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Stable nitrogen and carbon isotope ($\delta^{15}N$ and $\delta^{13}C$) variability in shallow tropical Pacific soft coral and black coral taxa and implications for paleoceanographic reconstructions

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Abstract

Soft corals and black corals are useful proxy tools for paleoceanographic reconstructions. However, most work has focused on deep-water taxa and few studies have used these corals as proxy organisms in shallow water (<200 m). To facilitate the use of stable nitrogen and carbon isotope ($\delta^{15}N$ and $\delta^{13}C$) records from shallow-water soft coral and black coral taxa for paleoceanographic reconstructions, quantification of the inherent variability in skeletal isotope values between sites, across depth, and among taxa is needed. Here, skeletal $\delta^{15}N$ and $\delta^{13}C$ values were measured in multiple colonies from eleven genera of soft corals and two genera of black corals from across a depth transect (5–105 m) at two sites in Palau located in the tropical western Pacific Ocean. Overall, no difference in skeletal $\delta^{15}N$ and $\delta^{13}C$ values between sites was present. Skeletal $\delta^{15}N$ values significantly increased and $\delta^{13}C$ values decreased with depth. This is consistent with changes in isotope values of suspended particulate organic matter (POM) across the photic zone, suggesting that the primary food source to these corals is suspended POM and that the stable isotopic composition of POM controls the skeletal isotopic composition of these corals. Thus, to compare the isotope records of corals collected across a depth range in the photic zone, first order depth corrections of $-0.013‰\ m^{-1}$ and $+0.023‰\ m^{-1}$ are recommended for $\delta^{15}N$ and $\delta^{13}C$, respectively. Average depth-corrected $\delta^{15}N$ values were similar between black corals and soft corals, indicating that corals in these orders feed at a similar trophic level. In contrast, average depth-corrected $\delta^{13}C$ values of black corals were significantly lower than that of soft corals, potentially resulting from metabolic processes associated with differing skeletal compositions among the orders (i.e., gorgonin vs. chitin based). Thus, a correction of $+1.0‰$ is recommended for black corals when comparing their $\delta^{13}C$-based proxy records to soft corals. After correcting for both the depth and order effects, variability in $\delta^{15}N$ values among corals within each genera was low (standard deviation (SD) of the mean $<\pm0.5‰$), with the exception of *Acanthorgorgia*. The calculated SD of $<\pm0.5‰$ provides a first order guideline for the amount of variability that could be expected in a $\delta^{15}N$ record, and suggests that these corals may be useful for $\delta^{15}N$-based paleoceanographic reconstructions. Variability in $\delta^{13}C$ values among corals within genera was also low (standard deviation of the mean $<\pm0.5‰$) with the exception of *Rhipidipathes* and *Villogorgia*. Similar to $\delta^{15}N$, records from the genera studied here with the exception of *Rhipidipathes* and *Villogorgia* may be useful for $\delta^{13}C$-based paleoceanographic reconstructions. Overall, using the recommendations developed here, stable isotope records from multiple sites, depths and taxa of these corals can be more rigorously compared.

1. INTRODUCTION

A vast array of proxy tools exist for reconstructing past ocean conditions. Yet few of these yield information at both high temporal resolution (i.e., sub-annual) and across a wide depth range. Soft corals and black corals, two

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separate orders within the class Anthozoa (Fabricius and Alderslade, 2001; Opresko and Sanchez, 2005), are a relatively new tool for paleoceanographic reconstruction. They have a global distribution, grow from the surface to several kilometers deep (Moore et al., 1956; Cimberg et al., 1981), and have a banded skeleton providing chronological control with the potential for sub-annual resolution (Risk et al., 2002; Sherwood et al., 2005a). While attention has mostly focused on deep-water taxa in mid-to-high latitudes, paleoceanographic reconstructions from shallow-water soft coral and black corals taxa in the tropics could prove essential to understanding past behavior of tropical oceanographic systems. Since large, and therefore old, colonies are rare, reconstructions from multiple soft coral and black coral taxa from a variety of sites and depths are inevitable. However, the natural variability that exists among specimens needs to be assessed so that corrections can be made when comparing records from multiple sites, depths, and/or taxa.

Measurements of the stable nitrogen ($\delta^{15}N$) and stable carbon ($\delta^{13}C$) isotopic composition of the organic skeleton is a primary method of obtaining paleoceanographic information from the skeleton of these types of corals (see review in Sherwood and Risk, 2007). In deep-water taxa (i.e., commonly found greater than 200 m), $\delta^{15}N$ and $\delta^{13}C$ values reflect sinking particulate organic matter (POM) (Heikoop et al., 2002; Roark et al., 2005; Sherwood et al., 2005b; Williams et al., 2007a). Since $\delta^{15}N$ and $\delta^{13}C$ values of sinking POM undergo minimal alteration with depth (Altabet and Francois, 1994), the isotope values of sinking POM, and therefore coral colonies at depth, record surface processes or sources of nutrients influencing the isotopic composition of surface organic matter. However, such reconstructions utilizing multiple specimens do not always account for differences in diet or metabolic fractionation among species, across depth, or in geographically distant locations in the ocean. In fact, in deep-water temperate taxa, these factors may be important as $\delta^{15}N$ values may vary up to 2.5‰ among colonies from the same location and up to 1.5‰ from a single skeletal ring within a colony (Sherwood et al., 2005b; Williams et al., 2007a,b). Quantifying and understanding the variability in organic skeletal $\delta^{15}N$ and $\delta^{13}C$ among deep-water taxa and among specimens within these taxa was the first step in developing proxy-based paleoceanographic reconstructions with these organisms.

Less is known about the natural isotope variability and the source(s) of that variability in tropical shallow-water taxa (<200 m). Similar to deep-water taxa, differences in diet (e.g., Grigg, 1965; Lewis, 1978; Ribes et al., 1998), growth rates (e.g., Khalesi et al., 2007; Bo et al., 2009), or metabolic fractionation rates (e.g., Sorokin, 1991) among shallow-water taxa could influence their skeletal isotope signatures independent of oceanographic conditions, making their derived proxy records difficult to compare. In addition, variable skeletal composition among taxa may override any environmental signal recorded in these corals since inherently different isotope signatures may characterize unique skeletal compositions. This may be particularly evident among orders, as the soft corals with internal skeletons (groups Scleraxonia, Holaxonia and Calcaxonia, formerly in the order Gorgonacea) suitable for paleoceanographic reconstructions are composed of gorgonin (an organic proteinaceous substance), sometimes in combination with calcite (Grasshoff and Zibrowius, 1983; Lewis et al., 1992), whereas black corals form a skeleton predominately composed of chitin complexed with proteins (Goldberg, 1976; Ellis et al., 1980).

$\delta^{15}N$ and $\delta^{13}C$ values of tropical shallow-water black coral and soft coral taxa could differ between sites, across depth, among colonies within a taxa, or among taxa if (1) the source of nitrogen and carbon differed among these parameters, and/or (2) if biological fractionation of acquired nitrogen and carbon were taxa-specific. A detailed study is needed to quantify the baseline isotope variability among genera in soft corals and black corals to facilitate comparison of isotope-based paleoceanographic proxy reconstructions from multiple taxa. With this in mind, we examined the organic skeletal $\delta^{15}N$ and $\delta^{13}C$ values among multiple coral colonies from different sites, depths, and taxa in the western tropical Pacific Ocean, and identified strategies for comparing the proxy records of these corals in paleoceanographic studies.

2. METHODS

2.1. Study site

Soft coral and black coral colonies were collected from Short Drop Off (7°16N, 134°31E) and Ulong Rock (7°17N, 134°14E) offshore of Palau. Both sites are 300 m vertical reef walls located offshore of the island Koror and experience similar seasonal seawater temperature patterns in the top 85 m of the water column (Colin, 2001). The temperature of the mixed layer is greater than 28 °C and the average temperature below the mixed layer is 23 °C. The base of the mixed layer fluctuates in depth on seasonal and El Niño-Southern Oscillation timescales with an average depth of 55 m (Zhang et al., 2007).

2.2. Colony identification

Colonies from a wide range of taxonomic groups were collected along a vertical wall from 5, 15, 25, 35, 45, and 85 m by SCUBA in 2006 and from 105 m by submersible in 2008. Colonies were growing outward into the water column, perpendicular to the wall. Photos showing gross colony morphology and branching pattern were taken of each colony after collection. A basal section of the stem from each colony was removed from below the lowest branches, and transported to the laboratory for isotope analyses. Taxonomic identification was made in the laboratory based on photos and sclerites. Soft corals were identified to the genus level according to Fabricius and Alderslade (2001) and with the assistance of Gary Williams of the California Academy of Sciences. Black corals were identified to the genus level by Dennis Opresko of the Oak Ridge National Laboratory. Identification below genus was not feasible as many species have not been described for both soft corals and black corals.

2.3. Laboratory analyses

The bottom three centimetres of the basal section from each colony was cut using a dremel drill for small specimens and rock saw for larger specimens. Working under a dissecting microscope, an area of approximately 2 mm × 2 mm of the external layer of tissue was removed with forceps from the outside of each basal section. At the same location, a 2 mm × 2 mm area of the outer layer of skeleton was gently cut off with a scalpel to a depth of 0.1–0.5 mm. The depth of sampled skeleton varied according to the thickness of the outer growth ring such that the sample was deeper (up to 0.5 mm) from specimens with thicker growth rings and shallower (at least 0.1 mm) from specimens with thinner growth rings. This strategy assumed that the outer growth ring of each colony represents the most recently formed skeletal material and covers a common period in time among all the specimens. Sufficient skeletal material was removed to obtain approximately 1 mg of dried skeleton. Each skeletal sample was individually acid washed in 1 N HCl in glass beakers for four hours to remove calcium carbonate and isolate the organic fraction of the skeleton, rinsed three times in 18 mΩ Milli-Q®, and dried over night at 60 °C. Carbon-to-nitrogen (C:N) ratio and stable isotope ($\delta^{15}N$ and $\delta^{13}C$) values of each sample were measured by combusting the organic fraction in a Costech Elemental Analyzer where the resulting N_2 and CO_2 gases were analyzed with a Finnigan Delta IV Plus isotope ratio mass spectrometer via a Finnigan ConFlow III open split interface. The standard Acetanilide was used for calibration of percent C and N, and the C:N ratios. $\delta^{15}N$ values were reported relative to air ($\delta^{15}N$ = per mil deviation of the ratio of stable nitrogen isotopes ^{15}N:^{14}N relative to air (Mariotti, 1984)). $\delta^{13}C$ values were reported relative to Vienna Peedee Belemnite Limestone Standard (V-PDB) ($\delta^{13}C$ = permil deviation of the ratio of stable carbon isotopes ^{13}C:^{12}C relative to V-PDB (Coplen, 1994)). The standard deviation of the mean of repeated measurements of internal standards ($n = 85$) was ±0.15‰ for $\delta^{15}N$ and ±0.06‰ for $\delta^{13}C$. Samples run in duplicate (10% of all samples) had a standard deviation of ±0.43‰ for $\delta^{15}N$ and ±0.37‰ for $\delta^{13}C$.

2.4. Statistical analyses

C:N ratios, $\delta^{15}N$, and $\delta^{13}C$ values among sites did not significantly differ (student's *t*-test, $p = 0.16$, $p = 0.32$, $p = 0.76$, respectively). Therefore, data from both sites were pooled to increase the statistical power in subsequent statistical analyses. Since lipid content can influence $\delta^{13}C$ values (DeNiro and Epstein, 1977; McConnaughey and McRoy, 1979), C:N ratios were used as a proxy for lipid content (Post, 2007) to assess if lipid content differed significantly between orders, and to determine if the $\delta^{13}C$ values needed to be "lipid-corrected" for organisms in each order. Visual examination of C:N ratios of each order showed a bimodal distribution. Therefore, a non-parametric signed rank was used to test for differences in C:N ratios of pooled data between orders.

Regression analysis was used to test for the effect of depth on soft coral skeletal $\delta^{15}N$ and $\delta^{13}C$ using SigmaPlot 10.0. Since black corals were not collected from all depths, they were excluded from this analysis. When significant, the effect of depth was removed from each value based on the slope of the regressions prior to further analysis. ANOVA analysis was used to test for significant differences in depth-corrected $\delta^{15}N$ and $\delta^{13}C$ values between orders (black coral vs. soft corals). The depth correction allowed for the comparison of orders independent of depth. A second ANOVA analysis was used to test for differences in depth- and order-corrected skeletal $\delta^{15}N$ and $\delta^{13}C$ among genera (*Antipathes*, *Rhipidipathes*, *Annella*, *Keroeides*, *Muricella*, *Acanthogorgia*, *Astrogorgia*, *Villogorgia*, *Paracis*, *Bebryce*, *Echinogorgia*, *Viminella*, *Muricella* and *Ellisella*). The taxanomic order effect and the depth effects were removed from all of the data where significant prior to ANOVA analysis in order to isolate the effect of genera on the isotope values. Only genera with more than one colony were included in the ANOVA, although genera represented by a single colony were also plotted for visual comparison purposes. *A posteriori* Tukey tests were used to explore significant effects. Residuals for $\delta^{13}C$ and $\delta^{15}N$ values were normally distributed according to the plots of the residuals versus predicted values for both variables. Statistical analyses were generated using SAS software, Version 8.02 of the SAS System for Windows [Copyright © 1999–2001 SAS Institute Inc. SAS and all other SAS Institute Inc. products and service names are registered trademarks or trademarks of SAS Institute Ind., Cary, NC, USA.]. All averages are reported ±1 standard deviation (SD). *p*-Levels $\leqslant 0.05$ were considered significant.

3. RESULTS

3.1. Coral colony collection and identification

Forty-seven soft corals and eight black corals were collected from 5 to 105 m (Table 1). The diameter of the skeletal base from collected colonies ranged from approximately 0.5 to 7 cm with heights of approximately 10 to 150 cm. Soft coral colonies were collected from the Scleraxonia group, and the suborders Holaxonia and Calcaxonia (Table 1). The highest abundance and diversity of collected colonies were Holaxonians, represented by 39 colonies in three families. Five colonies from a single genus were Scleraxonians, and two colonies from two separate genera but one family were Calcaxonians. Colonies from the genus *Astrogorgia* were abundant in shallow water and a large number were collected. Colonies from two genera and two separate families of black corals were collected from 5 and 26 m (Table 1). All specimens collected were azooxanthellate.

3.2. Isotope analyses

Skeletal $\delta^{15}N$ values ranged from 5.6‰ to 8.7‰ and skeletal $\delta^{13}C$ values ranged from −16.9‰ to −19.8‰ for all colonies (Fig. 1). Although skeletal carbon-to-nitrogen (C:N) ratios were significantly higher in soft corals than black corals (signed rank test, $p < 0.0001$), the C:N ratios

Table 1
Taxonomy and collection depth of colonies in this study.

Taxonomy	No of colonies	Depths (m)
Class Anthozoa		
Subclass Hexacorallia		
Order Antipatharia (Black corals)		
Family Antipathidae		
Genus *Antipathes*	1	5
Family Aphanipathidae		
Genus *Rhipidipathes*	7	26
Subclass Octocorallia		
Order Alcyonacea (Soft corals)		
Scleraxonia Group		
Family Subergorgiidae		
Genus *Annella*	5	5, 26, 33, 45
Suborder Holaxonia		
Family Keroeididae		
Genus *Keroeides*	1	33
Family Acanthogorgiidae		
Genus *Muricella*	2	85, 105
Genus *Acanthogorgia*	5	5, 85
Family Plexauridae		
Genus *Astrogorgia*	21	5, 13, 19, 26, 45
Genus *Villogorgia*	5	26, 33, 85
Genus *Paracis*	4	85
Genus *Bebryce*	1	85
Genus *Echinogorgia*	1	85
Suborder Calcaxonia		
Family Ellisellidae		
Genus *Viminella*	1	85
Genus *Ellisella*	1	85

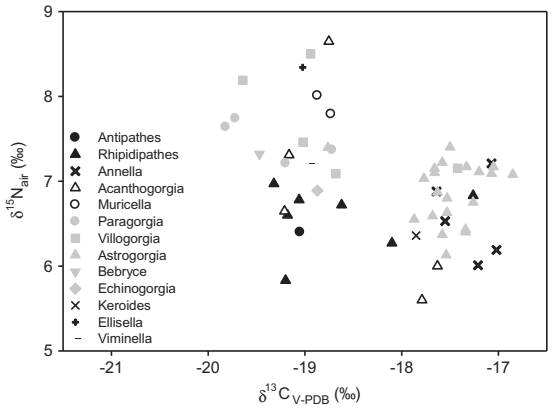

Fig. 1. Skeletal organic stable nitrogen isotope ($\delta^{15}N$) values versus stable carbon isotope ($\delta^{13}C$) values of each colony in the study. Detailed taxonomic information in Table 1.

were <3.5 for both orders. Thus corrections for lipid content would not significantly impact $\delta^{13}C$ values (Post et al., 2007) and none was applied. Raw coral $\delta^{13}C$ values fell into two clusters: one cluster was composed of black corals and soft coral genera that were collected predominately from the deeper depths (e.g., *Muricella* and *Paragorgia*) centered at −19.0‰ while a second cluster was primarily composed of the soft corals collected predominately from the shallower depths (e.g., *Astrogorgia* and *Annella*) centered at −17.5‰ (Fig. 1).

Regression analysis of the soft coral stable isotope values with depth revealed a significant increase in $\delta^{15}N$ values and a significant decrease in $\delta^{13}C$ values with depth (Fig. 2). Average $\delta^{15}N$ values increased by 1.3‰ and average $\delta^{13}C$ values decreased by 2.3‰ over an approximately 100 m depth transect. Therefore, a depth correction of -0.013‰ m^{-1} for $\delta^{15}N$ and $+0.023$‰ m^{-1} for $\delta^{13}C$ was applied to remove the effect of depth on isotope values prior to further statistical analysis. Average depth-corrected $\delta^{15}N$ values were similar between all black corals and soft corals (Fig 3A; $F = 1.92$, $df = 1$, $p = 0.17$). In contrast, average depth-corrected $\delta^{13}C$ values of black corals were significantly lower than that of soft corals by approximately 1‰ (Fig. 3B; ANOVA, $F = 29.22$, $df = 1, p < 0.0001$). Although the sample sizes of the soft corals ($n = 47$) and black corals ($n = 8$) were quite different, ANOVA is robust with respect to unbalanced design (e.g., Shaw and Mitchell-Olds, 1993). To be thorough, the ANOVA was repeated where only soft corals and black corals from similar depths (5 and 26 m) were included in the analysis and the results were identical with the average $\delta^{13}C$ value of black corals remaining ~1‰ lower than that of soft corals. Thus, a +1‰ order-specific correction to black coral $\delta^{13}C$ values was applied to remove the variability among orders on $\delta^{13}C$ values for further statistical analysis.

Depth-corrected $\delta^{15}N$ values significantly differed among genera (Fig. 4A; ANOVA, $F = 3.05$, $df = 6$, $p = 0.014$) with *Villogorgia* being significantly heavier than *Acanthogorgia* and *Rhipidipathes* (Fig. 4A). Average $\delta^{15}N$ values for *Villogorgia* were 0.9‰ higher than for *Acantho-*

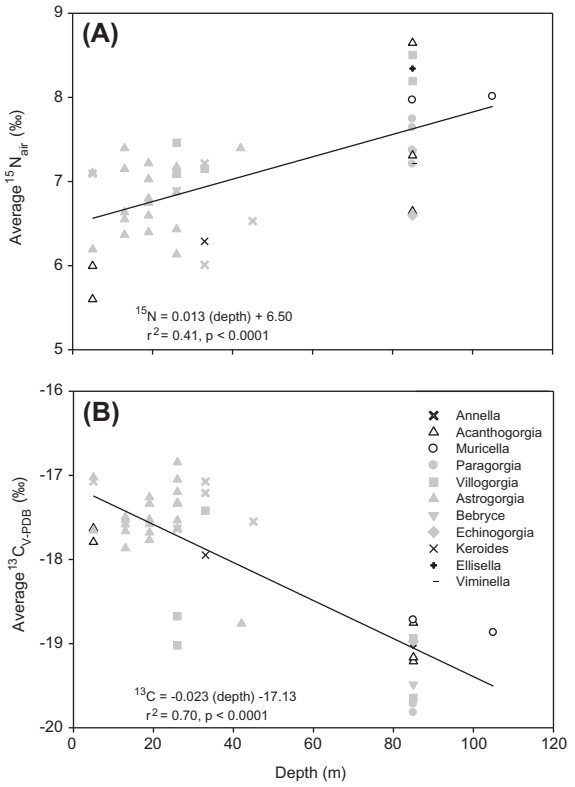

Fig. 2. Organic skeletal (A) $\delta^{15}N$ and (B) $\delta^{13}C$ values for all soft coral colonies across depth. Regression line and equation shown.

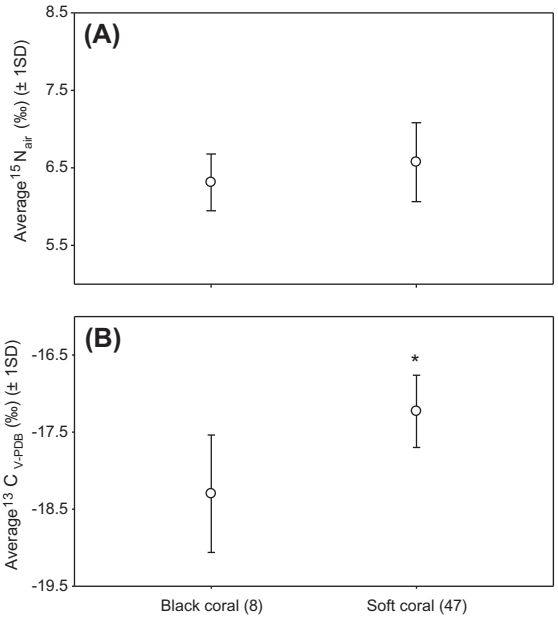

Fig. 3. Average (±1 standard deviation (SD)) depth-corrected organic skeletal (A) $\delta^{15}N$ and (B) $\delta^{13}C$ values for all black coral and soft coral colonies (sample size per order indicated on *x*-axis). * indicates significant differences at $p \leqslant 0.05$ between orders.

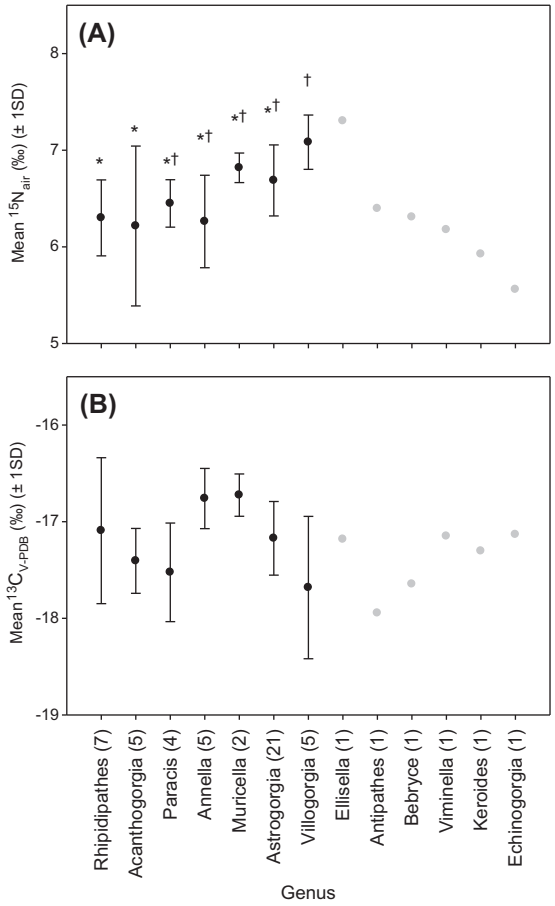

Fig. 4. Average (±1 standard deviation (SD)) depth-corrected organic skeletal (A) $\delta^{15}N$ and (B) depth- and order-corrected $\delta^{13}C$ values for all genera with more than one colony (black symbols, sample size per genus indicated on *x*-axis). Genera represented by a single colony at a given depth are plotted in gray, do not have error bars, and were not included in the statistical analyses. Genera averages with similar symbols (∗, †, no symbol) do not significantly differ from each other. Taxonomic information in Table 1.

gorgia, and represented the lowest and highest average values of all average genera. $\delta^{15}N$ values of all specimens ranged from 5.5‰ to 7.6‰, including those genera represented by a single specimen (Fig. 4A). In contrast to $\delta^{15}N$, average depth- and order-corrected $\delta^{13}C$ values did not significantly vary among genera although some variability was present (Fig. 4B; $F = 2.28$, $df = 6$, $p = 0.054$). $\delta^{13}C$ values of all specimens ranged from −15.7‰ to −18.5‰, including those genera represented by a single specimen (Fig. 4B). While it is not possible to statistically evaluate the $\delta^{15}N$ or $\delta^{13}C$ values for genera represented by a single colony, general observations suggest that these singly-represented $\delta^{15}N$ and $\delta^{13}C$ values fall within the range of the multi-colony represented genera at both shallow and deeper depths (Fig. 4).

4. DISCUSSION

4.1. Variability in stable isotopes between sites

Similar average $\delta^{15}N$ and $\delta^{13}C$ values between the two sites is consistent with a similar source of nitrogen and carbon to both sites. This suggests that direct comparisons of isotope proxy records among colonies within the same oceanographic region that are influenced by similar oceanographic conditions are valid.

4.2. Variability in stable isotopes with depth

4.2.1. Nitrogen

Increases in coral skeletal $\delta^{15}N$ with depth could be driven by either a shift in their source of food or changes in the $\delta^{15}N$ composition of their food source. $\delta^{15}N$ increases by approximately 3.4‰ with each trophic level in the food web as a result of trophic fractionation (i.e., the preferential use of lighter isotopes during metabolism leaving predators enriched in heavier isotopes than their prey) (DeNiro and Epstein, 1981; Minagawa and Wada, 1984). Thus, feeding higher in the food web (i.e., a proportionate increase in zooplankton versus particulate organic carbon in the diet) could drive the $\delta^{15}N$ enrichment with depth (Fig. 2A). However, a systematic shift in coral diet within the top 100 m of the water column is unlikely (see Section 4.2.2). In addition, coral $\delta^{15}N$ values of 6.4‰ in specimens from 5 m are several permil lower than the $\delta^{15}N$ values of zooplankton from surface waters in a lagoon offshore of Palau (Yamamuro et al., 1995) indicating that zooplankton does not notably contribute to the diet of soft corals and black corals in surface waters at this site.

A more likely explanation for the increase in $\delta^{15}N$ values with depth is that soft corals feed primarily on suspended

POM which becomes increasingly enriched with depth in the top 100 m of the water column (Benner et al., 1997). Since ^{14}N is preferentially used during bacterial degradation, suspended POM becomes increasingly enriched in ^{15}N over time as it very slowly sinks in the water column (Saino and Hattori, 1980; Wada et al., 1980; Macko and Estep, 1984). The present study shows an average increase of over 1‰ between shallow (5 m) and deeper (105 m) coral colonies, which is similar to the reported increase in $\delta^{15}N$ values of suspended POM across a similar depth range (Saino and Hattori, 1980; Altabet, 1988). Therefore, suspended POM is the likely food source of soft corals and a dominant control on the skeletal $\delta^{15}N$ composition of these corals within the photic zone. Similarly, Mintenbeck et al. (2007) predicted a 1–2.5‰ increase in tissue $\delta^{15}N$ values in suspension feeders across 100 m of the water column as a result of increases in $\delta^{15}N$ values of suspended POM across a similar depth range. This is consistent with our findings and supports, as a first order approach, the application of a correction factor of $-0.013‰\ m^{-1}$ to $\delta^{15}N$ values to compare soft corals $\delta^{15}N$ records from a range of depths in the photic zone. Due to the comparable ecology of black corals to soft corals, and similar food source availability, it is hypothesized that $\delta^{15}N$ values in black corals would also increase with depth and a similar correction factor would be needed when comparing isotope records from specimens collected across depths. Although additional data are needed to directly test this hypothesis, the depth corrections developed here for soft corals were applied to black coral $\delta^{15}N$ values to facilitate comparisons between the orders and among the genera.

In contrast to the shallow-water corals studied here, which feed predominately on suspended POM, deep-water corals from several hundred meters depth are known to feed primarily on sinking POM (Roark et al., 2005, 2006; Sherwood et al., 2005b; Williams et al., 2007a). Therefore across large depth ranges, the diet of soft corals and black corals must at some point shift from a diet predominately composed of suspended POM to one of sinking POM. This could reflect either an inherently different particle size preference between colonies in shallow and deep water, or since these corals feed opportunistically (Sherwood et al., 2008), a consequence in changes in food availability as sinking POM may be more abundant at depth than suspended POM (Loh and Bauer, 2000). Regardless, caution is needed when comparing colonies from this study to very deep-water taxa as their skeletal isotopic composition likely reflect very different food sources.

4.2.2. Carbon

$\delta^{13}C$ increases by approximately 1.1‰ with each trophic level in open-ocean food webs (DeNiro and Epstein, 1978; France and Peters, 1997). Thus, if feeding higher in the food web was driving the $\delta^{15}N$ enrichment with depth in the soft corals (Fig. 2A), then $\delta^{13}C$ values would also increase with depth. However, here the opposite is true and $\delta^{13}C$ value decrease with depth (Fig. 2B). Therefore, a dietary shift to higher or lower trophic level food sources within the top 100 m of the water column cannot explain the simultaneous $\delta^{15}N$ enrichment and $\delta^{13}C$ depletion with depth.

However, $\delta^{13}C$ values of suspended POM decrease by up to 2.4‰ with depth through the photic zone as a result of decreasing primary production (O'Leary et al., 2001) and/or due to preferential remineralisation of labile carbon molecules with high $\delta^{13}C$ values at the base of the pycnocline (e.g. amino acids and sugars (Jeffrey et al., 1983; Druffel et al., 2003)). Therefore, a diet of suspended POM is consistent with the observed decrease in skeletal $\delta^{13}C$ values with depth (Fig. 2B). Thus, to reliably compare $\delta^{13}C$-based proxy records from soft corals collected across a depth range in the photic zone, a correction factor of $+0.023‰\ m^{-1}$ is recommended as a first order approach to compare soft coral values independent of depth. It is hypothesized that a comparable decrease in $\delta^{13}C$ values with depth would be expected for black corals and that a similar correction factor would be needed when comparing isotope values from specimens collected across depth. Although additional data are needed to test this hypothesis, the depth corrections developed here for soft corals were applied to black coral $\delta^{13}C$ values to facilitate comparisons between the orders and among the genera.

4.3. Variability in stable isotopes between the taxonomic orders of black coral and soft coral

Based on their similar average depth-corrected $\delta^{15}N$ values, soft coral and black coral colonies feed at the same trophic level (Fig. 3A). Changes in both $\delta^{15}N$ and $\delta^{13}C$ values with depth (Fig 2) indicate that suspended POM is the primary food source to soft corals, and this is most likely true for black corals as well. Therefore, the depth-corrected skeletal $\delta^{13}C$ enrichment of soft corals compared to black corals (Fig. 3B) is not likely due to differences in their diets, but may be due to differences in their skeletal composition (i.e., gorgonin in soft corals versus chitin in black corals). Skeletal $\delta^{13}C$ of both gorgonin and chitin would be affected by the proportion of lipid, protein, and carbohydrates, where lipids are isotopically the most depleted (DeNiro and Epstein, 1977; McConnaughey and McRoy, 1979). However, C:N ratios of less than 3.5 in both taxonomic orders indicate that lipid content is insufficient to drive variability in $\delta^{13}C$ values. Therefore, skeletal composition does not explain the lower average depth-corrected $\delta^{13}C$ values in black corals than soft corals. Alternatively, amino acid concentrations differ between black coral and soft coral skeletons (Goldberg, 1991; Sherwood et al., 2006). Since $\delta^{13}C$ values of amino acids vary based on fractionation during metabolic processes while incorporating carbon (Hayes, 2001), differences in skeletal amino acid $\delta^{13}C$ values resulting from order-specific metabolic processes may cause differing carbon isotope signatures. Compound-specific analyses of the skeletal amino acids would be needed to test this hypothesis. On balance, it appears that differences in the metabolism of proteins in soft corals and black corals is the most likely source of their ~1‰ offset.

Regardless of the source of variability, a +1‰ correction is recommended to black coral $\delta^{13}C$-based proxy records when directly comparing them to soft coral $\delta^{13}C$ values to account for the offset present between the taxonomic orders (Fig. 3B). Interestingly, in deep-water corals

collected from the Newfoundland and Labrador continental slope in the northern Atlantic, the $\delta^{13}C$ values do not notably differ between black corals and soft corals (Sherwood et al., 2008) indicating that $\delta^{13}C$ values do not universally differ between these orders. The different $\delta^{13}C$ patterns observed in this and the Sherwood et al. (2008) study could be due to the different species compositions of black coral and soft coral orders in the two geographic locations (i.e., tropical Pacific versus northwestern Atlantic) or between depths (i.e., shallow (<200 m) versus deep (>200 m)). Further research is needed to determine if lower skeletal $\delta^{13}C$ values in black corals relative to soft corals is characteristic only of colonies in shallow water and/or is unique to the western tropical Pacific.

4.4. Variability in stable isotopes within and among genera

4.4.1. Nitrogen

Depth-corrected $\delta^{15}N$ values did not vary widely among colonies within a genus (SD for genera were $<\pm 0.5‰$), with the exception of *Acanthogorgia* ($SD \pm 0.8‰$) (Fig. 4A) where one specimen was 1.3‰ higher than all other individuals in this genus. Therefore, all genera except *Acanthogorgia* may respond similarly to environmental controls and may prove useful for $\delta^{15}N$-based paleoceanographic records.

The 0.9‰ lower average depth-corrected $\delta^{15}N$ values in *Acanthogorgia* and *Rhipidipathes* compared to *Villogorgia* (Fig. 4A) could reflect genus-specific differences in diet. A diet supplemented with smaller size fractions of organic matter would drive lower $\delta^{15}N$ values in *Acanthogorgia* and *Rhipidipates* relative to *Villogorgia*. Since soft corals are opportunistic feeders (e.g. Ribes et al., 1998; Coma et al., 2001; Sherwood et al., 2008) then even within a diet composed of suspended particulate organic matter, very slight differences in diet particle size could account for the genus-specific differences in depth-corrected skeletal $\delta^{15}N$ values. Irrespective of the exact source of the difference in $\delta^{15}N$ among these genera, the genus-specific offset must be taken into account before comparisons of $\delta^{15}N$-based proxy records from *Acanthogorgia* or *Rhipidipates* can be compared to *Villogorgia*.

4.4.2. Carbon

The standard deviation of the mean depth- and order-corrected $\delta^{13}C$ values of *Acanthogorgia, Paracis, Annella, Muricella,* and *Astrogorgia* was small at $<\pm 0.5‰$ (Fig. 4B). Therefore, all genera may respond similarly to environmental controls and may prove useful for $\delta^{13}C$-based paleoceanographic records. Depth- and order-corrected $\delta^{13}C$ values varied more widely within *Rhipidipathes* and *Villogorgia* ($SD \pm 0.7‰$ and $\pm 0.8‰$, respectively; Fig. 4B) indicating that these genera may be less useful for $\delta^{13}C$-based paleoceanographic records.

Carbon isotope values can be interpreted as a spectrum of feeding types, from pelagic (low $\delta^{13}C$) to benthic (high $\delta^{13}C$) (McConnaughey and McRoy, 1979; Nadon and Himmelman, 2006). This, in addition to inherent differences in metabolic fractionation related to genetic differences among individuals or variations in skeletal amino acid concentrations could drive the variability present within the genera *Rhipidipathes* and *Villogorgia*, and the non-significant differences among genera (Fig. 4B).

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