore, the loss of symbiodiniaceae directly leads to decreased levels of lipids and SFAs in corals. Under bleached conditions, corals may rely more heavily on stored lipid to sustain their normal physiological functions (Tolosa et al., 2011). Similar reductions in lipid levels of bleached corals in the Caribbean (Porter et al., 1989), Okinawa (Yamashiro et al., 2005), and Hawaii (Rodrigues et al., 2008) were attributed to decreases in translocated carbon from their symbionts. Moreover, marine organisms tend to preferentially metabolize SFAs to protect long-chain PUFAs (such as 20:4n6 and 22:6n3) from oxidation during starvation (Tocher, 2003; Liu et al., 2020). Thus, a large quantity of SFAs, as the preferred source of metabolic energy, was oxidized to provide energy for bleaching corals.

Interestingly, $C_{20–22}$ PUFAs were significantly reduced in bleached corals, whereas C_{18} PUFAs were increased significantly. The reduction in PUFAs in corals was reported following bleaching events (Tolosa et al., 2011; Tagliafico et al., 2017). Bachok et al. (2006) showed that completely bleached coral lost more than 70% of their PUFAs. Symbiodiniaceae transfer sufficient PUFAs for the hosts' requirements under ideal conditions (Chen et al., 2015), whereas in bleaching situations, the host just acquires PUFAs from heterotrophic feeding (Grottoli et al., 2006). Moreover, recent works showed that Cnidaria, including scleractinian corals, contain genes for de novo biosynthesis of PUFAs (Kabeya et al., 2018; Monroig and Naoki, 2018). C_{18} PUFAs, such as 18:2n6 and 18:3n3, are key precursors in the biosynthesis of $C_{20–22}$ PUFAs in marine invertebrates. Therefore, C_{18} PUFAs were abundant in bleached corals, indicating that corals could obtain PUFAs from biosynthesize or heterotrophic assimilation, but with low efficiency. Furthermore, 18:3n-6 and 18:2n6 and their metabolites can affect the expression of genes associated with immunity and apoptosis (Rocker et al., 2019), such as the aryl hydrocarbon receptor (AhR). Overall, considering the large consumption of lipids and SFAs and the inability to rapidly replenish essential FAs (long-chain PUFAs), long-term bleaching of corals inevitably leads to coral death.

4.3 Response to Environmental Changes of Branching and Massive Corals From the Perspective of Nutritional Ecology

Indeed, the nutritional status of corals can affect their resistance and resilience to bleaching. Branched corals have low total lipid content but high surface areas to volume ratio; hence, branched corals have lower levels of stored lipid than do massive corals. Such levels significantly influence the timing of onset of bleaching and subsequent mortality (Anthony and Willis, 2002; Grottoli et al., 2004). Conlan et al. (2017) suggested that corals with "full" initial lipid stores survive twice as long as those with low lipid stores under high bleaching rates. Therefore, branching corals with low initial lipid stores are disadvantaged in the face of environmental stress. Moreover, the ability to obtain extra lipids from the environment is also extremely

important for corals under adverse conditions (Houlbrèque and Ferrier-Pagès, 2009; Grottoli et al., 2014). Heterotrophy accounts for 0%–66% of the fixed carbon incorporated into coral skeletons and can meet 15%–35% of the daily metabolic requirements in healthy corals and up to 100% in bleached corals (Houlbrèque and Ferrier-Pagès, 2009; Conti-Jerpe et al., 2020). Yamashiro et al. (2005) found that massive corals were relatively rich in lipids even after a bleaching event, which was attributed to increased feeding rates. Massive corals, predominantly heterotrophic or mixotrophic, are less susceptible to bleaching and show higher resilience to stress than branching corals do.

FAs are the primary constituents of the cell and subcellular organelle membranes in organisms. Differences in FA compositions can affect membrane-associated physical features and biological functions such as fluidity, permeability, and related enzyme activity (Tchernov et al., 2004; Ernst et al., 2016; Liu et al., 2020). We found that massive corals have a higher composition of UFAs than that of branching corals. Compared to SFAs, homologous UFAs have a lower melting point and occupy a larger space within the membrane lipid bilayer to enhance their fluidity and stability (Hazel, 1979; Yeagle, 1989; Liu et al., 2018). Increased biomembrane fluidity may facilitate membrane-bound enzyme activity and material exchange (Conlan et al., 2020; Liu et al., 2020) and help minimize the influence of environmental stress. Tchernov et al. (2004) demonstrated that high levels of unsaturated in the membrane are a key determinant of thermal-stress sensitivity in symbiotic algae of cnidarians. Furthermore, PUFAs (such as 20:4n6, and 22:6n3) exert immune and reproductive functions and are used as precursors of some hormones (Berge and Barnathan, 2005). Therefore, massive corals with more PUFAs may have a survival advantage during environmental changes.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

CL, YZ, and HH designed experiments. CL, YZ, YS, LJ, YL, and XY carried out experiments. CL, YZ, SL, LH, and HH analyzed experimental results and wrote the manuscript. All authors contributed to the article and approved the submitted version.

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