

Proteinaceous corals as proxy archives of paleo-environmental change

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Abstract

High-resolution marine data are critical to evaluating anthropogenic impacts on our environment. Considering the spatial and temporal limitations of direct instrumental measurements, proxy data extracted from marine environmental archives are necessary to separate anthropogenic changes from those that would occur naturally. The majority of late-Holocene, high resolution environmental reconstructions are derived from marine carbonates including tropical scleractinian corals, bivalves, crustose coralline algae, and sclerosponges. However, these archives are restricted to the top hundreds of meters of the water column, and only preserve environmental variability that is captured by calcium carbonate skeletons. At a very few select locations, marine sediments archive annual environmental variability in organic and inorganic materials. Recently, additional types of corals are proving to yield information complimentary to these traditional marine archives, including cold water scleractinian corals and proteinaceous corals. A taxonomically-diverse group, the proteinaceous corals are broadly defined as those having a branching gross-morphology with skeleton comprised at least partly of protein-rich organic material. They encode characteristics of their food and ambient environment into the chemical and physical composition of their skeleton. This environmental-encoding combined with their banded skeleton and significant longevity means that proteinaceous corals hold information in their skeleton that helps fill the spatial and temporal gaps in our knowledge of past and present ocean conditions.

Here I review the environmental reconstructions derived from geochemical measurements of the proteinaceous coral skeletons. This information is grouped into the mesopelagic environmental variability captured in the skeleton of bamboo corals, surface processes captured in the organic skeletons of corals across all ocean depths, and environmental variability documented by skeletal radiometric isotopes. We include animals from two sepa-

rate subclasses within the class Anthozoa, including the parasitic Zoanthids that secrete a sclero-proteic skeleton. Since the proteinaceous corals are taxonomically diverse, we consider the unique features that define this group of corals including their distribution, morphology, nutrition, and longevity. We find that uncertainty surrounding biological parameters limits the precision of reconstructions derived from the calcitic skeleton; in contrast, analytical effort and cost constrains the number of reconstructions from the organic skeleton. Through this discussion, we provide insights into the uses, challenges, and directions for future research for this important environmental archive.

Keywords: corals, paleo-environmental proxy archives, organic skeleton, calcite, stable isotope geochemistry, trace element composition, radiometric dating

1. Introduction

The ocean is sensitive to environmental change, continuously experiencing and responding to variability in terrestrial inputs, atmospheric circulation, temperature, climate, productivity, cataclysms, and biodiversity (Levin and Le Bris, 2015; Hutchins and Fu, 2017; Yool et al., 2015; Jickells and Moore, 2015; Caesar et al., 2018). Direct measurements and monitoring of seawater conditions may capture this environmental variability; yet, these measurements are limited in time and space. Indeed, reliable instrumental measures of seawater conditions are restricted to the period after the mid-19th century (Woodruff et al., 2005) with the quality and variety of measured parameters largely constrained by technology (Kennedy, 2014). In fact, the uncertainty of these measurements decreases substantially only after the 1970s, in part because of the advent of satellites (Kennedy, 2014; Loveland and Dwyer, 2012). Furthermore, the spatial coverage of direct measurements is confined by the difficulties inherent to accessing remote areas of the ocean: instrumental time series are particularly limited in higher latitudes and generally devoid of detailed environmental information beyond temperature prior to the past several decades (Overland et al., 2012; Walsh et al., 2018). This lack of direct measurements is particularly worrisome in the context of global climate change: high-resolution data of ocean conditions are critical to constrain the anthropogenic component of recent, unprecedented changes (Neukom et al., 2019; Wu et al., 2019). Fortunately, a myriad of proxy records reconstructing environmental conditions can be extracted from geological and biological archives (Mackintosh et al., 2017;

25 Jones et al., 2009; Henderson, 2002), formed over much longer expanses of
26 time and from greater spatial areas than direct measurements. Such recon-
27 structions are pivotal to our understanding of the past ocean environment
28 (Nair and Mohan, 2017; Burke and Robinson, 2012; Freund et al., 2019;
29 Thornalley et al., 2018), long before direct measurements were possible.
30 Therefore, these archives fill the spatial and temporal gaps in our knowl-
31 edge of past and present ocean conditions.

32 Reconstructions derived from proxy measurements of environmental
33 archives provide a means to evaluate natural variability prior to any an-
34 thropogenic influence. Furthermore, reconstructions of "natural" variability
35 can serve as testing beds for evaluating mechanisms and feedbacks driving
36 environmental change. For example, an analysis of a suite of proxy paleo-
37 oclimate records, many ocean derived (PAGES2k Consortium, 2017), re-
38 constructed multidecadal temperature fluctuations spanning the past 2000
39 years; this work highlighted the spatial coherency of the recent and unparal-
40 leled warming (PAGES 2k Consortium, 2019; Neukom et al., 2019). Matched
41 with natural climate forcings, the temperature reconstructions identified the
42 role of volcanism in pre-industrial climate variability. Moving beyond tem-
43 perature, the carbon isotopic composition of marine calcifiers capture the
44 chemical signature of dissolved inorganic carbon (DIC) in seawater. The
45 DIC in turn captures the flux of anthropogenic carbon into the ocean, since
46 carbon derived from the burning of fossil fuels has a distinct carbon iso-
47 tope signature (Swart et al., 2010; Bacastow et al., 1996). Carbon isotopes
48 combined with trace elements (e.g., barium) prior to the industrial revo-
49 lution document changing high latitude primary productivity with links to
50 sea ice cover and solar insolation (Hou et al., 2018; Chan et al., 2017). The
51 nitrogen isotopic composition in the marine calcifiers document primarily
52 shifts in nitrogen source to a region (typically reflecting changing ocean cur-
53 rents), although this proxy can also capture changes in productivity and
54 trophic structure (Whitney et al., 2019; Gillikin et al., 2017). In a few select
55 locations anoxic conditions prevent bioturbation of marine sediments, yield-
56 ing annually-laminated sequences capturing environmental change, typically
57 changes in in situ primary production versus terrestrially-derived (eolian or
58 riverine) materials (Hughen et al., 1996; Thunell et al., 1993; Romero et al.,
59 2009; Lawton et al., 2003).

60 However, these proxy archives are not without their challenges (Schöne,
61 2013; Hetzinger et al., 2016; Hughes and Ammann, 2009). In tropical sclerac-
62 tinian corals (Table 1), compounding evidence suggests that biological effects
63 obscure some of the environmental signals encoded into the skeleton. For
64 example, coral growth typically positively correlates with seawater temper-

65 ature such that warmer temperatures generate faster growth (Saenger et al.,
66 2009); yet our current unprecedented warming may exceed the thermal max-
67 imum in some species (Lough et al., 2018). Where the thermal maximum
68 is exceeded, temperatures may in fact reduce growth; thus, warm temper-
69 atures may both increase and decrease growth (Anderson et al., 2017). In
70 turn, growth rates and other biological ("vital") effects may alter skeletal
71 geochemistry during the process of crystal calcification, making accurate
72 extraction of an environmental signal difficult (Saenger et al., 2008; Cohen
73 et al., 2006; Robinson et al., 2014). For example, calcification rate may
74 determine incorporation of elements into the skeleton more so than environ-
75 mental characteristics (Shirai et al., 2005). Similar issues are present in other
76 high-resolution marine archives: in bivalves, temperature and seawater $\delta^{18}O$
77 composition combine to determine the oxygen isotopic composition of the
78 mollusc skeleton, meaning that interpretation in variability of only one of
79 these parameters is challenging (Wanamaker et al., 2007). Many trace ele-
80 ments in bivalves vary with organismal growth and metabolic processes also
81 making it difficult to extract an environmental signal (Elliot et al., 2009).
82 In sclerosponges, the absence of consistent periodicity of growth bands pre-
83 vents accurate chronological assignment to time in the skeleton (Swart et al.,
84 2002). For crustose coralline algae, significant specimen-specific variability
85 suggests that replication is needed to reduce uncertainty around reconstruc-
86 tions (Williams et al., 2017a; Halfar et al., 2011). In the sediments, ocean
87 locations with anoxic conditions are rare, thus annually-laminated marine
88 sediments are geographically restricted (Lawton et al., 2003). Finally, re-
89 cent work has shown that small errors in chronological uncertainty can sig-
90 nificantly alter interpretation of environmental variability (Comboul et al.,
91 2014).

92 Proteinaceous corals are proving to be important archives of past ocean
93 conditions over multiple spatial and temporal scales: their growth can span
94 up to multiple millennia (Roark et al., 2009) and their distribution extends
95 throughout the global ocean (Figure 2). Taxonomically, they are colonial
96 Anthozoans in the phylum Cnidaria, including two suborders (Holaxonia and
97 Calcaxonia) and one subgroup (Scleraxonia) of Alcyonaceans (soft corals or
98 gorgonian corals) in the subclass Octocorallia, and two orders Antipathar-
99 ians (black corals) and some Zoanthids (gold corals) in the subclass Hexa-
100 corallia (Figure 1) (van Ofwegen, 2018). The unifying feature of proteina-
101 ceous corals is that they accrete biomass that includes recalcitrant protein
102 and contains organic matter derived from seawater and dietary sources. The
103 skeleton archives ambient environmental conditions because: 1) it is both
104 protected by a continuous external tissue layer and resistant to diagenesis

105 even when exposed to seawater, 2) forms as a core in concentric, coeval
 106 bands such that the outer layer of skeleton is the most recently formed, and
 107 3) captures environmental variability in its physical, chemical, and/or bio-
 108 logical properties (Sherwood et al., 2006; Williams et al., 2006; Risk et al.,
 109 2002). In some species, the formation of both organic and inorganic skeleton
 110 provide dual recorders of ambient and surface water processes (Griffin and
 111 Druffel, 1989). Because of these traits, sclerochronological and geochemical
 112 techniques can extract approximately annually-resolved records of a broad
 113 range in environmental variability over the past several thousands of years.

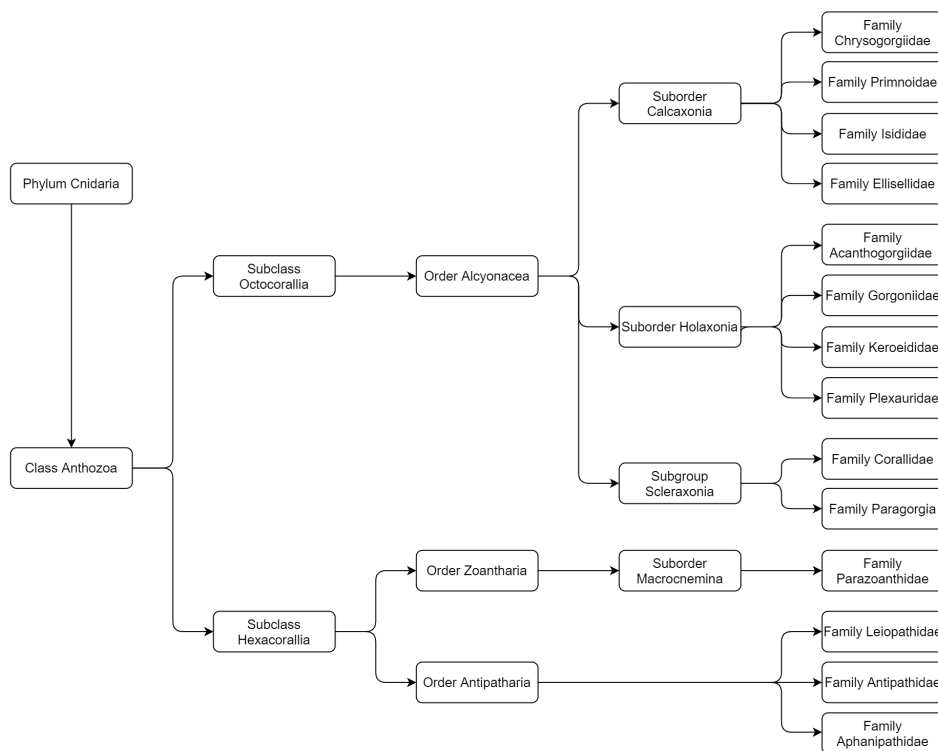


Figure 1: Taxonomic relationship from the World Register of Marine Species (van Ofwegen, 2018) of the major proteinaceous coral families considered for environmental reconstructions.

114 To date, records of seawater temperature (Thresher et al., 2010), nitro-
 115 gen fixation (Sherwood et al., 2013), ocean circulation (Williams and Grot-
 116 toli, 2010a), land use change (Prouty et al., 2014), phytoplankton dynamics
 117 (McMahon et al., 2016), water mass reservoir age (Komugabe et al., 2014),
 118 and terrestrial effluent (Risk et al., 2009b) have been reported over various

119 timescales from both deep and shallow-water proteinaceous coral specimens.
120 Yet, there remain substantial gaps in our understanding of how the records
121 are incorporated and preserved in the corals. This review aims to provide
122 a synthesis of the current knowledge of proteinaceous coral skeletal charac-
123 teristics, including methods for incorporation of environmental signatures
124 in the skeleton and chronological assignment with associated uncertainties.
125 At the same time, I provide a comprehensive review of the environmental
126 reconstructions derived from this group of corals with a discussion on the
127 emerging techniques and the current limitations in extracting environmental
128 variability from the coral skeletons. This work helps to frame our recom-
129 mendations for advancing the field of environmental reconstructions from
130 these important archives.

131 **2. Characteristics of proteinaceous corals**

132 *2.1. Distribution*

133 The distribution of proteinaceous corals is determined largely by habi-
134 tat requirements, and not limited by latitude or depth. They are found
135 throughout the world's oceans from the tropics to the poles (Figure 2), and
136 from surface waters to greater than 8600 m (Wagner et al., 2012; Pasternak,
137 1977). Black corals are largely deep-sea taxa, with approximately 75% of
138 the nearly 250 species found deeper than 50 m (Cairns, 2007). Similarly,
139 several prominent families of gorgonian Octocorals are found in the deep-
140 sea (Perez et al., 2016; Zapata Guardiola et al., 2012). In some species,
141 temperatures does restrict latitudinal and depth distribution (Mortensen
142 and Buhl-Mortensen, 2004; Wagner et al., 2012). Otherwise, most species
143 require hard substrate or host organism for which to settle on and larger-
144 scaled topographic features to create strong and regular currents to provide
145 food (Wagner et al., 2012; Mortensen and Buhl-Mortensen, 2004; Gori et al.,
146 2011; Giusti et al., 2014; Edinger et al., 2011; Sinniger et al., 2013). The pro-
147 teinaceous corals also require low-sedimentation environments to reduce the
148 occurrence of smothering (Mortensen and Buhl-Mortensen, 2004; Wagner
149 et al., 2012). Finally, distribution of some species is a function of ecological
150 connectivity and habitat selection by larvae (Jordán-Dahlgren, 2002; Lasker
151 and Kim, 1996). Where the corals are able to settle with suitable habitat,
152 they can sometimes reach significant densities, becoming the dominant eco-
153 logical organisms and/or supporting significant diversity of other organisms
154 (Wagner et al., 2012; Cerrano et al., 2010; Grigg, 1977; Stone et al., 2015).

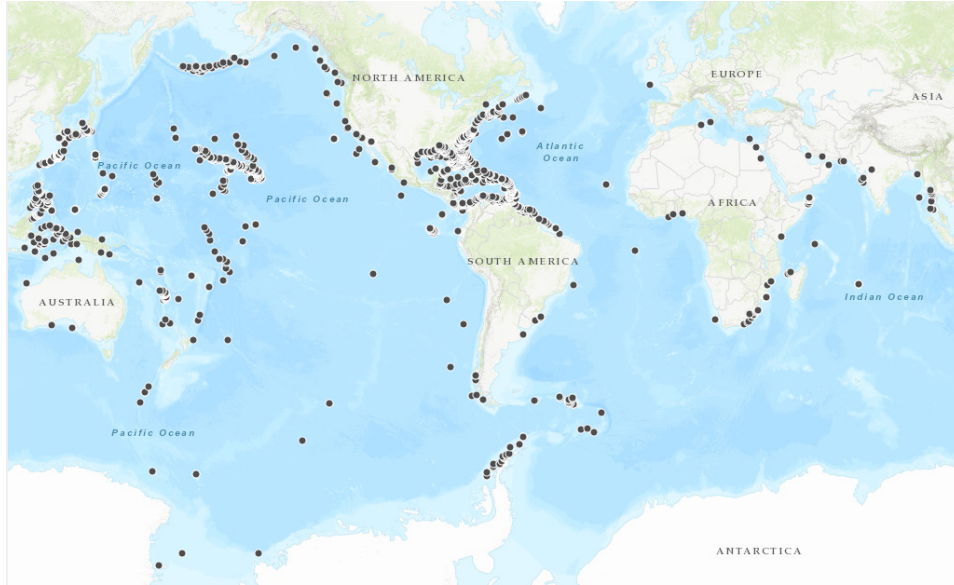


Figure 2: Map of gorgonian coral locations identified from the Smithsonian Institution (<https://deepseacoraldata.noaa.gov>).

155 *2.2. Morphology*

156 The proteinaceous corals are ahermatopic, colonial organisms with an
 157 epithelial tissue covering a scleroproteic skeleton. The coral’s epithelial tis-
 158 sues secrete the scleroproteic skeleton in concentric layers around a central
 159 core. The core itself may be solid, hollow, or even another organism. This
 160 skeleton builds up over time into significant growth structures: individuals
 161 attaining several meters in width and height are not uncommon (Figure 3)
 162 (Grigg, 1965; Lasker and Sanchez, 2002; Leversee, 1976).

163 The gross colony morphology of skeletons varies widely from unbranched
 164 and wire-like to heavily branched and arborescent. The gross colony mor-
 165 phology of proteinaceous corals is likely an adaptation to microhabitat and
 166 functional niche: the smaller and more irregular bushy gorgonian *Primnoa*
 167 *resedaeformis* is adapted to variable currents in near-bottom environments
 168 while *Paragorgia arborea* is generally taller and wider, adapted to reach-
 169 ing above the turbulent near-bottom currents (Buhl-Mortensen and Buhl-
 170 Mortensen, 2005). The stiffness of the skeleton varies with environment as
 171 well: corals with rigid and inflexible skeletons are generally found in calm,
 172 deep-water environments while taxa with more flexible skeletons are more
 173 prevalent in high-energy areas (Esford and Lewis, 1990). Arborescent mor-

174 phologies are advantageous since branch bifurcation increases colony sur-
175 face area. The increased surface area provides more support for resource
176 acquisition, waste removal, gas exchange and reproductive tissues; the lat-
177 ter being a benefit that is particularly important to old colonies (Brazeau
178 and Lasker, 1992). In addition to surface area, reduced polyp size is also
179 linked to productivity in symbiotic gorgonians (Baker et al., 2015). As a
180 result, morphological characters such as colony shape and polyp sizes may
181 be convergent amongst the diverse groups of proteinaceous corals but serve
182 different functions for acquiring nutrition (Porter, 1976). Convergent evo-
183 lution is supported by the different taxonomic relationships amongst the
184 morphologically-similar proteinaceous corals (Figure 1).

185 2.3. Nutrition

186 Most proteinaceous corals are omnivorous suspension feeders, exploiting
187 a wide variety of food sources (Elias-Piera et al., 2013). These food sources
188 include zooplankton (Coma et al., 1994), microplankton (Ribes et al., 1998),
189 suspended particulate organic matter (POM) (Lasker, 1981; Williams and
190 Grottoli, 2010b), sinking POM (Roark et al., 2005; Sherwood et al., 2005a;
191 Druffel et al., 1995) and dissolved organic matter (Murdock, 1978). The size
192 of their food source ranges from 4 μm (nanoeukaryotes) to several hundred
193 microns (seston particles) (Ribes et al., 2003). A corals adaptability to a
194 diversity of food sources makes use of seasonal fluctuations in food supply
195 (Coma et al., 2000). For example, shallow water gorgonians can shift from
196 a plankton-dominated diet in winter to resuspended organic matter in the
197 summer when plankton concentrations decline (Cocito et al., 2013) along
198 with shifting the size class of its diet based on the natural abundance of prey
199 items (Leal et al., 2015). Since gorgonian's store energy primarily as lipids,
200 and reductions in food availability may reduce lipid (energy) reserves (Rossi
201 et al., 2006; Rossi and Tsounis, 2007), an opportunistic feeding strategy may
202 reduce stress to the corals. In deep-water corals, the primary food source
203 is POM produced in the surface waters that has sunk to depth (Griffin and
204 Druffel, 1989; Sherwood et al., 2005b; Roark et al., 2006).

205 In addition to heterotrophy in proteinaceous corals, a diversity of gor-
206 gonians found in warm, sunlit waters use photoautotrophic food obtained
207 from *Symbiodinium* (dinoflagellate microalgae) symbionts located within the
208 polyp endoderm (Kanwisher and Wainwright, 1967). In fact, the net gain
209 of carbon from *Symbiodinium* photosynthesis may be similar to many scler-
210 actinian corals (Kanwisher and Wainwright, 1967). This, combined with
211 contraction of gorgonian polyps at night when other species are actively cap-
212 turing prey, suggests a predominantly autotrophic nutrition in some of these

213 corals (Wainwright, 1967). Similarly, heterotrophy supplies less than 20% of
214 the annual nitrogen demand in symbiotic gorgonians with rod morphologies
215 and large polyps (Ribes et al., 1998). Thus, nitrogen must be coming from
216 *Symbiodinium* to meet the metabolic demands of growth and reproduction.
217 However, while most symbiotic gorgonians benefit at least somewhat from
218 *Symbiodinium* photosynthesis, only species with high polyp and colony-level
219 surface area:volume are net autotrophs (Baker et al., 2015).

220 Black coral nutrition is largely reliant on heterotrophy, and not depen-
221 dent on *Symbiodinium* (Wagner et al., 2012): Hawaiian black corals live in
222 low-light environments that do not support photosynthesis even when they
223 are living with intercellular *Symbiodinium* (Wagner et al., 2012). In deep-
224 water corals, the functional role of the symbiont to the coral is unknown.

225 **3. Taxonomic considerations**

226 Proteinaceous corals are gorgonian corals, black corals, and some zoan-
227 thids in the class Anthozoa of the phylum Cnidaria (Figure 1). Anthozoans
228 are exclusively polypoid, and may be colonial, clonal, or solitary, skeleton-
229 less or with a mineralic and/or proteinaceous skeleton (Daly et al., 2007).
230 They are divided into the subclasses Octocorallia and Hexacorallia. The
231 Octocorallia have eight tentacles and eight mesenteries of octocoral polyps
232 (Bayer, 1981) while the Hexacorallia generally have hexamerous symme-
233 try, although eight- or ten-part symmetry is present. All Hexacorallia have
234 spirocysts, a type of cnida with a singlewalled capsule and a tubule com-
235 posed of tiny entangling sub-threads (Mariscal et al., 1977), and includes
236 the Antipatharia and Zoanthidea (Daly et al., 2007).

237 Species identifications are sometimes problematic, as descriptions are
238 made from inadequate specimens and/or the type specimen is not avail-
239 able (Daly et al., 2007; Wagner et al., 2012). In addition, advancements in
240 molecular techniques are refining taxonomic relationships.

241 *3.1. Gorgonians*

242 Gorgonian is the common name for Octocorallia falling within the sub-
243 orders Holaxonia and Calcaxonia, and the subordinal group Scleraxonia of
244 the order Alconacea (Horvath, 2019; Daly et al., 2007); they were formerly
245 within the order Gorgonacea, a term which is no longer taxonomically ac-
246 cepted (van Ofwegen, 2018; Perez et al., 2016; Grasshoff, 1999). Gorgonian
247 corals are sometimes colloquially referred to as sea whips or sea fans. The
248 common feature of these corals is soft tissue encompassing the coenchyme
249 and covering the coral animal polyp that secretes a scleroproteic skeleton

250 comprised of some combination of non-scleritic calcite and gorgonin (Daly
251 et al., 2007). In the tissue, calcite sclerites provide skeletal support and
252 protection, and are one of the primary taxonomic identifiers (Bayer, 1961).
253 The gorgonin material in the skeleton is a structural, fibrillar organic keratin-
254 like protein material with a heterogenic chemical composition (see review by
255 (Ehrlich, 2019)). The relative amounts and arrangement of the gorgonian
256 and calcite skeleton varies among species and taxa. The Holaxonians form
257 an axial skeleton derived largely of layered gorgonin fibers built around a hol-
258 low, cross-chambered central core. Small amounts of embedded calcite are
259 sometimes deposited in non-scleritic calcareous inclusions (Figure 3) (Bond
260 et al., 2005; Lewis et al., 1992; Daly et al., 2007). The Calcaxonians form a
261 solid axial skeleton of gorgonian with large amounts of non-scleritic calcite
262 with no central hollow core (Daly et al., 2007). The Scleraxonia form an ax-
263 ial (or axial-like) skeleton of sclerites which can be fused together or bound
264 by gorgonin (Horvath, 2019; Daly et al., 2007).

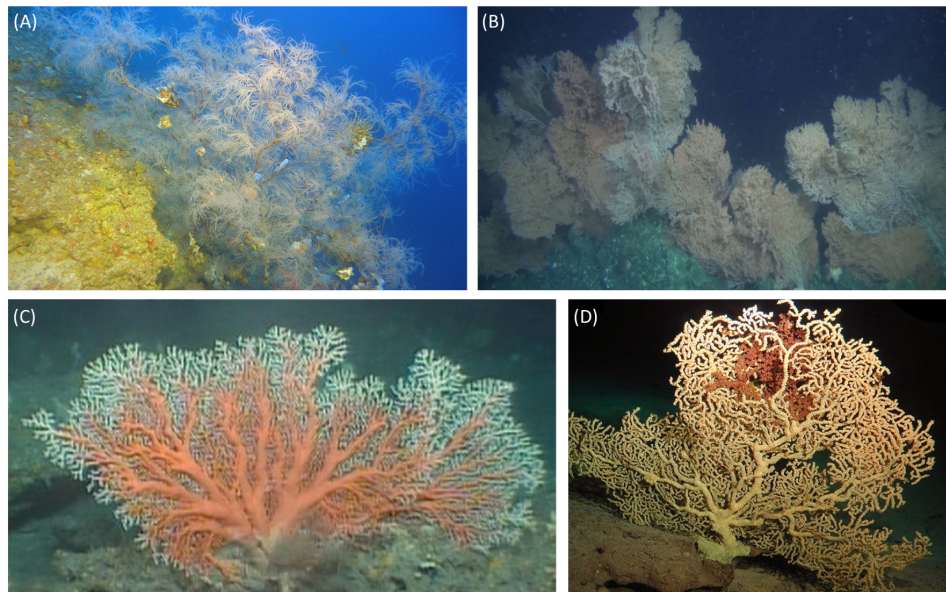


Figure 3: Proteinaceous corals viewed *in situ* (A) Black coral (*Antipathes grandis*), (B) Primnoid gorgonian coral (*Primnoa pacifica*), (C) Scleraxonian gorgonian coral (*Coralium elatius*), and (D) Gold corals (*Kulamanamana haumeaa*). Photos from (A) Hawaii Undersea Research Laboratory, provided by Daniel Wagner, (B) Alaska Fisheries Science Center, provided by Bob Stone, (C) (Nonaka et al., 2012), and (D) (Sinniger et al., 2013).

265 The gorgonin in the skeleton provides flexibility to an otherwise rigid
266 calcified skeleton (Grasshoff and Zibrowius, 1983; Lewis et al., 1992; Wain-

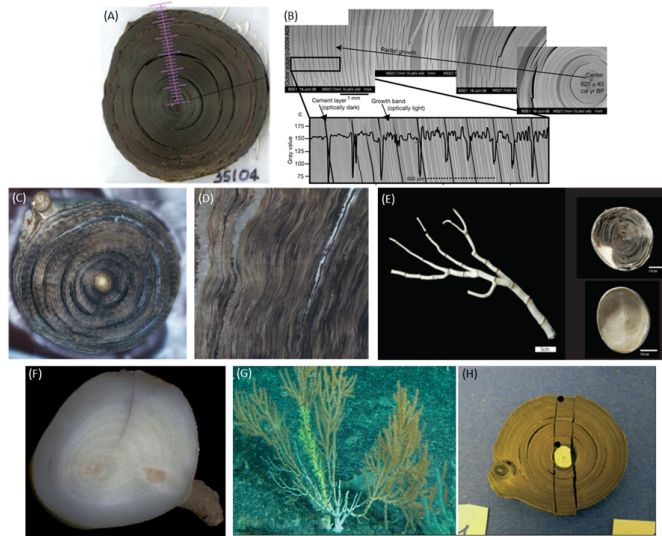


Figure 4: Cross-section and banding patterns in (A-B) Black corals, (C-D) Primnoid gorgonian, (E) Bamboo gorgonian coral with skeletal branch showing node and internode with cross-section sin subset, (F) Scleraxonian gorgonian coral, and (G-H) Gold coral showing the zoonthid subsuming a bamboo coral host. Photos from (A) (Hitt et al., 2020), (B) (Prouty et al., 2011), (C) (Williams et al., 2019), (E) (Hill et al., 2014), (F) (Hasegawa et al., 2012), (G-H) (Sinniger et al., 2013).

267 wright and Dillon, 1969). Gorgonin contains significant concentrations of
 268 glycine, proline, hydroxyproline, and hydroxylysine with 1% by weight
 269 concentrations of saccharides, glucose and galactose, suggesting that col-
 270 lagen is a major structural component of the gorgonin (Szmant-Froelich,
 271 1974; Goldberg, 1978, 1976). In addition, the skeleton is rich in tyrosine
 272 and quinones-containing compounds, an important tanning agent promot-
 273 ing cross-linking of protein chains in the gorgonin (Goldberg, 1976). The
 274 gorgonin composition provides the mechanical flexibility that lets the corals
 275 grow in high velocity areas but may eventually not be able to structurally
 276 support very tall (>1 m) specimens (Wainwright and Dillon, 1969; Ehrlich,
 277 2019). The calcite in gorgonian corals is composed of high-Mg calcite precip-
 278 itated from surrounding seawater DIC (Noé and Dullo, 2006; Roark et al.,
 279 2006), with some contribution of metabolically produced carbon dioxide in
 280 the sclerites of some species (Lucas and Knapp, 1997). The formation of
 281 calcite is induced in vitro because of an extracellular protein, even when
 282 the calcifying solution favors aragonite precipitation (Rahman et al., 2011).
 283 The sclerites are small (10-100 μ m) polycrystalline aggregates of the mag-

284 nesium calcite forming spindle-shaped rods covered with small protrusions
285 and embedded in the coenenchyme. Functionally, the sclerites limit com-
286 pression and extension of the axial skeleton (Lewis and Wallis, 1991) and
287 structural defense against predators (West, 1998). In the same species, the
288 sclerites also contain insoluble organic matrices that are predominately col-
289 lagenous (Kingsley, 2013). In the Holaxonians the axis may be contain
290 non-scleritic calcareous deposits (loculi) while the Calcaxonians may have
291 significant amounts of non-scleritic calcareous material, either embedded or
292 as internodes between gorgonin nodes. In the Scleraxonia, the axial skeleton
293 is comprised primarily of sclerites and may have minimal to no gorgonin,
294 although are often still included as gorgonian corals (Horvath, 2019). In
295 deep-water Calcaxonians reaching significant size, skeletogenesis shifts from
296 the calcite-organic alterations to fibrous Mg-calcite skeleton encompassing
297 the central axis (Noé et al., 2008). The causes of this could be due to the
298 lower energy costs of forming calcite versus gorgonin skeleton, potentially
299 related to shifts in food availability (Mistri, 1996) or shifts in hydrographic
300 regimes requiring stiffer axial structures (Noé et al., 2008).

301 The banding in gorgonian corals occurs within both the gorgonin and
302 calcite fraction of the skeleton and/or by alteration of calcite and gorgonin
303 in the skeleton (e.g., Figure 3). In the gorgonin, more cross-linkages be-
304 tween the protein chains have higher tyrosine content, producing a darker
305 ("tanned") colour (Goldberg, 1976; Szmant-Froelich, 1974). The degree of
306 cross-linkages directly reflects the amount of time the axial skeleton re-
307 mains in contact with the epithelium such that periods of faster growth
308 result in fewer cross-linkages with less tyrosine and lighter skeleton while
309 slower growth creates more time for cross-linkages with higher tyrosine and
310 darker skeleton (Goldberg, 1976; Szmant-Froelich, 1974). As a result, band-
311 ing within the gorgonin skeleton may reflect changes in growth in response
312 to coral biology or environmental variability, such food availability (Szmant-
313 Froelich, 1974).

314 Within the calcite skeletal fraction, bands are formed because of varia-
315 tions in crystal growth combined with inclusion of organic matter. Calcite
316 fibers nucleate on calcification centers or gorgonin surfaces and then grow
317 spherically to form crescent shaped fibrous crystal bundles. Repetition of
318 crystal growth and nucleation events laterally fuse together to create bands
319 (Risk et al., 2002). In Calcaxonian Isididae corals, changes in orientation of
320 the crystal bundles surrounding by thin organic seams relative to the plain
321 of imaging also contribute to the banding patterns (Noé and Dullo, 2006).
322 The longitudinal axes of the crystals are oriented parallel to the section plan
323 in the darker rings while they are oriented oblique to vertical in the lighter

324 bands. Changes in biomineralization likely determine the orientation of the
325 crystals. In the same corals, there are no changes in density of the crystal
326 structure contributing to the banding structure (Noé and Dullo, 2006), un-
327 like calcium carbonate scleractinian corals. In Scleraxonia, annual banding
328 patterns relate to the concentration of organic matter such that seasonally,
329 higher concentrations of organic matter are present, or might not be present
330 at all (Marschal et al., 2004; Mortensen and Buhl-Mortensen, 2005). Gor-
331 gonin may be present in the calcite skeleton, forming an insoluble structural
332 framework surrounding the crystal. In this role, gorgonin scaffolds the calcite
333 but does not initiate biomineralization (Ehrlich, 2019). Foreign particulate
334 organic matter is also incorporated into the skeleton along growth bands,
335 but probably only in significant accumulations during growth hiatuses (Noé
336 and Dullo, 2006).

337 In gorgonian corals forming alternating couplets of calcite-gorgonin skele-
338 ton, the calcite secretions by the coral may be constant while fluctuating
339 rates of gorgonin production produce the calcite-gorgonin banding. Since
340 the biosynthesis of the gorgonin skeleton requires more energy than the
341 secretion of a calcite crust, pulses of increased food may trigger the pro-
342 duction of gorgonin (Noé et al., 2008). Food availability as a trigger is
343 consistent with formation of the dark, more gorgonin-rich portion of the
344 calcite-gorgonin ring couplet coinciding with the the spring/summer plank-
345 ton bloom in *Primnoa resedaeformis* (Sherwood et al., 2005b).

346 Some gorgonian corals form their bands annually: shallow water gor-
347 gonians *Muricea californica* and *Muricea fruticosa* (Grigg, 1974) and the
348 deep-sea Tasmanian *Keratoisis* (Thresher et al., 2004) form annual bands
349 in either the gorgonian or calcite fraction of the skeleton while *Primnoa*
350 *resedaeformis* forms annual couplets of gorgonin and calcite (Andrews et al.,
351 2002; Sherwood et al., 2005b). In the Isididae *Lepidisis* sp., counts of the cal-
352 citic banding in the internode combined with ^{210}Pb dating suggest the bands
353 form bi-annually, with two light and dark couplets deposited per year. How-
354 ever, scanning electron microscopy of the calcite internode produced much
355 higher band counts, potentially driven by the downward transport of organic
356 blooms associated with lunar cycles (Tracey et al., 2007; Roark et al., 2005).
357 *P. resedaeformis* forms sub-annual banding of unknown periodicity that is
358 evident within their annual bands (Risk et al., 2002) Thus, clear annual
359 or lunar bands are not evident in all gorgonian coral taxa (Martinez-Dios
360 et al., 2016); nor are they consistently present even within specimens of the
361 same taxa at different locations or using different band counting techniques.
362 These discrepancies perhaps reflects stability in local environments, timing
363 of reproduction, and/or food abundance (Grigg, 1974; Buhl-Mortensen and

364 Mortensen, 2005). Taken together, environmental conditions with strong
365 seasonal fluctuations drive annual periodicity in skeletal banding in the gor-
366 gonian corals rather than a characteristic inherent to a specific coral genus
367 itself; however, additional unknown mechanisms driving banding are present.

368 3.2. *Black corals*

369 Black corals are the common name for families within the order An-
370 tipatheria, which is comprised of seven families all under the umbrella of
371 proteinaceous corals (Figure 1). They have six unbranched tentacles, six pri-
372 mary mesenteries, and zero, four, or six secondary mesenteries. The number
373 of mesenteries and the morphology of the corallum, polyps, and axial spines
374 are the principal taxonomic characters used in classification (Opresko, 2006;
375 Wagner et al., 2010), although DNA sequencing is becoming more common
376 (Brugler et al., 2013). The spines radiate from the central growth axis out-
377 ward (Goldberg, 1991); likely serving to strengthen the skeleton (Kim et al.,
378 1992).

379 The skeleton in black corals is entirely proteinaceous (no calcium car-
380 bonate) with a significant contribution from a chitin-like polysaccharide.
381 The skeleton in the genera *Antipathes* is comprised primary of non-fibrillar
382 protein (60%), chitin fibrils (15%), and other minor contributions of lipid,
383 carbohydrate, phenols, and sterols (Goldberg, 1991; de la Rosa et al., 2007).
384 The amino acid composition of the protein fraction is 35% glycine, 15% ala-
385 nine, and 13% histidine with 4-6% serine, glutamine, and leucine, and less
386 than 4% of 11 other amino acids. These corals have the highest concentra-
387 tion of halogens (iodine and bromine) in a biological material (Goldberg,
388 1978), although concentrations of these halogens vary in the skeleton, likely
389 in response to environmental availability (Goldberg, 1978; de la Rosa et al.,
390 2007; Williams and Grottoli, 2011; Prouty et al., 2018).

391 The banding in black corals is formed by layers of chitin fibrils. The
392 corals accrete the chitin molecules which connect by hydrogen bonds to
393 form sheets with proteins. The proteins attached to the chitin sheets group
394 together through cross-linking to form growth layers building the hardened
395 skeleton (Kim et al., 1992; de la Rosa et al., 2007)). The periodicity of
396 these growth layers (rings) varies among taxa: rings are formed daily in
397 *Stichopathes gracilis* (Noome and Kristensen, 1976), annually in *Antipathes*
398 spp. (Williams et al., 2006; Grange and Goldberg, 1993), or with no identi-
399 fied periodicity in *Bathypathes patula* (Marriott et al., 2020).

400 3.3. *Gold corals*

401 Marine organisms within the order Zoanthidea (= Zoantharia, Zoanthi-
402 naria) are clonal, soft bodied polyps with two rows tentacles, and a sin-
403 gle ventral siphonoglyph linked together by a coenenchyme (Daly et al.,
404 2007). Of the zoanthids, those classified as proteinaceous corals are the
405 taxa that secrete a scleroproteic skeleton (Sinniger et al., 2013) through
406 parasitizing other proteinaceous coral skeletons (Sinniger et al., 2005; Cer-
407 rano et al., 2010). Initial taxonomic classification was done by morphology
408 based mostly on septa characteristics (Ryland and Lancaster, 2003), with
409 more recent work using rRNA to infer molecular phylogeny (Sinniger et al.,
410 2005). Gold coral is the common name for *Kulamanamana haumea* and
411 potentially used synonymously to *Savalia* (Sinniger et al., 2013). Current
412 classification recognizes the genera *Kulamanamana* and *Savalia*, both with
413 a scleroprotein skeleton and both which may have previously been referred
414 to as *Gerardia* (Cerrano et al., 2010; Parrish and Roark, 2009; Griffin and
415 Druffel, 1989).

416 The scleroproteinaic skeleton of the zoanthid resembles that of other
417 proteinaceous corals: it is rich in histidine and glycine, the latter which
418 may provide structural strength to the skeleton by tightly binding protein
419 polymers through hydrogen bonding (Druffel et al., 1995; Sherwood et al.,
420 2013). It also forms growth layers, potentially analogously to the black
421 corals (Griffin and Druffel, 1989; McMahan et al., 2016). Unique to these
422 zoanthids is that the secreted skeleton is dependent on a host skeleton, and
423 often actually ends up subsuming the original host (Parrish, 2015).

424 4. Geochronology

425 Accurate dating of proteinaceous corals is critical to assigning time to
426 environmental records derived from their skeletons. Annual bands in corals
427 collected live from a known date provide the best chronologies (e.g., annual
428 resolution within minimal uncertainty). In the absence of annual bands or
429 in corals collected dead, geochemical dating techniques provide estimations
430 of time in the skeleton. The duration of the corals, both as living organisms
431 and also preservation of the skeleton once dead, informs the periods of time
432 for which environmental information is captured by these corals.

433 4.1. *Geochemical dating techniques*

434 Radiocarbon measurements in the organic skeleton yields chronological
435 information in two ways. The first method measures the amount of radio-
436 carbon in the skeleton to backtrack the amount of time that has passed since

437 the skeleton was formed, based on the radioactive decay of ^{14}C with a half
438 life of 5730 years. This technique requires information about the amount of
439 ^{14}C in the atmosphere at the time of the skeletal formation, and a correc-
440 tion, termed the marine reservoir age, to account for the difference between
441 the atmospheric ^{14}C content and the local ^{14}C content of the seawater which
442 ends up in the food to the corals (Stuiver and Braziunas, 1993; Griffin and
443 Druffel, 1989). Thus, the usefulness of ^{14}C dating is limited by knowledge
444 of past seawater ^{14}C variability driven by seawater circulation changes and
445 natural or anthropogenic changes in local seawater ^{14}C and the calculation
446 of an accurate correction value (Druffel et al., 1995). In addition, local vari-
447 ability in the marine reservoir age and atmospheric variability result in the
448 possibility of multiple calibrated ages, yielding numerous potential ages of
449 the skeleton.

450 The second method by which radiocarbon measurements can provide
451 chronological control is through correlation of anthropogenic perturbations
452 in atmospheric radiocarbon content with known timing in the skeleton of
453 the coral colonies. Anthropogenic burning of fossil fuels since the 1850s is
454 emitting ^{14}C -depleted carbon into the atmosphere. The ^{14}C -depleted carbon
455 dissolves into the surface waters, reducing the ^{14}C content of the mixed sur-
456 face layer (Keeling, 1979; Tans et al., 1979), and decreasing the ^{14}C content
457 of proteinaceous coral skeletons formed in the early-to-mid 1900s. Beginning
458 in the 1950s, thermonuclear bomb-testing increased the ^{14}C content in the
459 atmosphere by an order of magnitude, resulting in a near doubling of the
460 radiocarbon content of the surface oceans by the mid-to-late 1970s. Since
461 then, the excess ^{14}C in surface water has been decreasing due to radioac-
462 tive decay and mixing with low- ^{14}C content deeper waters. The increase
463 and subsequent decrease in ^{14}C content is measurable in the ocean surface
464 waters. The ^{14}C perturbation is incorporated into the marine carbon cycle,
465 then into the food source to the corals, and finally into the coral skeletons.
466 Coral skeletal measurements of ^{14}C through time in the skeleton can iden-
467 tify the start of ^{14}C -bomb carbon mixing into the oceans in the mid-1950s,
468 peak in the late 1970s, and subsequent decline in values to the present day.
469 Through identification of these time points, including a known date of collec-
470 tion, three time points can be assigned to skeletal growth providing the basis
471 for a first order chronology (Figure 5) (Roark et al., 2006, 2005; Sherwood
472 et al., 2005b; Prouty et al., 2014; Williams and Grottoli, 2010a).

473 Radiocarbon measurements of the calcitic portion of deep-sea proteina-
474 ceous coral skeletons does not yield chronological information. Instead, the
475 carbon in the calcite skeleton of these corals is incorporated from ambi-
476 ent carbon at the depth of the coral and not derived from organic carbon

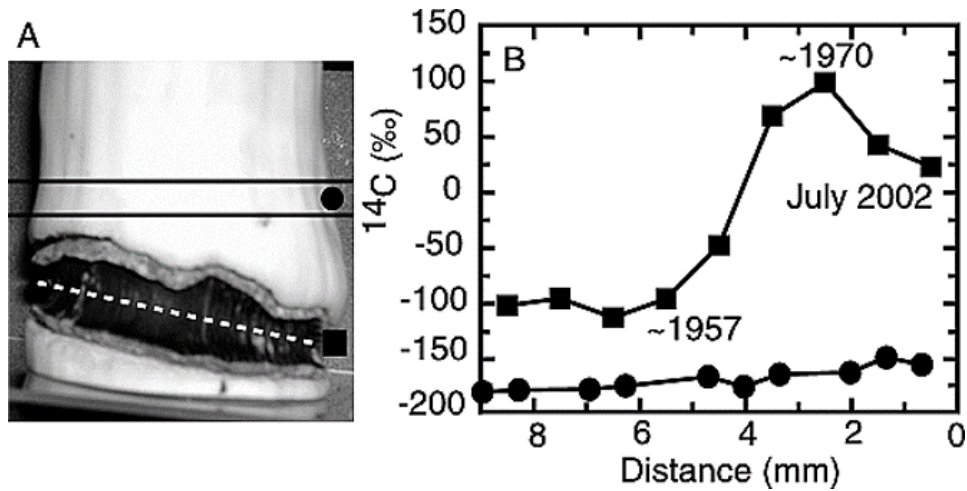


Figure 5: Radiocarbon (^{14}C) measured across two cross-sections of the axial skeleton of a bamboo coral showing bomb-carbon derived from surface waters encapsulated in the organic internode and ^{14}C from ambient water at depth in the calcitic internode. Figure from Roark et al. (2005).

477 exported from the surface (Figure 5). Thus, these corals capture the ^{14}C
 478 content of the dissolved inorganic carbon at depth, which reflects oceano-
 479 graphic processes (Griffin and Druffel, 1989; Roark et al., 2005).

480 The decay of ^{210}Pb measured in the organic skeleton of proteinaceous
 481 corals provides estimates of specimen age (Andrews et al., 2002). The low
 482 solubility of lead in the water column causes it to adhere to particulate
 483 matter that is the food source to proteinaceous corals, forming a source of
 484 exogenous (or unsupported) ^{210}Pb ($^{210}\text{Pb}_{ex}$) to the skeleton. Since decay of
 485 the ^{210}Pb starts after incorporation into the skeleton, the amount of $^{210}\text{Pb}_{ex}$
 486 remaining in the skeleton can provide an estimate of the time that has passed
 487 since the skeleton was formed, once the additional sources of ^{210}Pb in the
 488 skeleton are accounted for. Since the half life of ^{210}Pb is relatively short
 489 (22.26 years), measuring $^{210}\text{Pb}_{ex}$ can determine the age of coral skeletons
 490 that are less than a century old. Beyond this, the amount of ^{210}Pb will
 491 decrease to background levels. Additional sources of lead (supported and in-
 492 growth fractions) include detrital particles in the water column derived from
 493 the decay of ^{238}U and the in situ decay of ^{226}Ra taken up from the skeleton
 494 during skeletal formation. The supported and in-growth fractions are likely
 495 negligible in specimens in which the asymptote of the curve of measured
 496 ^{210}Pb against time is essentially zero and do not need to be accounted for
 497 in determining $^{210}\text{Pb}_{ex}$ (Williams et al., 2006).

498 Amino acid racemization measures changes in amino acid molecules that
499 occur at a set rate. In corals, the ratio of D- to L-handed isomers in aspartic
500 acid moves toward an equilibrium value once the skeleton is formed. The
501 rate of equilibrium is a function of age and temperature. Thus, if tempera-
502 ture is constant as it is in the deep sea, than the amount of the D-isomer can
503 be used to calculate age (Goodfriend, 1992). Amino acid racemization has
504 successfully determined age in a fossil specimen of *Primnoa resedaeformis*
505 with an error marginally better than that of ^{14}C dating over the past 100-
506 200 years or where the model ^{14}C ages are invalid (50-90 years BP AD 2000)
507 (Sherwood et al., 2006). Prior to 200 years BP, the error associated with the
508 D/L age exceeds that of ^{14}C and post 1960, bomb-carbon provides better
509 age estimates than the amino acid racemization. In gorgonians, the fibrillar
510 nature of the protein has caused problems with the use of acid racemization:
511 experiments heating the skeleton likely overestimate racemization rates, re-
512 sulting in younger apparent ages. The overestimation from heating likely
513 explains the discrepancy between amino acid racemization-determined ages
514 of 250 years and radiocarbon-derived age of 1800 years for *Salvia* (= *Ger-*
515 *ardia*) (Collins and Riley, 2000; Goodfriend, 1997; Sherwood et al., 2006;
516 Reimer and Sinniger, 2010).

517 U/Th-dating is used to provide chronological control of skeletal growth
518 by determining the level to which the the radioactive isotope ^{234}U has de-
519 cayed into its daughter isotope ^{230}Th . The extent of the decay reflects
520 the amount of time that has passed since the skeleton was formed. In
521 the ocean, ^{234}U co-precipitates from the seawater into the skeleton during
522 skeletal formation while ^{230}Th concentrations are often negligible (Edwards,
523 2003; Adkins, 1998). Thus, the age of the coral skeleton is determined by
524 calculating the measured amount of ^{230}Th to accumulate from the decay
525 of ^{234}U , as the isotopes moves toward secular equilibrium (Adkins, 1998;
526 Bradley, 1999). While this dating technique is used in shallow water and
527 deep-sea scleractinian corals (Cheng et al., 2000; Schröder-Ritzrau A., 2005;
528 Cobb et al., 2003), it has not been heavily applied to the calcitic skeleton in
529 proteinaceous corals: in gorgonian corals, low amounts of uranium, particu-
530 larly relative to potential contamination, make dating with U/Th difficult,
531 and some taxa (*Coralliidae*) display display U-series open-system behaviour
532 making U/Th dating completely unsuitable in these corals (Sinclair et al.,
533 2011; Thresher et al., 2004; Robinson et al., 2007; Gutjahr et al., 2013). In
534 contrast, antipatharians have sufficient concentrations and display U-series
535 closed system behaviour; U/Th-dating is successfully used in these corals
536 (Komugabe et al., 2014; Komugabe-Dixon et al., 2016).

537 *4.2. Longevity, Growth, and Fossil Preservation*

538 Extreme longevity is reported in some taxa of proteinaceous corals: both
539 antipatharians and gold corals can live for centuries to millennia (Komugabe-
540 Dixon et al., 2016; Roark et al., 2009; Hitt et al., 2020; Prouty et al.,
541 2015; Marriott et al., 2020). For the antipatharian corals, growth rates and
542 longevity may be taxa specific such that slower growing species live longer
543 (Hitt et al., 2020). In contrast, maximum reported ages for gorgonians are
544 in the decades to centuries with one reported colony exceed a millennium
545 in age (Martinez-Dios et al., 2016; Sherwood and Edinger, 2009; Prouty
546 et al., 2015). Broadly, deep-water taxa tend to grow slower and live longer
547 than shallow-water taxa. Both decreasing temperatures with depth and
548 lower availability of surface-derived food to deeper specimens could drive
549 this depth-growth relationship (Thresher, 2009; Roberts et al., 2009). Verti-
550 cal growth (linear extension) rates within a single coral colony may remain
551 constant through time (Thresher, 2009) or more commonly decrease with
552 age such that colony height rarely exceeds one meter in gorgonians (Andrews
553 et al., 2002; Coma et al., 1998; Mitchell et al., 1993; Buhl-Mortensen and
554 Buhl-Mortensen, 2005). The strength of the coral connection to the sub-
555 stratum may ultimately drive coral size/height (Kinzie and Robert, 1973);
556 the connection of which is a reflection of strong skeletal composition and
557 moderate ocean currents providing food but not physical stress. However,
558 vertical growth rates also vary through the course of a year; this variabil-
559 ity is likely linked to temperature fluctuations, changes in food availability
560 (Coma et al., 1998) and/or changes in respiration related to oxygen diffu-
561 sion into the coral tissues as a function of changing water current altering
562 boundary layer thickness (Sebens, 1987). And, predation by other organisms
563 may reduce vertical growth: algae abrading branching tips or consumption
564 by fish may slow growth or even erode colony apical tissue (Grigg, 1974).
565 Taken together, many of the factors driving longevity and vertical growth
566 are taxonomic and location(habitat)-specific, and the oldest corals may be
567 those taxa with the strongest skeletons growing in communities dominated
568 by few organisms (reducing competition and predation) and with optimal
569 environmental conditions (moderate currents with low sedimentation rates).

570 Once dead, the tissue layer recedes and the skeleton is exposed to seawater.
571 Skeletal preservation in the proteinaceous corals relates more to com-
572 position than taxa: calcitic skeletal fragments and holdfasts are reported in
573 the geological record from the early Cenozoic and even as far back as the
574 Lower Ordovician (Giammona and Stanton, 1980; Cope, 2005; Stolarski,
575 1996). The organic component of the skeleton is vulnerable to microbial ac-
576 tivity, sponge and bivalve boring, leaving the skeleton weakened and prone

577 to decay (Noé et al., 2007; Grasshoff and Zibrowius, 1983). In fact, the
578 gorgonian *Paragorgia* has little preservation once dead, degrading to just
579 the calcite spicules within a year (Edinger and Sherwood, 2012). In other
580 species, consistency in skeletal amino acid composition is preserved few at
581 least a few thousand years (Sherwood et al., 2006), and Primmoid gorgonin
582 is preserved back to 10,880, albeit with some evidence of bioerosion (Noé
583 et al., 2007). Similarly, sub-fossil gold corals dating back approximately
584 10,000 years have been reported (Parrish and Roark, 2009). In Antipathar-
585 ians, the chitin-like components components of the skeleton do not preserve
586 well (Gupta and Briggs, 2011) although the phosphatised skeletons dating
587 back to the Ordovician are reported (Baliński et al., 2012; Baliński and Sun,
588 2017).

589 **5. Mesopelagic seawater reconstructions from the calcitic skeleton**

590 Reconstructions from the calcitic skeleton in gorgonian corals are largely
591 limited to bamboo corals. As the bamboo corals grow vertically, their skele-
592 ton alternates between forming calcitic nodes interspersed between organic
593 internodes. Both the nodes and internodes grow radially with age so contin-
594 uous measurements across the radius of the calcitic node spans the lifespan of
595 the coral. The source of elements to the calcitic skeleton is typically ambient
596 dissolved elements. As a result, environmental changes in ambient dissolved
597 elements are encoded in the isotopic composition of the coral calcitic intern-
598 odes. However, encoding of that environmental signal is complicated: the
599 biomineralization pathways leading to the calcite precipitation produces a
600 mineral with an isotopic composition that is offset from seawater. If the
601 offset is not constant, then this "vital" effect signal obscures any environ-
602 mental signal captured in the skeleton. Here we explore investigations into
603 overcoming the influence of vital effects on coral skeletal composition.

604 *5.1. Isotopic composition*

605 The source of carbon to the calcite in deep-sea bamboo corals is ambient
606 dissolved inorganic carbon (Roark et al., 2006) with $\delta^{13}C_{seawater}$ values of
607 approximately 0.5 to 2.5 ‰ (Gruber et al., 1999). However, vital effects
608 alter the $\delta^{13}C_{coral}$ from that of seawater, generating values ranging from
609 -5.5 to 2 ‰ (Hill et al., 2014). These vital effects are potentially enhanced
610 during the linear extension phase of the central core axis of these corals,
611 as $\delta^{13}C_{coral}$ in the central core are commonly 1 ‰ depleted relative to rest
612 of the specimen (Hill et al., 2014). Furthermore, $\delta^{13}C_{coral}$ values varied 3
613 ‰ within a single year in one specimen (Hill et al., 2014). In the calcitic

614 sclerites of shallow-water gorgonian corals, vital effects impacting the pro-
615 portion of metabolic carbon uptake during calcification is potentially related
616 to variations in growth rates or ontogenetic effects (Grossowicz et al., 2020).
617 Thus the vital effect-driven offset in $\delta^{13}C_{coral}$ values is not constant, and
618 cannot be accounted for with a simple offset correction factor. For these
619 reasons, direct interpretation of environmental variability from the calcitic
620 $\delta^{13}C$ values is difficult (Farmer et al., 2015).

621 The boron isotopic composition of marine calcifiers broadly reflects the
622 isotopic composition of borate in seawater, which in turn reflects the pH of
623 seawater (Hemming and Hanson, 1992; Zeebe and Wolf-Gladrow, 2001). In
624 Atlantic Ocean bamboo corals, $\delta^{11}B_{coral}$ in recently formed skeleton matches
625 that of the isotopic composition of borate anion in seawater, calculated as
626 a function of seawater pH (Farmer et al., 2015). However, the wide range
627 in $\delta^{11}B_{coral}$ values within these specimens exceeds that which can be ex-
628 plained by variability in seawater pH alone. In addition, in eastern Pacific
629 specimens, $\delta^{11}B_{coral}$ is elevated 0.2 to 2 ‰ higher than calculated for each
630 specimen based on ambient seawater pH (Farmer et al., 2015). Therefore,
631 in bamboo corals, the environmental signal of seawater pH encoded in the
632 $\delta^{11}B_{coral}$ values reflects that of ambient seawater with some additional im-
633 print due to coral’s biological processes when saturation state is greater than
634 1 (e.g., in the Atlantic Ocean). Conversely, seawater with calcite saturation
635 less than 1, active modification of pH during coral calcification disconnect
636 $\delta^{11}B_{coral}$ from the ambient seawater pH (Farmer et al., 2015). In the calcitic
637 skeleton of Scleraxonian corals, the $\delta^{11}B$ composition is similar to that of the
638 bamboo coral, and both are lower than that of deep-sea scleractinian corals
639 (McCulloch et al., 2012; Rollion-Bard et al., 2017). This might suggest that
640 gorgonian corals play less of an active role in controlling the calcifying fluid
641 pH than scleractinian corals (Rollion-Bard et al., 2017).

642 The oxygen isotopic composition of seawater and the temperature at the
643 time of calcite calcification determines the $\delta^{18}O$ composition of marine calci-
644 fiers (Shackleton, 1974). For the deep-sea bamboo corals, the $\delta^{18}O_{seawater}$ is
645 likely consistent over the lifespan of the corals because the surface processes
646 of precipitation/evaporation and sea ice formation/melt that change the
647 seawater $\delta^{18}O$ composition don’t impact deep water on the timescales that
648 these corals live. As a result, seawater temperature should be retrievable
649 from the $\delta^{18}O_{coral}$ values. However, vital effects offset the $\delta^{18}O$ compo-
650 sition of the corals from seawater (Hill et al., 2011; Kimball et al., 2014;
651 Thresher and Neil, 2016). Since this offset is not consistent (Hill et al.,
652 2011), the offsets confounds efforts to retrieve seawater temperature from
653 the $\delta^{18}O_{coral}$ values directly. The deviations in $\delta^{18}O_{coral}$ from equilibrium

654 (e.g., the magnitude of the offset) are associated by proportional deviations
 655 in $\delta^{13}C_{coral}$ from equilibrium. Therefore, the slope of the $\delta^{18}O$ - $\delta^{13}C$ rela-
 656 tionship finds the $\delta^{18}O$ value when $\delta^{13}C$ is at equilibrium. This $\delta^{18}O_{coral}$
 657 value can then be used to back track seawater temperature (Hill et al.,
 658 2011), as has been demonstrated in deep-sea aragonitic scleractinian and
 659 stylasterid corals (Smith et al., 2000; Samperiz et al., 2020). Initial stud-
 660 ies used $\delta^{13}C_{coral} - \delta^{13}C_{DIC} = 0$ ‰ to determine the $\delta^{13}C_{coral}$ equilibrium
 661 value; however, there is no a priori reason why $\delta^{13}C_{coral}$ is equal to $\delta^{13}C_{DIC}$
 662 (Saenger and Erez, 2016): the $\delta^{13}C_{coral}$ may itself be offset from equilib-
 663 rium. More recently, a $\delta^{13}C_{coral}$ equilibrium value was calculated using an
 664 ion-by-ion model of calcite growth (Saenger and Erez, 2016). The model of
 665 calcite growth requires growth rates and pH as inputs, which can be determined
 666 from radiometric dating and $\delta^{11}B$ measurements, respectively (Saenger and
 667 Erez, 2016). The calculated growth rates and pH, thus, determine the pre-
 668 cision of the proxy-derived temperatures, with current estimates limiting
 669 the reconstructed temperature uncertainty to $\pm 2 - 3^\circ C$ (Saenger and Erez,
 670 2016).

671 A second approach to extracting temperature from the calcitic skeleton
 672 of deep-sea corals is the clumped isotopic composition ($\Delta 47$) of the skele-
 673 ton. This technique measures the degree to which rare isotopes bond with
 674 each other versus bonding to the more abundant isotope. In calcium car-
 675 bonate calcifiers, the deviations in abundance of $^{18}O^{13}C$ bonds relative to
 676 a stochastic distribution of carbon isotopologues can vary with tempera-
 677 ture (Eiler, 2007). The $\Delta 47$ value depends on the internal isotopic exchange
 678 between isotopes in a single phase, and as a result, the $\Delta 47$ value is indepen-
 679 dent of the bulk skeletal isotopic composition (Schauble et al., 2006). Thus,
 680 the clumped isotope technique is advantageous because it does not require
 681 either the equilibrium value of the $\delta^{18}O_{coral}$ nor the bulk $\delta^{18}O_{seawater}$ to
 682 extract temperature. However, the $\Delta 47$ value is sensitive to pH and vital
 683 effects in marine calcifiers (Tripathi et al., 2015; Kluge et al., 2014; Eiler,
 684 2011). Potentially because of the role of vital effects, the $\Delta 47$ value in the
 685 gorgonian corals is depleted relative to other measured carbonates, result-
 686 ing in different $\Delta 47$ -temperature calibrations between deep-sea scleractinian
 687 corals and gorgonian corals (Kimball et al., 2016). Specifically, gorgonian
 688 corals calcify from a DIC pool with higher CO_3^{2-} and moderately elevated
 689 pH than abiogenic experiments which may impact the skeletal $\Delta 47$ value
 690 (Saenger et al., 2017). The use of this technique to accurately and precisely
 691 reconstruct past seawater temperature might be therefore dependent on de-
 692 termining calcifying fluid pH in each calcifier. The calcifying fluid pH can be
 693 back tracked from $\delta^{11}B$ measurements of the skeleton but this measurement

694 would introduce similar uncertainties as determining the equilibrium value
695 for $\delta^{13}C_{coral}$.

696 5.2. Elemental composition

697 Finally, Mg/Ca ratios in coral calcitic skeleton may reflect ambient sea-
698 water temperatures. In high-Mg calcite, the substitution of Mg for Ca into
699 the $CaCO_3$ lattice is an endothermic reaction: thus, the ratio of Mg/Ca in
700 the calcite skeletons of marine organisms varies with seawater temperature
701 (Lea et al., 1999). In gorgonian corals, sclerite Mg/Ca ratios are gener-
702 ally higher in warmer-water shallower specimens than colder-water deeper
703 specimens, although this relationship may vary among species (Weinbauer
704 and Vellmirov, 1995; Maté et al., 1986; Velimirov and Böhm, 1976). Within
705 a single shallow-water gorgonian, temperature effects Mg/Ca values with
706 a sensitivity of 0.47 mmol/mol per $^{\circ}C$ (Bond et al., 2005), although the
707 temperature effect on Mg/Ca values may be non-linear (Weinbauer and
708 Vellmirov, 1995; Matsumoto, 2007). For example, the relationship depends
709 on the ambient temperature in deep-water corals: $T(^{\circ}C) = 0.048Mg/Ca +$
710 0.50 (mmol/mol) within a range of 3-6 $^{\circ}C$ while $T(^{\circ}C) = 0.19Mg/Ca - 12.31$
711 within a range of 5-10 $^{\circ}C$ (Sherwood et al., 2005c; Thresher et al., 2010).
712 In addition, reproducibility of Mg/Ca profiles within a single colony is low,
713 indicating influence of variables in addition to temperature driving skeleton
714 Mg/Ca values. These variables may include disparate radial growth results
715 limiting accuracy of assigned chronologies, instrumental uncertainty, vari-
716 able vital effects related to growth rates, incorporation of organic material,
717 and seasonality of the proxy (Sherwood et al., 2005c; Sinclair et al., 2011;
718 Aranha et al., 2014; Vielzeuf et al., 2013). As a result, these studies suggest
719 that Mg/Ca-temperature proxy is sensitive to temperature changes occur-
720 ring on the timescales of five years and longer (Sinclair, 2005; Flöter et al.,
721 2019).

722 Environmental effects on gorgonian Sr/Ca values vary. In shallow-water
723 taxa, the Sr/Ca composition of the calcite sclerites varied in colonies across
724 depths in water with consistent Sr/Ca ratios and did not correlate with tem-
725 perature (Weinbauer and Vellmirov, 1995; Bond et al., 2005). This suggests
726 a potential growth effect on Sr incorporation into the skeleton (Weinbauer
727 and Vellmirov, 1995). In deep-sea *Primnoa resedaeformis*, Sr/Ca values
728 broadly correlate to temperature, which could either reflect either a direct
729 temperature influence or an indirect relationship between Sr content and
730 growth rates or seawater content (Heikoop et al., 2002). In deep-sea bam-
731 boo corals, Sr/Ca values tracked seawater Sr/Ca ratios (Figure 6), with some
732 small unexplained intrinsic variability that did not vary with growth rates,

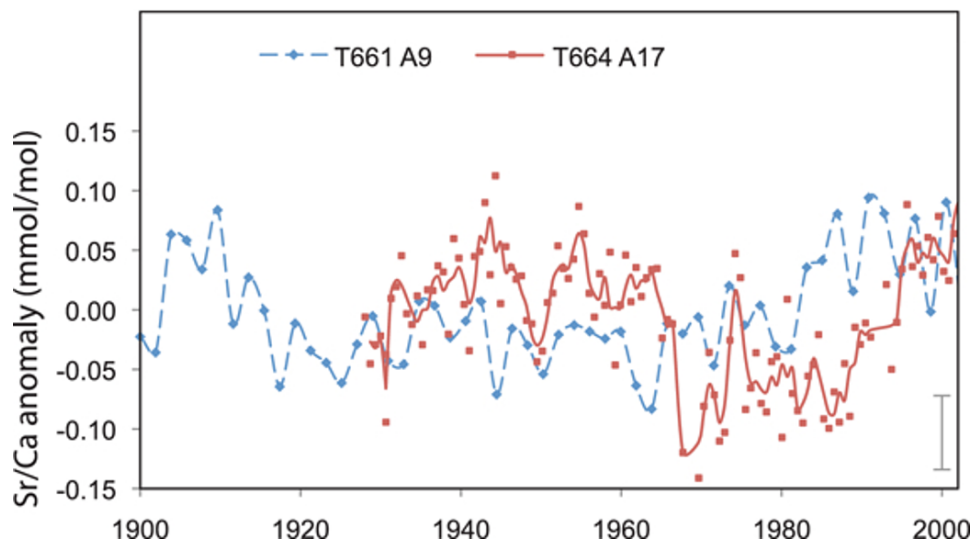


Figure 6: Sr/Ca ratios measured across the calcitic nodes in two bamboo coral recording ambient seawater Sr/Ca content. Figure from Hill et al. (2012).

733 temperature, or on annual timescales (Hill et al., 2012; Sinclair et al., 2011;
 734 Thresher, 2009; Thresher et al., 2009, 2010). In summary, Sr/Ca may vary
 735 intrinsically in all gorgonian corals but may also be influenced by growth
 736 rates in faster growing shallow-water taxa (Weinbauer and Vellmirov, 1995)
 737 and the seawater Sr/Ca content in slower growing deep-water taxa (Wein-
 738 bauer and Vellmirov, 1995; Hill et al., 2012).

739 In deep-sea bamboo corals, generally reproducible replicate time series of
 740 Ba/Ca within a single specimen supports an environmental driver of Ba/Ca
 741 values (Serrato Marks et al., 2017; Thresher et al., 2016; Sinclair et al., 2011;
 742 Strzepek et al., 2014). Furthermore, the Ba-isotopic composition of the
 743 corals may record ambient seawater Ba-isotope chemistry (Geyman et al.,
 744 2019). The environmental driver is likely ambient seawater Ba incorporated
 745 into coral skeleton via cationic substitution because the slope relating
 746 skeletal to seawater Ba/Ca values is similar between bamboo corals from dif-
 747 ferent locations (LaVigne et al., 2011; Thresher et al., 2016). Although the
 748 timescales of the intracolony reproducibility varies among colonies (indicat-
 749 ing some intrinsic variability), filtering time series Ba/Ca data and averaging
 750 multiple transects can extract the environmental-derived Ba contributions
 751 to improve the quality of seawater Ba/Ca reconstructions (Serrato Marks
 752 et al., 2017; Sinclair et al., 2011).

753 **6. Reconstructions of surface processes from the organic skeleton**

754 *6.1. Stable isotopic composition*

755 The stable isotopic composition of a proteinaceous coral's polyp and
756 skeletal tissues are determined by the food to the corals and the coral's
757 biochemical pathways that synthesize new tissue biomass from that food
758 (Heikoop et al., 2002; Sherwood et al., 2005a; McMahan et al., 2018). Con-
759 sequently, the carbon and nitrogen stable isotopic composition of the coral
760 skeleton yields information about source nutrients and a coral's biological
761 processes. However, extracting information from the coral stable isotopic
762 composition is complicated because unique biochemical pathways charac-
763 terize the formation of the two types of coral tissue resulting in skeleton
764 with higher $\delta^{13}\text{C}$ values and lower $\delta^{15}\text{N}$ values than polyp tissue (Sherwood
765 et al., 2005a; McMahan et al., 2018). The systematic offsets between the
766 tissues means that the corals' biological processes are modifying the sta-
767 ble isotopic information from the food recorded in the corals polyps and/or
768 skeleton.

769 The offset in stable isotopic composition may reflect differences in either
770 the amino acid composition or the isotopic composition of individual amino
771 acids, as the isotopic composition of amino acids varies (McClelland and
772 Montoya, 2002; Keil and Fogel, 2001). For carbon, the amino acids separate
773 into two groups: essential amino acids that the corals obtain from their food
774 and non-essential amino acids that the corals can synthesize themselves. The
775 essential amino acids have unique $\delta^{13}\text{C}$ values because primary producers
776 have a wide diversity in metabolic pathways of essential amino acid synthesis
777 (Hayes, 2001; Scott et al., 2006; Larsen et al., 2009, 2013). The $\delta^{13}\text{C}$ values
778 of these essential amino acids (threonine (Thr), leucine (Leu), isoleucine
779 (Ile), valine (Val), and phenylalanine (Phe)) are unmodified during trophic
780 transfer and the original isotopic composition of the amino acid is preserved
781 in the corals (Schiff et al., 2014; McMahan et al., 2016). In contrast, the
782 $\delta^{13}\text{C}$ values of the non-essential amino acids (glutamic acid (Glu), aspartic
783 acid (Asp), alanine (Ala), proline (Pro), glycine (Gly), and serine (Ser)) are
784 not reflective of the source carbon in the coral's food and instead can reflect
785 biological fractionation occurring within the coral. The minimal offset in the
786 $\delta^{13}\text{C}$ values of both the essential and non-essential amino acids between the
787 coral polyp and skeleton in gorgonian corals indicates minimal differences
788 in pathways characterizing the movement of these elements from the food
789 to the coral polyp and skeleton material (McMahan et al., 2018). Instead,
790 the amount of amino acids varies between the coral materials: polyp tissue
791 has higher concentrations of essential amino acids and lower concentrations

792 of non-essential amino acids than than the skeleton (Sherwood et al., 2006).
793 Therefore, the offset in the carbon isotopic composition of the coral materials
794 reflect differences in the abundance of the amino acids and not the isotopic
795 composition of the amino acids.

796 For nitrogen, the amino acids are generally divided into two groups:
797 those that enrich with trophic transfer (Ala, Asp, Glu, Ile, Leu, Pro, Val) and
798 those that do not enrich with trophic transfer, i.e., the source amino acids
799 (Gly, Lys, Phe, Ser, Tyr) (Chikaraishi et al., 2014; Popp et al., 2007). There is
800 a third grouping of amino acids containing Thr, which is metabolically active
801 and does not fit into either either of the two main categories (McMahon
802 et al., 2018). In *P. resedaeformis*, the total of 13 amino acids (Asp, Thr,
803 Ser, Glu, Gly, Ala, Val, Met, Ile, Leu, Tyr, Phe, and Arg) account for 78%
804 and 87% of the mass of the tissue and gorgonin, respectively (Sherwood et
805 al., 2006). Higher concentrations of the $\delta^{15}\text{N}$ enriched trophic amino acids
806 characterize the tissue of a Primnoid coral which could start to explain the
807 $\delta^{15}\text{N}$ offset. However, the $\delta^{15}\text{N}$ values of trophic amino acids in tissue are
808 consistently enriched by 3-4 ‰ than in the skeleton ((McMahon et al., 2018).
809 Therefore, both the amino acid concentrations and isotopic composition of
810 the trophic amino acids cause the $\delta^{15}\text{N}$ offset between the tissue and the
811 skeleton.

812 In zooxanthellate proteinaceous corals, carbon supplied by the symbiotic
813 algae influences the $\delta^{13}\text{C}$ values of the coral material. The symbiotic algae
814 in the zooxanthellate corals derive carbon from ambient dissolved HCO_3^-
815 ($\delta^{13}\text{C}$ of approximately 0.8 ‰) as a base for photosynthesis. The result-
816 ing $\delta^{13}\text{C}$ values in zooxanthellate coral polyp tissue is higher than that of
817 nearby azooxanthellate corals, although the $\delta^{13}\text{C}$ offset varies among coral
818 taxa (Cocito et al., 2013; Baker et al., 2015). Similarly, nitrogen is also
819 processed differently in zooxanthellate gorgonians: nitrogen generated as
820 metabolic waste products from the coral are re-absorbed by the symbiotic
821 algae rather than excreted into the seawater, as in heterotrophic organisms.
822 This resorption of enriched nitrogen increases the $\delta^{15}\text{N}$ composition of the
823 polyp tissue (Cocito et al., 2013). As a result, symbiotic algae impact the
824 isotopic composition by increasing both the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of
825 zooxanthellate corals.

826 Combined with the biological processes, the food source to the coral de-
827 termines its isotopic composition. The diversity in food sources to shallow-
828 water and mesopelagic proteinaceous corals complicates interpretation of iso-
829 topic measurements of their skeletons (Williams and Grottoli, 2010b; Coma
830 et al., 1994; Ribes et al., 1998; Chang-Feng and Ming-Chao, 1993), although
831 in some cases dramatic shifts in nutrient sources are evident in the coral

832 isotopic composition (Ward-Paige et al., 2005). Since deep-water corals feed
833 primarily on the surface-derived POM (Griffin and Druffel, 1989; Sherwood
834 et al., 2005b; Roark et al., 2006), changes in the POM dynamics - either the
835 source of the POM to the corals or the isotopic composition of the POM -
836 is captured in the coral skeleton. Below we discuss the environmental re-
837 constructions extracted from the coral proteinaceous skeleton when stable
838 isotopes are measured over the lifespan of a coral colony.

839 The $\delta^{13}\text{C}$ composition of the POM to deep-water corals is driven by
840 1) the baseline carbon-source signatures of the dissolved inorganic carbon
841 (DIC), 2) that is imprinted upon by fractionation during incorporation into
842 organic matter, and 3) subsequent enrichment due to trophic transfer. The
843 resulting $\delta^{13}\text{C}$ values of proteinaceous corals range from -20 to -15 ‰ (Sher-
844 wood et al., 2005a; Williams et al., 2006). While changes in any of the steps
845 in carbon processing from the baseline DIC to incorporation into the coral
846 will change the $\delta^{13}\text{C}$ composition, time series records of coral $\delta^{13}\text{C}$ largely
847 track anthropogenic changes in the baseline carbon-source signature of the
848 DIC (Baker et al., 2010b; Williams et al., 2007a,b). These anthropogenic
849 changes manifest as the ^{13}C -Suess effect, the gradual depletion of $\delta^{13}\text{C}$ val-
850 ues of atmospheric carbon over the past several decades resulting from the
851 burning of ^{13}C -light fossil fuels (Keeling, 1979). This isotopically-depleted
852 carbon has entered the marine carbon cycle, depleting $\delta^{13}\text{C}_{DIC}$ values and
853 thus also $\delta^{13}\text{C}_{POM}$ values and $\delta^{13}\text{C}_{coral}$ (Quay et al., 2003; Bentaleb and
854 Fontugne, 1996; Williams et al., 2007a,b; Sherwood et al., 2005a; Baker
855 et al., 2010b).

856 In some cases, proteinaceous corals document ^{13}C values that decline
857 at a faster rate than the ^{13}C -Suess effect, or do not document the ^{13}C -
858 Suess effect at all. These corals are thought to be capturing changes in
859 primary productivity, changes in terrestrial contribution to the baseline DIC,
860 or a shift in food source (Druffel et al., 1995; Williams et al., 2007b; Ward-
861 Paige et al., 2005). For example, skeletal $\delta^{13}\text{C}$ records in shallow-water
862 zooxanthellate gorgonians decrease with a shift to heterotrophic feeding with
863 increased terrestrial dissolved organic matter (Ward-Paige et al., 2005).

864 Measuring the ^{13}C composition of the essential amino acids in the coral
865 skeleton yields additional information to aid in the interpretation of changes
866 in bulk skeletal ^{13}C values. Similarities in the $\delta^{13}\text{C}$ of the essential amino
867 acids with bulk $\delta^{13}\text{C}$ values inform if changes in the bulk $\delta^{13}\text{C}$ values reflect
868 processes occurring prior to carbon incorporation into the coral (Schiff et al.,
869 2014). Since the $\delta^{13}\text{C}$ values of these essential amino acids (EAA) is unique
870 to the primary producer that fixes the carbon at the base of the food chain,
871 the coral $\delta^{13}\text{C}_{EAA}$ reflects the dominant primary producers. In long-lived

872 proteinaceous corals, shifts in $\delta^{13}\text{C}_{EAA}$ through the past 1000 years reflect
873 changes in the plankton community regimes in the North Pacific Ocean
874 that corresponded in timing with regional climate regimes (McMahon et al.,
875 2015). The most recent regime spanning less than the past 200 years was a
876 cyanobacterial community, characterized by strongly enhanced N_2 fixation
877 (McMahon et al., 2015). This approach in other proteinaceous corals may
878 yield information about environmental reconstructions, in addition to the
879 $\delta^{13}\text{C}$ -Suess effect.

880 Time series $\delta^{15}\text{N}$ measurements from the skeleton of proteinaceous corals
881 reconstructs changes in marine nitrogen biogeochemistry. The primary
882 drivers of these changes are 1) the baseline nitrogen-source signatures of the
883 bioavailable nitrogen to the primary producers, typically nitrate, 2) that is
884 imprinted upon by fractionation during incorporation into organic matter
885 that feeds the coral, and 3) subsequent enrichment due to trophic transfer.
886 The different sources of bioavailable nitrogen and subsequent processing
887 of that nitrogen all impacts a unique $\delta^{15}\text{N}$ signature (e.g., (Owens, 1988;
888 Montoya, 2008)) on the food that is available to corals, and thus the $\delta^{15}\text{N}$
889 composition of the skeleton.

890 The main sources of nitrogen to the ocean that determines the baseline
891 nitrogen-source signatures are biological nitrogen fixation (Capone et al.,
892 1997; Mahaffey et al., 2003), atmospheric deposition (Duce et al., 2008; Fo-
893 gel and Paerl, 1993), and terrestrially-derived nitrogen supplied via riverine
894 inputs (Walsh, 1991). Additional processes can also provide nitrogen: up-
895 welling and vertical mixing of nitrate-rich seawater (Williams et al., 2000;
896 Williams and Follows, 1998) and diffusion across the thermocline (Lewis
897 et al., 1986; Planas et al., 1999). In nitrate-limited surface waters in which
898 all of the biologically available nitrogen is consumed by phytoplankton dur-
899 ing primary production, the isotopic composition of generated POM reflects
900 that of the source of nitrogen to phytoplankton (i.e. $\delta^{15}\text{N}$ of the substrate
901 nitrogen). In contrast, in surface water where the biologically available ni-
902 trogen is not fully consumed, the $\delta^{15}\text{N}$ composition of the POM depends on
903 the degree of nitrogen consumption (Altabet and Francois, 1994; Wu et al.,
904 1997; Thibodeau et al., 2017). These fluctuations in $\delta^{15}\text{N}_{\text{NO}_3^-}$ are incorpo-
905 rated into the resulting POM (Wu et al., 1997). Thus, the $\delta^{15}\text{N}$ composition
906 of the food to the corals captures the $\delta^{15}\text{N}$ signature of the source nitrogen
907 to the region and/or nitrate utilization, depending on the regional nutrient
908 biogeochemistry.

909 The $\delta^{15}\text{N}$ composition of the POM produced during primary production
910 is altered during subsequent incorporation into the larger marine food web.
911 Isotopic enrichment during incorporation of the nitrogen into consumers

912 yields higher $\delta^{15}\text{N}$ values than the food because the ^{14}N -abundant nitrogen
913 is more readily excreted than the heavier isotope, leaving the remaining
914 organism with enriched $\delta^{15}\text{N}$ values. This is also true for the proteinaceous
915 corals, which are enriched in $\delta^{15}\text{N}$ relative to their food (e.g., (Sherwood
916 et al., 2008)). As a result of this trophic enrichment, bulk $\delta^{15}\text{N}$ values in
917 coral skeletons could also trace changes in the length of the food chain in the
918 organisms that contribute materials to the POM feeding the corals (Heikoop
919 et al., 2002).

920 Time series measurements of nitrogen isotopic composition of the pro-
921 teinaceous coral skeleton thus reflects potentially complex changes in the
922 environment and ecological structure of the ocean. To date, bulk $\delta^{15}\text{N}$
923 records document increases in terrestrial effluent to coastal and deep sea
924 regions (Baker et al., 2010b; Risk et al., 2009a,b; Sherwood et al., 2010;
925 Ward-Paige et al., 2005; Williams et al., 2007b), increasing in agricultural
926 fertilizer to coastal oceans (Baker et al., 2010b), and degree of variability in
927 oceanic conditions (Williams and Grottoli, 2010a; Sherwood and Edinger,
928 2009). However, these changes may occur simultaneously and perhaps offset
929 each other. This limits our interpretation of the nitrogen isotopic records
930 from these corals.

931 Refining interpretation of the bulk nitrogen isotopic composition is ac-
932 cessible by measuring the $\delta^{15}\text{N}$ values of individual amino acids: the $\delta^{15}\text{N}$
933 value of the source amino acids in the corals reflects the $\delta^{15}\text{N}$ composition
934 of the biologically available nitrogen while the trophic amino acids track the
935 number of trophic transfers in the marine food web (Sherwood et al., 2011;
936 Williams et al., 2017b). By using this approach, several studies have demon-
937 strated significant shifts in source nitrate to a region with no corresponding
938 changes in microbial resynthesis and alteration or change in relative trophic
939 position of the corals (Figure 7) (Sherwood et al., 2011, 2013; Prouty et al.,
940 2014; Williams et al., 2017b). Therefore, similar to carbon, isotopic mea-
941 surements of the individual amino acids benefits interpretation of the bulk
942 stable isotopic composition of the skeleton.

943 *6.2. Elemental composition*

944 In the black coral skeleton, reproducible replicate analyses of trace ele-
945 ment concentrations suggest a coherent incorporation of individual elements,
946 pointing toward an environmental driver of skeletal trace element concen-
947 trations (Williams and Grottoli, 2011). For example, skeletal rhenium and
948 iodine concentrations vary with environmental concentrations linked with
949 continental material flux to the oceans (Prouty et al., 2014, 2018). The

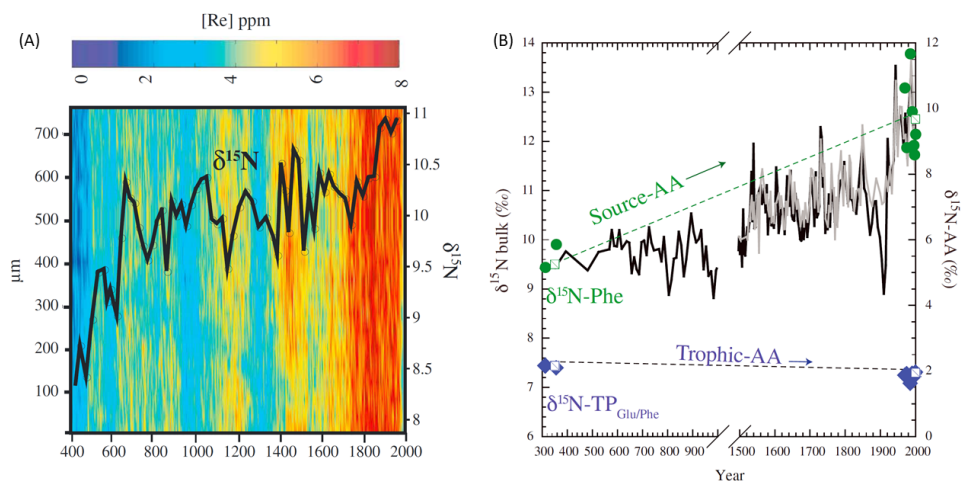


Figure 7: (A) Map of rhenium concentrations in a black coral plotted with bulk $\delta^{15}\text{N}$ values through time and (B) change in bulk $\delta^{15}\text{N}$ values along two transects in a black coral along with compound specific $\delta^{15}\text{N}$ measurements of source and trophic amino acids, showing that changes in source nitrogen values (and not trophic status) drive the enrichment in bulk values through time. Figure from Prouty et al. (2014).

950 source of the iodine to the coral skeleton is likely iodine bound to the or-
 951 ganic particles that the coral feeds on (Prouty et al., 2018). An environ-
 952 mental driver of iodine in black corals is further supported by co-elevation
 953 of the isotopic composition of the iodine ($^{129}\text{I}/^{127}\text{I}$ ratios) in the black corals
 954 during periods of nuclear bomb-testing: this is consistent with the ^{129}I ra-
 955 tio in the corals documenting seawater ^{129}I variability (Prouty et al., 2014).
 956 These results suggest that trace element concentrations, particularly iodine,
 957 in black corals yield useful environmental information.

958 Concentrations of trace elements vary between taxa of proteinaceous
 959 corals: chromium, nickel, and selenium are elevated and lead is lower in
 960 black corals than gorgonians (Raimundo et al., 2013; Williams and Grottoli,
 961 2011). These differences could reflect biological processes of elemental in-
 962 corporation into the skeleton between the different taxa, or, perhaps more
 963 likely, differences in ambient environmental concentrations, since gorgonians
 964 bioaccumulate heavy metals when exposed to heavy metal contaminated sea-
 965 water (Chan et al., 2012). Concentrations of manganese, zinc, and lead were
 966 comparable in the skeletons of deep-sea gorgonians from disparate locations,
 967 while cadmium was lower in colonies from the western tropical Pacific re-
 968 lative to the Atlantic Ocean (Williams and Grottoli, 2011; Raimundo et al.,
 969 2013). The elevated cadmium measurements in the Atlantic gorgonians

970 from the Azores is consistent concentrations in recent sediments from the
971 Azores-Iceland Ridge, and could reflect increased concentrations reflecting
972 hydrothermal activity (Grousset and Donard, 1984). In addition, the Pacific
973 corals were from the mesophotic zone, which typically is lower in cadmium
974 than deeper waters (Bruland, 1983). However, despite potential explanations
975 for bulk differences in trace elements among gorgonian colonies that
976 potentially reflects environmental concentrations, trace element concentrations
977 within a single colony gorgonian were not reproducible in replicate
978 analyses through the lifespan of that gorgonian (Williams and Grottoli,
979 2011). This points toward limitations in using elemental composition of
980 gorgonian corals as archives of environmental changes into the past.

981 *6.3. Radiometric isotopic composition*

982 Radiometric measurements of proteinaceous corals largely provide a
983 means to develop growth chronologies for the coral skeletons. The excep-
984 tion to this is radiocarbon measurements which can also yield information
985 about the global carbon cycle. Similar to stable isotopes, the ^{14}C con-
986 centration in the skeleton of deep-water proteinaceous corals reflect that
987 of the coral's food, primarily the POM that is rapidly exported from sur-
988 face waters (Roark et al., 2009; Sherwood et al., 2005b; Griffin and Druffel,
989 1989). In long-lived specimens pre-dating anthropogenic alternations of the
990 global ^{14}C cycle (i.e., the ^{14}C -Suess effect and bomb-carbon, see below), the
991 amount of ^{14}C measured reflects the relative contribution of older, lower ^{14}C
992 and younger, higher ^{14}C seawater to a region. This approach reconstructed
993 the relative influence of the East Australian Current to the South Tasman
994 through the past 4500 years (Komugabe-Dixson et al., 2016).

995 **7. Conclusions**

996 Using geochemical tools, we can extract substantial environmental in-
997 formation from the skeletons of the proteinaceous corals. Yet, there are
998 challenges in doing so. The calcitic skeleton in most gorgonians corals is
999 difficult to physically isolate because it is tightly coupled with the organic
1000 skeleton (Figure 3). In the bamboo corals with calcite disks, variable growth
1001 rates across the radius lowers the resolution of the resulting time series data
1002 (Sinclair et al., 2011). However in the bamboo corals, trace elemental con-
1003 centrations of the calcite skeletons may track ambient seawater temperature
1004 in deeper settings with stable ocean temperatures. When reconstructing
1005 past temperature is of interest, there are several potential methods to re-
1006 trieve ambient temperature from the skeletons; however, the precision of

1007 the temperature reconstructions are compromised by vital effects or limita-
1008 tions on estimating biological parameters to reduce uncertainty. Efforts to
1009 improve our understanding of the coral biology, particularly the calcifying
1010 fluid pH and growth rates may improve temperature estimates. Alterna-
1011 tively, application of newer techniques developed in other marine carbonates
1012 may provide estimates for reconstructing past temperatures (Table 1). Al-
1013 though, initial studies of newer proxies such as Mg/Li are suggesting unique
1014 geochemistry in high-Mg calcite compared to aragonite (Chaabane et al.,
1015 2019; Vielzeuf et al., 2018; Stewart et al., 2020; Anagnostou et al., 2019).

1016 In the organic skeleton, the proteinaceous corals provide unparalleled
1017 records of high-resolution carbon and nitrogen dynamics, surpassing those
1018 available from nitrogen incorporated into carbonate skeleton of corals and
1019 bivalves. However, interpreting variability in carbon and nitrogen bulk iso-
1020 topes can be difficult because of the multiple factors that drive changes in
1021 the nutrient composition of the food to the corals. Measuring the isotopic
1022 composition of the individual amino acids provides substantially more in-
1023 sights into nutrient cycling but these measurements are time consuming and
1024 expensive. Furthermore, the period in which a coral’s food is assimilated
1025 into their skeleton is unknown as is mechanisms driving sub-annual banding.
1026 Efforts into understanding the processes by which the corals incorporate nu-
1027 trients into their skeleton, any resulting alteration of the chemistry of those
1028 nutrients, and the time frame for which this occurs would improve strategi-
1029 cally sampling and interpreting skeletal measurements.

1030 Despite the challenges, the extreme longevity in some of the proteina-
1031 ceous corals combined with their widespread distribution across the shallow
1032 to deep ocean means that they can provide critical data to identify mecha-
1033 nisms of natural and anthropogenic ocean variability. The largest challenges
1034 are conservation of the corals from large-scale fishing while at the same time
1035 providing means for deep-sea exploration to locate and selectively collect
1036 the invaluable environmental archives.

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Table 1: Example reconstructions of environmental variability derived from proxies archived in high resolution marine archives.

Archive	Material	Proxies	Reconstruction	References
Scleractinian corals	Inorganic	$\delta^{18}\text{O}$	temperature	(Carriquiry et al., 1988)
		$\delta^{18}\text{O}$	seawater $\delta^{18}\text{O}$ /salinity	(Wellington et al., 1996)
		$\delta^{13}\text{C}$	DIC/ $\delta^{13}\text{C}$ -Suess effect	(Swart et al., 2010)
		$\delta^{13}\text{C}$	terrestrial contributions	(Moyer and Grottoli, 2011)
		$\delta^{13}\text{C}$	photosynthesis/heterotrophy/respiration	(Grottoli, 2000; Allison and Finch, 2012)
		$\delta^{15}\text{N}$	seawater $\delta^{15}\text{N}$ /nutrient dynamics	(Murray et al., 2019)
		$\delta^{11}\text{B}$	seawater pH/calcifying fluid pH	(McCulloch et al., 2012; Anagnostou et al., 2012)
		^{14}C	reservoir age	(Yu et al., 2010; Hirabayashi et al., 2017)
		Nd isotopes	seawater Nd isotopic composition	(Copard et al., 2010; van de Flierdt et al., 2010)
		Sr/Ca	temperature	(Jimenez et al., 2018)
		Li/Mg	temperature	(Cuny-Guirriec et al., 2019; Montagna et al., 2014)
		growth rates	temperature	(Saenger et al., 2009)
		density/calcification	temperature	(Lough and Barnes, 1997)
Ba/Ca, Mn/Ca, Y/Ca	riverine flux	(Carriquiry and Horta-Puga, 2010; Moyer et al., 2012)		
Bivalves	Inorganic	$\delta^{18}\text{O}$	temperature / seawater $\delta^{18}\text{O}$	(Mette et al., 2016; Wanamaker et al., 2008b)
		$\delta^{15}\text{N}$	seawater $\delta^{15}\text{N}$	(Whitney et al., 2019)
		^{14}C	reservoir age	(Wanamaker et al., 2008a)
		growth rates	temperature	(Poitevin et al., 2019)
Sclerosponges	Inorganic	$\delta^{18}\text{O}$	temperature / seawater $\delta^{18}\text{O}$	(Rosenheim et al., 2009)
		$\delta^{13}\text{C}$	DIC/ $\delta^{13}\text{C}$ -Suess effect	(Böhm et al., 2002)
		Sr/Ca	temperature	(Rosenheim et al., 2004)
Crustose coralline algae	Inorganic	$\delta^{13}\text{C}$	DIC/ $\delta^{13}\text{C}$ -Suess effect	(Williams et al., 2011)
		$\delta^{13}\text{C}$	DIC/productivity	(Hou et al., 2018)
		$\delta^{11}\text{B}$	pH	(Anagnostou et al., 2019; Fietzke et al., 2015)
		Mg/Ca	temperature	(Williams et al., 2017a)
		Mg/Li	temperature	(Anagnostou et al., 2019)
		Ba/Ca	seawater Ba/Ca / glacial runoff	(Chan et al., 2011)
		Ba/Ca	seawater Ba/Ca / productivity	(Chan et al., 2017)
growth rates	temperature + light	(Halfar et al., 2011; Adey et al., 2013)		
Sediments	Combined	grey scale/laminar thickness	productivity / eolian flux	(Hughen et al., 1996; Thunell et al., 1993)
		varve thickness	terrestrial contributions	(Lückge et al., 2001)
	Inorganic	Cd/Ca	upwelling	(Reuer et al., 2003)
		$\delta^{18}\text{O}$	seawater temperature	(Lückge et al., 2001)
		^{14}C	radiocarbon calibration	(Hughen et al., 1998)
		taxa abundance	production	(Sancetta and Calvert, 1988; Romero et al., 2009)
		biogenic silica	sedimentation rate	(Fan et al., 2011)
		Ti/Al	fluvial discharge	(Lückge et al., 2001)
		K/Al	eolian input	(Lückge et al., 2001)
		Organic	alkenones	seawater temperature

Table 2: Reconstructions of environmental variability derived from proxies archived in proteinaceous corals

<u>Coral</u>	<u>Skeletal material</u>	<u>Proxy</u>	<u>Environmental variable</u>	<u>References</u>
Shallow water gorgonian corals	Inorganic	$\delta^{18}\text{O}$	temperature	(Chaabane et al., 2016)
	Organic	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ -Suess effect	(Baker et al., 2010b)
	Organic	$\delta^{15}\text{N}$	terrestrial (agricultural fertilizers)	(Baker et al., 2010b)
	Organic	$\delta^{15}\text{N}$	terrestrial (effluent)	(Baker et al., 2010a, 2013; Ward-Paige et al., 2005)
	Inorganic	Mg/Ca	temperature	(Chaabane et al., 2019; Maté et al., 1986; Bond et al., 2005)
Bamboo corals	Inorganic	$\delta^{18}\text{O}$	temperature	(Hill et al., 2011; Saenger and Erez, 2016)
	Inorganic	$\Delta 47$	temperature	(Kimball et al., 2016; Saenger et al., 2017)
	Inorganic	Mg/Ca	temperature	(Thresher et al., 2010; Flöter et al., 2019)
	Inorganic	Sr/Ca	Sr/Ca content	(Weinbauer and Vellmirov, 1995; Hill et al., 2012)
	Inorganic	Ba/Ca	Ba/Ca content	(LaVigne et al., 2011; Thresher et al., 2016; Flöter et al., 2019)
	Inorganic	Ba-isotopes	seawater Ba-isotopic composition	(Geyman et al., 2019)
Primonidae gorgonians	Organic	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ -Suess effect	(Williams et al., 2007a)
	Organic	$\delta^{15}\text{N}$ AA	ocean currents	(Sherwood et al., 2011)
	Organic	^{14}C	water mass	(Sherwood et al., 2008)
Antipatharians	Organic	$\delta^{13}\text{C}$	$\delta^{13}\text{C}$ -Suess effect	(Williams et al., 2007b)
	Organic	$\delta^{13}\text{C}$	primary productivity	(Williams et al., 2007b)
	Organic	$\delta^{15}\text{N}$	terrestrial (effluent)	(Williams et al., 2007b; Risk et al., 2009a,b)
	Organic	$\delta^{15}\text{N}$ AA	riverine nitrate flux	(Prouty et al., 2014)
	Organic	Re	terrestrial (agro-industrialization)	(Prouty et al., 2014)
	Organic	$^{129}\text{I}/^{127}\text{I}$	nuclear weapons testing	(Prouty et al., 2018)
Organic	^{14}C	water mass reservoir age	(Komugabe et al., 2014; Komugabe-Dixson et al., 2016)	
Zoantharians	Organic	$\delta^{13}\text{C}$ AA	planktonic community composition	(McMahon et al., 2015; Glynn et al., 2019)
	Organic	$\delta^{15}\text{N}$ AA	nitrogen fixation/supply	(Sherwood et al., 2013; Glynn et al., 2019)

AA = amino acid