

**Evidence for
benthic-pelagic food
web coupling and
carbon export**

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Evidence for benthic-pelagic food web coupling and carbon export from California margin bamboo coral archives

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Received: 20 January 2014 – Accepted: 23 January 2014 – Published: 13 February 2014

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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Abstract

Deep-sea bamboo corals (order Gorgonacea, family Isididae) are known to record changes in water mass chemistry over decades to centuries. These corals are composed of a two-part skeleton of calcite internodes segmented by gorgonin organic nodes. We examine the spatial variability of bamboo coral organic node $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ from thirteen bamboo coral specimens sampled along the California margin (37–32° N; 792 to 2136 m depth). Radiocarbon analyses of the organic nodes show the presence of the anthropogenic bomb spike, indicating the corals utilize a surface-derived food source (pre-bomb D^{14}C values of $\sim -100\%$, post-bomb values to 82%). Carbon and nitrogen isotope data from the organic nodes ($^{13}\text{C} = -15.9\%$ to -19.2% ; $^{15}\text{N} = 13.8\%$ to 19.4%) suggest selective feeding on surface-derived organic matter or zooplankton. A strong relationship between coral ^{15}N and habitat depth indicate a potential archive of changing carbon export, with decreased ^{15}N values reflecting reduced microbial degradation (increased carbon flux) at shallower depths. Using four multi-centennial length coral records, we interpret long-term ^{15}N stability in the California Current. Organic node ^{13}C values record differences in carbon isotope fractionation dictated by nearshore vs. offshore primary production. These findings imply strong coupling between primary production, pelagic food webs, and deep-sea benthic communities.

1 Introduction

Recent studies have shown that deep-sea corals (DSC) are an important archive of geochemical information for reconstructing past ocean circulation and environmental variability (e.g., Smith et al., 2000; Adkins et al., 2003; Thresher et al., 2004; Robinson et al., 2005; Sherwood et al., 2005, 2009a, b; Sherwood and Edinger, 2009). Bamboo corals (family Isididae) are gorgonian octocorals commonly found on exposed hard-grounds in areas such as the Gulf of Alaska (Roark et al., 2005), south/southeast of

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Tasmania (Thresher et al., 2004), New Zealand (Noe and Dullo, 2006), and the California margin (Hill et al., 2011, 2012; LaVigne et al., 2011). These corals derive their name from a skeletal structure of calcite internodes segmented by gorgonin organic nodes, forming a bamboo-like structure (Roark et al., 2005; Hill et al., 2011; Noe and Dullo, 2006). Bamboo corals live up to 400 yr (Thresher et al., 2004) and extend both their calcite skeleton and organic nodes in concentric rings, thereby producing temporally-linked organic and inorganic material for geochemical analyses that record annual to subannual environmental information.

Calcite internode geochemistries ($D^{14}C$, $\delta^{18}O$, $\delta^{13}C$) of bamboo corals indicate that the calcite skeleton is derived from dissolved inorganic carbon (DIC) in the surrounding intermediate waters (Roark et al., 2005; Hill et al., 2011). In contrast, radiocarbon ($D^{14}C$) analyses of several different types of DSC, including bamboo corals, demonstrate that the organic skeletal material reflects a surface derived signal (Roark et al., 2005; Griffin and Druffel, 1989; Sherwood et al., 2009; Sherwood and Edinger, 2009). DSC feed on sinking particulate organic matter (POM) or zooplankton (Griffin and Druffel, 1989; Sherwood et al., 2005, 2009). Thus, through proxy development and validation, bamboo corals may provide a unique opportunity to reconstruct past surface and deepwater processes from the same coral specimens.

This study examines $\delta^{13}C$, $\delta^{15}N$, and $D^{14}C$ variability in thirteen bamboo coral specimens sampled along the California margin from intermediate water depths (792–2136 m). In this region, the southward-flowing California Current dominates this system for most of the year while the weaker northward-flowing Davidson Current becomes more prevalent during the winter months (Chelton et al., 1982; Largier et al., 1993). Strong northerly winds along the western North America coast allow for coastal upwelling on the California margin generally commencing during March and continuing until winter (Huyer, 1983; Strub et al., 1987; Largier et al., 1993). Previous investigations of bamboo corals from this region indicate that their calcite geochemistry is a proxy for temperature ($\delta^{18}O$, $\delta^{13}C$) and refractory nutrient concentrations (Ba/Ca) of local intermediate waters, as well as an advected signal of productivity (Sr/Ca) from

the North Pacific Gyre (Hill et al., 2011, 2012; LaVigne et al., 2011). The goals of this study were to utilize organic node geochemistry to: (1) assess the use of the anthropogenic radiocarbon “bomb spike” as a potential chronological tool; (2) determine the primary food source of bamboo corals using isotopic tracers; and, (3) evaluate the utility of organic node geochemistry in recording surface water processes.

2 Materials and methods

2.1 Coral samples

Specimens of bamboo corals utilized in this study were collected as part of two expeditions on the MBARI vessel R/V *Western Flyer* utilizing the ROV *Tiburón* along the California margin, including six seamounts and Monterey Canyon in (2004 and 2007; Table 1; Fig. 1). These specimens were collected at depths ranging from 792–2136 m and at latitudes of 31.9–37.4° N (Fig. 1). Corals with no polyp material at the base of the skeleton, or complete absence of polyps were noted as “dead”; live corals were characterized by the presence of polyp material extending across the entire specimen. For live specimens, the polyp material was removed from the coral skeleton post-collection and the corals were archived dry, at UC Davis Bodega Marine Laboratory.

Organic nodes from the basal section (that nearest the attachment to substrate) of the coral were selected for subsequent analyses. Separation of the organic nodes from the calcite internodes was accomplished by cutting the calcite above and below the node with a diamond saw and subsequent immersion of the node in dilute HCl (0.6N HCl) to remove the remaining calcite interspersed throughout the node. Once the calcite was removed, the nodes were stored in deionized water prior to sub-sampling for isotopic analyses. Individual nodes were sampled at ~ 1 mm intervals using forceps and scalpel under a stereomicroscope. These samples were then dried overnight at 90 °C and stored in polyethylene vials at room temperature.

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2.2 Radiocarbon analyses

Ten coral specimens were sampled radially for radiocarbon analyses, at ~ 1 mm sample resolution. Radiocarbon analyses of the organic nodes were performed by the Center for Accelerator Mass Spectrometry (CAMS) at the Lawrence Livermore National Laboratory. Samples were converted to CO₂ and then reduced to graphite targets in the presence of iron catalyst. Results include a ¹⁴C-free background correction, and $\delta^{13}\text{C}$ normalization. Results are reported as conventional (uncorrected) radiocarbon age and per mil (‰) D¹⁴C as per international convention put forth in Stuiver and Polach (1977).

2.3 Isotopic analyses

Ten coral specimens were sampled for organic node stable isotopic composition. Corals were sampled along a radial cross-section at 1 mm resolution to a maximum distance of 20–35 mm for the larger corals. Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of the organic nodes were performed by the Stable Isotope Facility at the University of California, Davis. Organic node samples were combusted at 1020 °C and analyzed on a PDZ Europa ANCA-GSL elemental analyzer coupled to a PDZ Europa 20–20 isotope ratio mass spectrometer using helium as a carrier gas, with the resulting N₂ and CO₂ samples separated on a Carbosieve GC column prior to mass spectrometer analysis. Stable isotope values are reported in standard‰ notation, where the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ reference standards are Vienna-Pee Dee Belemnite or AIR respectively.

3 Results

3.1 Radiocarbon analyses

Organic nodes from the coral specimens investigated here exhibit pre-anthropogenic D¹⁴C values of $-101 \pm 15\text{‰}$ in the interior of the skeleton. Six of the coral specimens,

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primarily those that were collected alive, exhibit a range of positive and clearly post-bomb (post-1957) values near the outer edge of the skeleton (0–5 mm), with $D^{14}C$ ranging from +22 to +68‰ (Table 2; Fig. 2). We note that all of these corals occur within 250 km of the coastline, across a range of sampling depths (Table 1, Table 2).

5 Interior samples exhibit typical (pre-bomb) $D^{14}C$ values of -101 ± 15 ‰.

3.2 Isotopic analyses

$\delta^{13}C$ and $\delta^{15}N$ data are presented in Fig. 3. For specimens with more than 15 subsamples along a radial transect, we only present the first 15 mm in Fig. 3 to limit interpretation to recent skeletal precipitation. The total range of $\delta^{15}N$ values observed from these specimens was 13.8–19.4‰ ($1\sigma = \pm 1.81$ ‰). Variation within a single coral skeleton (intracolony) in $\delta^{15}N$ was 1–2‰. The total range in $\delta^{13}C$ composition was –15.9 to –19.2‰ ($1\sigma = \pm 0.70$ ‰). Maximum intracolony variation in $\delta^{13}C$ composition was 2‰.

4 Discussion

4.1 Radiocarbon analyses and calculation of extension rates

$D^{14}C$ data from all organic node samples from live-collected specimens exhibit a strong positive excursion near the outer 5 mm of the coral. Two of the dead specimens also exhibit this trend. The remaining bamboo corals collected dead exhibit relatively constant $D^{14}C$ values. The elevated $D^{14}C$ signal observed in six of the corals is consistent with increased ^{14}C in the atmosphere and surface waters due to atmospheric nuclear bomb testing during the 1950's and early 1960's (the "bomb spike") (Nydal and Lovseth, 1983; Broecker et al., 1985). Bomb radiocarbon has been previously observed in surface waters, surface water organisms, and other DSC investigations (Broecker et al., 1985; Ebert and Southon, 2003; Roark et al., 2005; Sherwood et al., 2009; Benavides and Druffel, 1986; Rosenheim and Swart, 2007; Moore et al., 1997). We interpret the

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presence of the anthropogenic bomb spike in these bamboo corals as indicative of a surface-water food source influencing the organic node geochemistry (Fig. 2).

The presence of “bomb radiocarbon” ($D^{14}C$ values of $\geq -85\text{‰}$ for surface waters in this region) (Ingram and Southon, 1996) can be utilized as a chronologic marker (Roark et al., 2005; Sherwood et al., 2009). We note that prior to the presence of bomb radiocarbon in our samples (Fig. 2) that radiocarbon values are mostly constant and imply little time since incorporation, or that values were changing at a rate to compensate ^{14}C -decay. These type of features are well known in the atmospheric record of ^{14}C : the so called radiocarbon plateaus (Stuiver and Brazunias, 1986; Reimer et al.). We infer that the nearly constant values that we observe are associated with the plateau and relative insensitivity of radiocarbon in surface waters between the mid to late 1600s and ~ 1950 AD (Stuiver, 1965; Stuiver and Quay, 1981; Reimer et al., 2013).

The timing of the surface ocean expression of the rise in bomb- ^{14}C allows for a consistent relative age dating among these corals, given that the onset of ^{14}C increase in Northern Hemisphere surface waters is dated to 1957 ± 2 yr (Manning et al., 1990; Kerr et al., 2005); we utilize this date for the onset of $D^{14}C$ increase in the corals. We further utilize a tiepoint to the $D^{14}C$ “peak” (maximum) age of 1980 as presented in Roark et al. (2005), as we expect this to be regionally coherent. These two tie points, plus the year of sampling, are utilized to calculate gorgonin $D^{14}C$ -based extension rates (Fig. 2; Table 3). The use of these tie-points assumes rapid transport of POM/zooplankton to the deep sea, thus no delay in the $D^{14}C$ signal reaching the DSC via the food web. This assumption is supported by regional studies of carbon export as discussed below. The calculated radial extension rates are within the previously published calcite extension rates for bamboo corals in this region (Hill et al., 2011). In this regard, the gorgonin extension rate from one coral (T664 A1) of $72 \mu\text{m yr}^{-1}$ can be directly compared to calcite extension rates estimated using $D^{14}C$ and growth bands for the same coral of $38\text{--}89 \mu\text{m yr}^{-1}$ (Table 3) (Hill et al., 2011). Calculated extension rates are assumed to reflect average rates for the lifetime of the coral; however, we acknowledge

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that the coral chronologies are the most robust between 1950–2000, near tie-points in the post-bomb era.

4.2 Isotope values

To estimate intercolony reproducibility we compare $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ records from two corals collected from the same location (both with D^{14}C chronological construction: T1104 A7, 870 m; T1104 A3, 917 m; Fig. 4). This comparison indicates intercolony $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ reproducibility of $< 0.5\text{‰}$, and $< 0.4\text{‰}$, respectively. A similar comparison of two corals (T1101 A12, T1101 A13) collected at 1012 m from Pioneer seamount indicates intercolony $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ reproducibility of 0.1–1.5‰ and 0.1–1.2‰, respectively (both typically $< 0.5\text{‰}$). These corals do not have D^{14}C -based chronologies so an assumption of equivalent growth rates is required and may introduce error. Similarly, Sherwood et al. (2009) found an intercolony reproducibility of $\delta^{15}\text{N}$ of $\sim 0.5\text{--}1.5\text{‰}$ in bamboo corals from Tasmanian seamounts.

During collection dives, corals were observed being preyed upon by sea stars. We suggest that the lack of a bomb carbon signal in the dead corals is likely due to the removal of the outer gorgonin material due to predation on living polyps by predators, or degradation following polyp predation or coral death. The exposure of the organic nodes could potentially lead to biologic consumption and/or chemical degradation from the surrounding water, removing the outer portion of the organic nodes that contain the anthropogenic bomb spike signal. Such removal of node material could also introduce hiatuses or cause additional diagenesis that would influence the isotopic record, as discussed below. Dead corals may also reflect growth from prior to 1957, so have no record of the atmospheric bomb spike. While previous research has shown little evidence of diagenesis or reworking of coral organic material (Sherwood et al., 2005), we observe that one specimen (T1102 A3) exhibits $\delta^{13}\text{C}$ values that indicate wide variability and offsets from the rest of the dataset (-18 to -20‰ ; Fig. 3). We hypothesize that this specimen may have a superimposed signature due to diagenesis or degrada-

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tion of the gorgonin. While $\delta^{15}\text{N}$ values do not appear significantly altered, this coral is removed from further discussion beyond Fig. 3.

4.2.1 $\delta^{15}\text{N}$ composition

Organic node $\delta^{15}\text{N}$ (13.9–20.2‰) shows significant enrichment when compared to surface particulate organic matter $\delta^{15}\text{N}$ (3–10‰), sinking fecal pellets (2–5‰) and zooplankton $\delta^{15}\text{N}$ (8–15‰) (Fig. 3) (Saino and Hattori, 1987; Rau et al., 2003; Ohman et al., 2012; El-Sabaawi et al., 2012; Altabet and Small, 1990; Walker and McCarthy, 2012). Along the California margin, denitrification contributes to the isotopic enrichment of NO_3^{2-} , resulting in organic matter $\delta^{15}\text{N}$ values of 8–10‰ (Altabet et al., 1999). Temporal variability in nitrogen isotopes from sediment trap samples record the upwelling of denitrified NO_3^{2-} from subthermocline waters and incorporation of this signal into phytoplankton (Altabet et al., 1999). We note that $\delta^{15}\text{N}$ composition of coral gorgonin is more enriched here than in previously documented investigations from elsewhere in the world (Heikoop et al., 2002; Sherwood et al., 2005, 2009). Such values are consistent with more positive baseline $\delta^{15}\text{N}$ values in phytoplankton due to denitrification, which is then transferred to successive trophic levels.

Field studies indicate that on average the enrichment of bulk $\delta^{15}\text{N}$ through trophic steps is $\sim 3.0\text{‰}$ per trophic level (Deniro and Epstein, 1981; Macko et al., 1982; Michener and Schell, 1994). Given their isotopic composition, $\sim 10\text{‰}$ enriched relative to POM and 5‰ enriched relative to zooplankton, these corals appear to feed on sinking zooplankton, marine snow, or deeper water zooplankton species (Fig. 3). Utilizing $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values recorded here together with previously published work (Drazen et al., 2008), we suggest that bamboo corals occupy a similar trophic level as other benthic macrofaunal predators and suspension feeders, such as caridean shrimp, deep sea fish (*macrourids*), polychaete worms (*Laetmonice* sp.) and anemones (*B. australis*) (Drazen et al., 2008). These findings are also consistent with trophic interpretations from previous DSC studies (Heikoop et al., 2002; Sherwood and Edinger, 2009; Sher-

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wood et al., 2005, 2009; Walker and McCarthy, 2012). Centennial length records of compound specific $\delta^{15}\text{N}$ composition also support a stable trophic position for bamboo corals over long timescales (Batista et al., 2014). Samples from coral polyp tissue ($n = 8$) exhibit a similar range of isotopic values ($\delta^{15}\text{N} = 6.1$ to 16.4 ‰, Hill et al., 2014).

5 We acknowledge the possibility that corals may feed on more degraded POM, which was found in previous gorgonin $\delta^{15}\text{N}$ studies (Sherwood et al., 2009), thus the radio-carbon tiepoints may require some “lag” from surface waters, which would lead to an underestimation of growth rates in Table 3.

10 We consider three factors that may influence coral gorgonin $\delta^{15}\text{N}$: water depth, distance from shore, and consumption of particles that carry a fractionated $\delta^{15}\text{N}$ signature associated with denitrification. In contrast to previous DSC investigations (Heikoop et al., 2002) on *Primnoa* species, we do not find a linear relationship between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values. Instead, $\delta^{15}\text{N}$ values cluster around two means: ~ 15 ‰ and ~ 18 ‰ (Fig. 3). These two “clusters” of data are determined by coral habitat depth; all corals exhibiting enriched $\delta^{15}\text{N}$ values (16.5 – 18.8 ‰) were found below 1954 m water depth (regression of depth: $\delta^{15}\text{N}$ yields R^2 of 0.77 , $n = 12$). A broad investigation of suspension and deposit feeders in the Southern Ocean documents a significant depth effect of $\delta^{15}\text{N}$, such that increased isotopic enrichment is observed with depth (Mintenbeck et al., 2007). This isotopic enrichment is interpreted to reflect the degree of microbial degradation of POM prior to consumption by suspension feeders (Mintenbeck et al., 2007); thus we interpret the depth-dependent patterns in $\delta^{15}\text{N}$ in much the same manner.

25 During time periods of increased productivity, particles have been shown to sink quickly to the deep ocean with less remineralization and decomposition, likely due to aggregation (Wong et al., 1999). Studies in the Southern California Bight indicate a very short time lag (days) between the onset of upwelling and an observable increase in POC export (Collins et al., 2011). Sinking rates of particles in the North Pacific have been observed from 175 to 300 m d^{-1} (Wong et al., 1999). At 1000 m water depth, POM fluxes at Station P (North Pacific Gyre) peak in the month of August ($\sim 15 \text{ mg m}^{-2} \text{ d}^{-1}$)

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but maintain fluxes $> 2 \text{ mg m}^{-2} \text{ d}^{-1}$ year round (Wong et al., 1999). Thus, corals in this study may be feeding on particles less than 1 week old during peak productivity periods.

A sediment trap in Monterey Bay (450 m water depth) documented seasonal peaks in mass particle flux, with highest flux in July and lowest in December. Synchronous with these trends in particle flux are variations in the $\delta^{15}\text{N}$ of sinking POM, with lower $\delta^{15}\text{N}$ values in summer (7‰) and enriched (higher) $\delta^{15}\text{N}$ values in winter (8.5‰) (Altabet et al., 1999). Thus, decreased isotopic enrichment is associated with peak flux periods, and is interpreted to reflect better preservation of the particle $\delta^{15}\text{N}$ (Altabet et al., 1999). In contrast, $\delta^{15}\text{N}$ enrichment in zooplankton has been linked to food chain elongation, and/or an increase in ^{15}N -rich denitrified waters from the equatorial Pacific (Rau et al., 2003; Ohman et al., 2012). Long-term investigations of zooplankton $\delta^{15}\text{N}$ in the California Current show an inverse linear relationship between $\delta^{15}\text{N}_{\text{zooplankton}}$ and average nitrate concentration, where increased NO_3^{2-} is linked to lower $\delta^{15}\text{N}$ (Ohman et al., 2012). These decadal scale zooplankton $\delta^{15}\text{N}$ records record long-term stability in these records, providing evidence for the similarity of trophic position and broad scale productivity through time.

We investigate latitude as a proxy for exposure to denitrified water masses, since corals in the southern part of our study area would experience more influence of Eastern Tropical North Pacific (ETNP) waters with significant denitrification (Altabet et al., 1999; Liu and Kaplan, 1989; Gruber and Sarmiento, 1997). While denitrification would not directly influence coral gorgonin $\delta^{15}\text{N}$, this process would fractionate the available nitrate pool that is utilized by the base of the food web. To avoid interpretation of overprinting of the $\delta^{15}\text{N}$ signal from microbial degradation of particles with depth, we utilize only corals from the shallower portions of our study (792–1285 m) for this analysis. We find that with the removal of deeper specimens ($> 1900 \text{ m}$), there is no significant relationship between coral gorgonin $\delta^{15}\text{N}$ and latitude (using the average of the outer 15 mm of gorgonin samples, regressed with latitude). While bamboo corals have the potential to record the denitrification history in this region, this signal appears over-

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printed by the microbial degradation of particles with depth. Coral gorgonin $\delta^{15}\text{N}$ does not show a significant relationship with distance from shore, although we do observe higher variability in $\delta^{15}\text{N}$ values in specimens that are > 200 km offshore.

Thus, we hypothesize that temporal changes in $\delta^{15}\text{N}$ of bamboo coral gorgonin primarily reflect surface productivity/carbon export, with increased $\delta^{15}\text{N}$ reflecting lower productivity. This relationship has been previously proposed in other DSC investigations of *Primnoa* and bamboo corals (Heikoop et al., 2002; Sherwood et al., 2009). Centennial-length records from T1104 A7 (870 m), T1104 A3 (917 m), T1101 A13 (1012 m) and T1100 A4 (1285 m) provide evidence for the long-term stability of the $\delta^{15}\text{N}$ of sinking particles in this region (Fig. 5). These records extend to a centennial-scale the previous interpretation of long-term stability in isotopic values, productivity, and trophic relationships in the California Current (Ohman et al., 2012).

4.2.2 $\delta^{13}\text{C}$ composition

The carbon isotopic composition of the bamboo coral gorgonin documented here is consistent with marine carbon sources such as those documented from copepod organic matter from the California Current ($\delta^{13}\text{C} = -15$ to -21 ‰) (Miller et al., 2008). We expect a biochemical fractionation (positive offset) from POM due to coral gorgonin being dominantly composed of amino acids, resulting in the loss of isotopically light material. Since the biochemically induced offset is likely constant, trends over space and time should reflect mechanistic processes in the overlying water column. We again consider the same factors when interpreting the $\delta^{13}\text{C}$ results as we did with $\delta^{15}\text{N}$: water depth, distance from shore, and latitude as potential controlling factors. We find no significant relationship between water depth or latitude and gorgonin $\delta^{13}\text{C}$. However, we do observe a relationship between distance from shore and $\delta^{13}\text{C}$ (Fig. 6), with declining $\delta^{13}\text{C}$ values occurring offshore. This relationship may be nonlinear, but this is difficult to determine with the current small sample size ($n = 12$; utilizing outer 15 mm of coral gorgonin). As previously noted, we also observe that anthropogenic “bomb”

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spike' ^{14}C is only observed in corals < 250 km from the shoreline, providing further evidence that particle geochemistry, and potentially source, differs between nearshore and offshore regimes.

The observation of an onshore/offshore difference in $\delta^{13}\text{C}$ composition has been previously noted on smaller spatial scales for both copepods (up to 70 km offshore) and a variety of other nekton and gelatinous zooplankton (up to 50 km offshore, Miller et al., 2008). A variety of mechanisms could contribute to these differences, including isotopic composition and concentration of CO_2 (draw-down of CO_2 during inshore blooms), species composition and associated differences in growth rates and fractionation, and differing inputs from benthic macrophytes to the food web (e.g., Miller et al., 2008; Burton and Koch, 1999; Michener and Schell, 1994; Pancost et al., 1997; Fry and Wainright, 1991; Rau et al., 1992). Taken together, this study and previously published literature indicate that POM, copepods, gelatinous zooplankton, nekton, and deep-sea gorgonins all document a decrease in $\delta^{13}\text{C}$ with distance offshore (Miller et al., 2008; Perry et al., 1999; Kline, 1999). This conclusion is also supported by investigations of migratory vs. non migratory pinnipeds which document an onshore/offshore $\delta^{13}\text{C}$ difference (Burton and Koch, 1999). The addition of bamboo coral $\delta^{13}\text{C}$ composition to this nearshore/offshore dataset provides strong evidence for benthic-pelagic coupling given the reproducibility of these $\delta^{13}\text{C}$ trends within both planktonic and benthic community members. We also note that the intercept of the regression line for $\delta^{13}\text{C}$ of copepods (-16.64%) is very similar to that of bamboo corals (Miller et al., 2008).

5 Conclusions

Here we investigate the D^{14}C , $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ composition of bamboo coral organic node material to understand controls on organic node geochemistry and refine proxies for paleoceanographic use. The presence of the anthropogenic bomb spike in bamboo coral organic node D^{14}C confirms that their food source is surface derived, and allows for development of gorgonin radial-extension rates based upon D^{14}C tiepoints.

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$\delta^{15}\text{N}$ composition provides evidence for a zooplankton-derived food source, with isotopic enrichment in deeper water due to increased particle reworking and fractionation. Centennial scale $\delta^{15}\text{N}$ records provide evidence for long-term $\delta^{15}\text{N}$ stability in the California Current. $\delta^{13}\text{C}$ of coral gorgonin provides strong evidence for benthic-pelagic coupling in food webs based upon a clear nearshore/offshore $\delta^{13}\text{C}$ gradient.

Acknowledgements. We thank the crew and scientific party of the R/V *Western Flyer* (Seamounts 2004 and 2007 expeditions) and D. Clague for support of this investigation. Seamount sampling and geochemical analyses were supported by NOAA West Coast Polar Regions Research Program (NA030AR4300104 to TMH and HJS) and NSF (OCE 0647872 to TMH). A portion of this work was performed under the auspices of the US Department of Energy by Lawrence Livermore National Laboratory (contract W-7405-Eng-48 and DE-AC52-07NA27344) including LLNL IGPP funding (HJS, TMH, and TPG). Additional support was provided by NA05OAR4310021 (TPG). We appreciate the technical support of the UC Davis Stable Isotope Facility and LLNL CAMS. This is a contribution of Bodega Marine Laboratory.

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Table 1. Coral samples utilized in this investigation. All corals were collected from seamounts on the California margin, with the exception of corals collected within the Monterey Canyon area.

Sample ID	Location	Depth (m)	Latitude	Longitude	Alive/Dead
T668 A13	Little Joe	2136	31.906	−120.046	Dead
T669 A1	San Marcos	2043	32.636	−121.482	Dead
T664 A2	San Juan	1954	33.149	−120.887	Live
T664 A1	San Juan	2055	33.151	−120.882	Dead
T670 A20	Rodriguez	1093	34.004	−121.116	Dead
T661 A9	Rodriguez	792	34.054	−121.084	Live
T1102 A3	Davidson	1647	36.742	−122.717	Live
T1104 A7	Monterey Canyon	870	36.744	−122.037	Live
T1104 A3	Monterey Canyon	917	36.744	−122.037	Dead
T1100 A4	Pioneer	1285	37.359	−123.394	Live
T1101 A13	Pioneer	1012	37.371	−123.409	Live
T1101 A12	Pioneer	1012	37.371	−123.409	Dead
T892 A8	Pioneer	1202	37.393	−123.428	Dead

Table 2. Radiocarbon analyses on organic nodes presented in Fig. 2.

ID	Distance from edge (mm)	D ¹⁴ C (‰)	±	Water depth (m)	Distance from shore (km)
T668 A13	0.7	-99	4.8	2055	237
	5	-92.9	4.7		
	10.2	-106.6	4.3		
T669 A1	0.7	-95.9	3.4	1954	237
	2.9	-101	3.5		
	4.8	-85.1	4		
	6.6	-93.1	3.4		
	22.8	-102.8	3.4		
T670 A20	2.7	-85.1	3.6	1012	82.09
	5.7	-86.7	3.2		
	8.7	-96.3	3.4		
	11.7	-81.3	3.4		
	14.7	-83.6	3.4		
	17.7	-83.1	3.4		
T892 A8	4.2	-107.5	4.9	1093	390
	7.2	-104.1	5.7		
	12.2	-106.4	4.5		
T1100 A4	0.7	64.5	3.8	1202	85
	1.7	56.1	3.9		
	2.7	-42.3	3.1		
	3.7	-84.7	4.1		
	4.7	-96.6	3.4		
T1101 A13	0.5	46	4.6	917	20
	1.5	63.4	4.3		
	2.5	66.9	3.7		
	3.5	67.7	6.4		
	4.5	27.8	4.9		
T1104 A3	1.5	22.2	4.2	870	20
	2.5	37.5	4.2		
	3.5	46.8	4.3		
T1104 A7	4.5	36.9	4.3	870	20
	0.5	26.9	4.7		
	1.5	67.4	4.3		
	2.5	56.1	4.4		
	3.5	58.7	4.4		
T664 A1	4.5	-72.8	3.8	2055	237
	2	81.3	4		
	3.4	-74.2	3.5		
	5.5	-100.5	3.4		
	5.8	-86.2	3.4		
T664 A2	8	-116.9	3.1	1954	237
	0.7	68.8	4.3		
	3.3	-80.8	4		
	5.5	-97.7	3.8		
	9.1	-96.3	3.6		

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Table 3. Calculated radial extension rates based upon D¹⁴C and correlation to bomb carbon.

Coral ID	Onset of D ¹⁴ C increase	extension rate μm yr ⁻¹	Peak of D ¹⁴ C	extension rate μm yr ⁻¹
	1957 mm from edge		1980 mm from edge	
T664 A1	3.4	72		
T664 A2	3.3	70		
T1100 A4	2.7	54	0.7	26
T1101 A13			3	111
T1104 A3			2.5	93
T1104 A7	4.5	90	1.5	56

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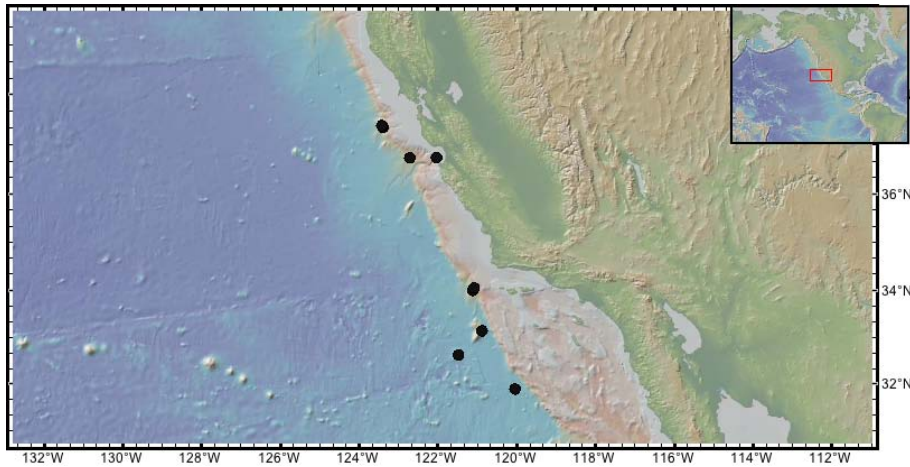


Fig. 1. Bathymetric map of study area with coral sampling locations noted. Map generated using GeoMappApp.

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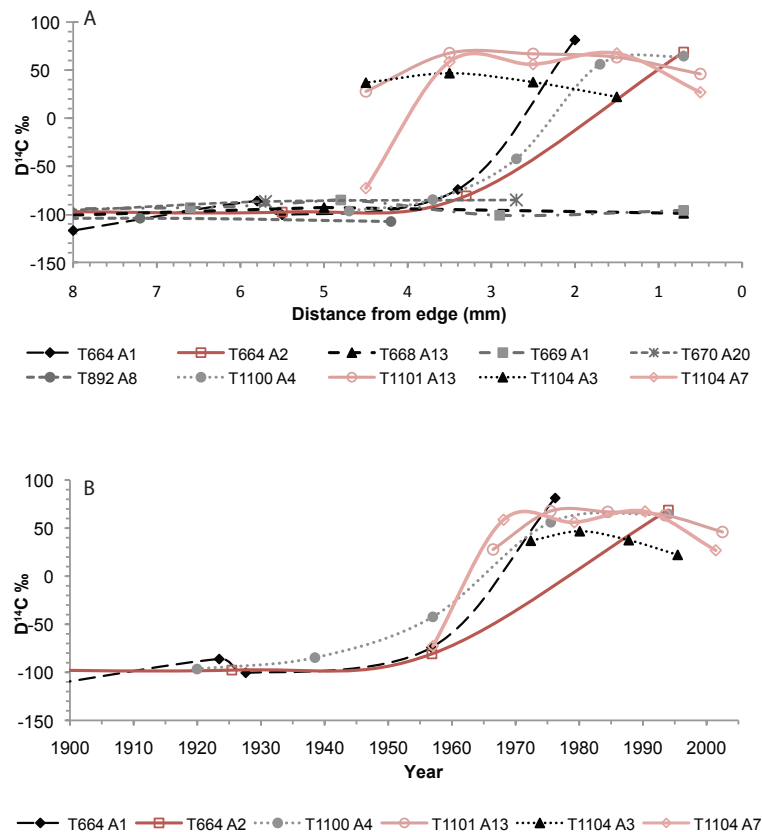


Fig. 2. (A) Radiocarbon analyses on live (red symbols) and dead (black or grey symbols) coral specimens, plotted as distance from edge. (B) Radiocarbon analyses on corals with the “bomb spike” apparent, plotted vs. age. Coral chronologies are based upon growth rates calculated in Table 3.

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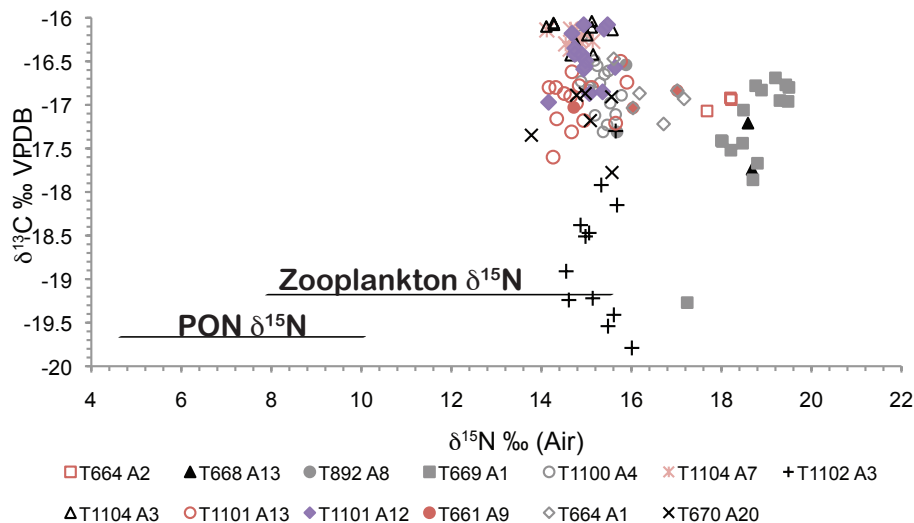


Fig. 3. Stable isotopic ($\delta^{15}\text{N}$, $\delta^{13}\text{C}$) composition for samples from thirteen coral specimens. Symbols follow the key, and are the same symbols used in Fig. 2 (live corals, red symbols; dead corals, black or grey symbols). Typical PON and zooplankton $\delta^{15}\text{N}$ ranges from the California Current are provided for comparison (see text for references).

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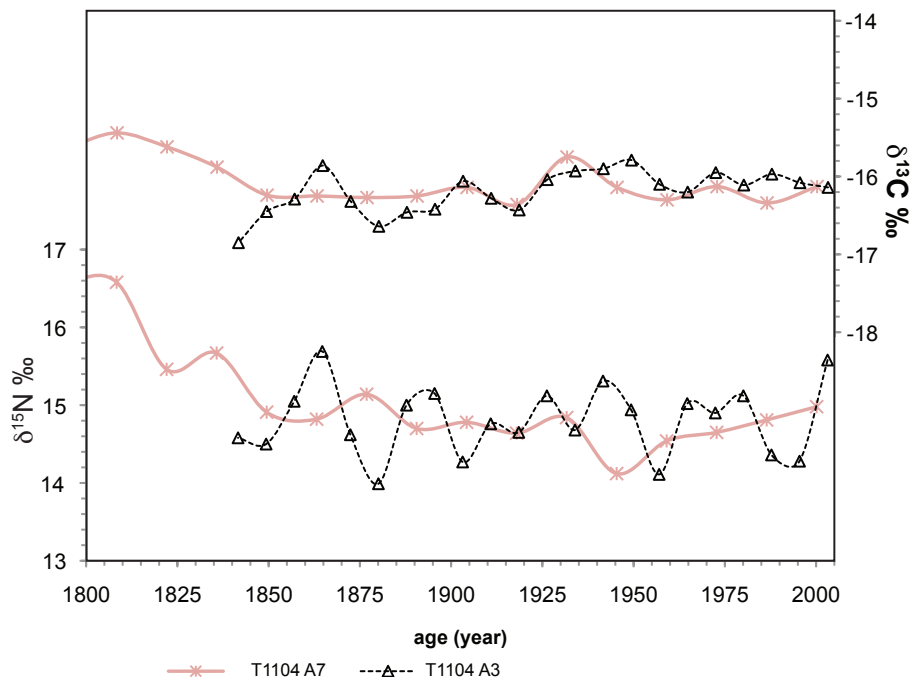


Fig. 4. Intercolony comparison: $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from two corals sampled from the same region (Monterey Canyon), and < 50 m apart in depth. Isotopic values plotted vs. age, based upon extension rates established for each coral in Table 3. These data establish point to point reproducibility typically < 0.5‰.

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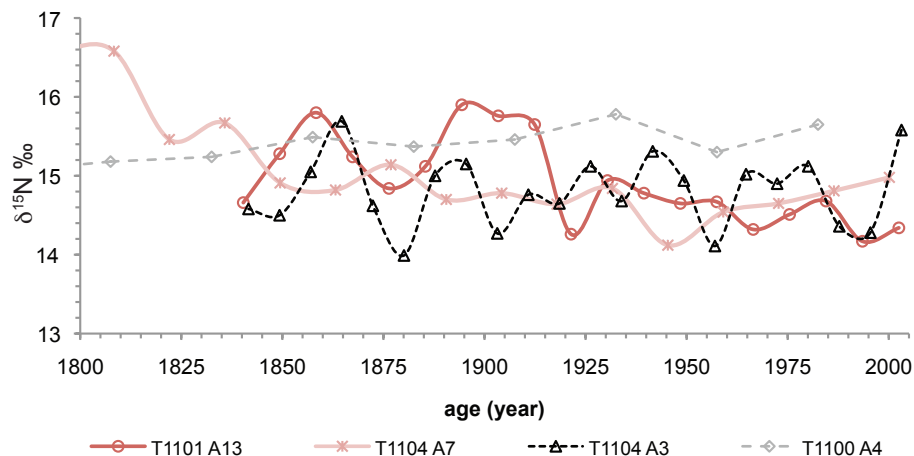


Fig. 5. Centennial-length $\delta^{15}\text{N}$ records from four corals: T1101 A13 (hollow circles, solid line), T1104 A7 (*), T1104 A3 (hollow triangles) and T1100 A4 (hollow circles, dashed line). Age models based upon calculated extension rates in Table 3, and assume a constant extension rate throughout the sampling of the coral. Records show overall stability in $\delta^{15}\text{N}$ over time.

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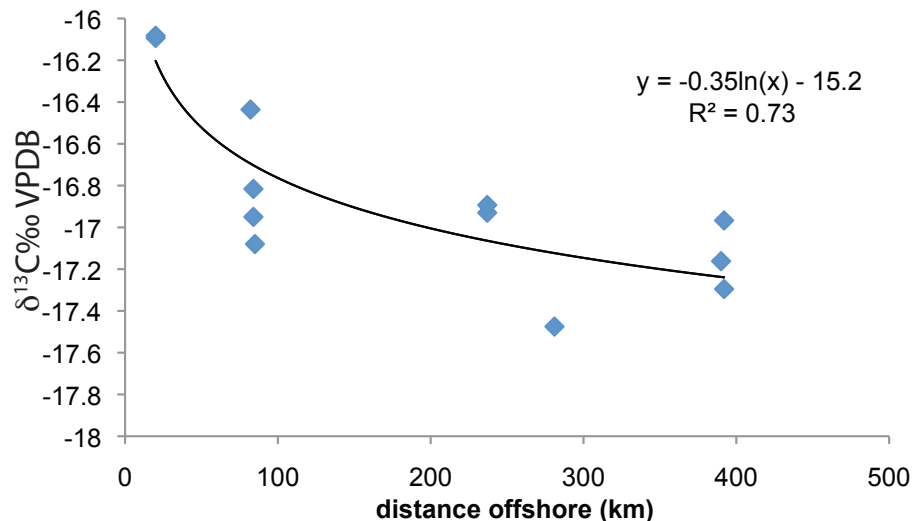


Fig. 6. The relationship between $\delta^{13}\text{C}$ of coral gorgonin and distance from shore indicates declining $\delta^{13}\text{C}$ values offshore, particularly > 250 km offshore. This relationship has been previously observed in zooplankton and nekton up to 70 km offshore (Miller et al., 2008). This relationship may be nonlinear (as indicated) but would require higher sample density to resolve.

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