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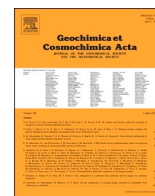
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Proteinaceous deep sea coral amino acid isotope records reveal climate-driven decadal-scale planktic ecosystem fluctuations

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ABSTRACT

Decadal-scale climate variability drives important fluctuations in nutrient availability and productivity in highly productive eastern boundary current upwelling ecosystems, but the relatively brief duration of most monitoring efforts limits understanding of these dynamics. When applied to high-resolution paleoarchives such as deep-sea proteinaceous coral skeletons, stable carbon and nitrogen isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis can provide useful new insight into biogeochemical and ecological changes beyond the instrumental record. However, interpretation of bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ records is often complicated by multiple possible drivers of variability. Here, we addressed these challenges by applying both bulk and compound-specific amino acid $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysis to two bamboo coral specimens from Sur Ridge on the central California margin, generating sub-decadal resolution records spanning c. 1810 to present. Our overarching goals were to first test amino acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ proxies in proteinaceous deep-sea bamboo coral archives, and second to investigate links between climate forcing and biogeochemical responses on the California margin over the Anthropocene.

Together, comparison of deep-sea coral amino acid trophic position results to local sediment traps and end-member mixing analysis indicate that bamboo coral feed directly on exported sinking particles, which are comprised primarily of zooplankton fecal pellets (>70 %). This new evidence contradicts some past work based on bulk $\delta^{15}\text{N}$ analysis alone and validates bamboo coral as archives of euphotic zone processes. Amino acid $\delta^{15}\text{N}$ proxies also reveal that trophic position, not baseline $\delta^{15}\text{N}$ of nitrate or phytoplankton production, is the primary driver of bulk $\delta^{15}\text{N}$ variability in these coral records from a highly-productive coastal upwelling environment.

Our approximately 200-year reconstruction shows overall long-term ecosystem stability since the pre-industrial period, overlain by major multidecadal-scale fluctuations in bamboo coral trophic position and $\delta^{13}\text{C}$ of primary production. Relatively high (low) trophic position and low (high) $\delta^{13}\text{C}$ values of primary production occurred during negative (positive) phases of the Pacific Decadal Oscillation over the 20th century. Counter to expectations, these results suggest lower primary production likely occurred during past periods of high nitrate availability in our study region. Modern satellite chlorophyll-*a* observations corroborate this finding. We hypothesize that offshore transport and subduction of nutrients and phytoplankton and/or precipitation-mediated changes in iron availability may link climate variability and planktic ecosystem dynamics in this region.

1. Introduction

In the California Current System (CCS), a highly dynamic eastern boundary current ecosystem, equatorward alongshore winds cause upwelling of nutrient-rich subsurface waters, fueling high primary and secondary production (Checkley and Barth, 2009). Multiple modes of

climate variability, including the El Niño Southern Oscillation (ENSO), Pacific Decadal Oscillation (PDO) and North Pacific Gyre Oscillation (NPGO), drive interannual- to interdecadal- scale fluctuations in sea surface temperatures, intensity and phenology of upwelling-favorable winds and the strength of major currents in the CCS (Bograd et al., 2009; Di Lorenzo et al., 2013; Jacox et al., 2014). These physical

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changes have major impacts on plankton ecology and productivity which then propagate through CCS ecosystems, ultimately impacting higher trophic levels and fisheries productivity (Hare and Mantua, 2000; Chavez, 2003; Di Lorenzo et al., 2013; Barth et al., 2020). Decadal-scale modes of climate variability have been implicated in ecological “regime shifts”- fundamental alterations in community structure and abundance (Hare and Mantua, 2000; Chavez, 2003). In the face of intensifying anthropogenic changes, understanding how marine ecosystems respond to low-frequency modes of climate variability is critical for projecting outcomes in economically, ecologically, and culturally significant marine resources.

One major obstacle for characterizing links between basin-scale climate and regional ecosystem variability is the short duration of instrumental records. Dominant low-frequency modes of North Pacific climate variability, including the PDO and NPGO, have long periodicities that span nearly the entire length of most existing biological monitoring efforts (MacDonald and Case, 2005). Paleooceanographic reconstruction is therefore needed to gain a longer-term perspective on linked climate-ecosystem dynamics. Sedimentary records can reach back many millennia; however, apart from several anoxic basins limited to the Southern California Bight (Deutsch et al., 2014; Davis et al., 2019), the relatively coarse resolution of most sedimentary archives in the CCS (Lewis et al., 2002) prevents reconstruction with sufficient resolution to examine decadal-scale or higher-frequency fluctuations.

Long-lived deep-sea coral skeletal archives provide a unique solution to challenges associated with traditional sedimentary paleoarchives. Certain deep-sea coral taxa form concentric bands of skeletal material throughout their lifetimes, creating living archives of past ocean change on centennial to millennial time scales with annual to decadal resolution (Roark et al., 2005; Sherwood et al., 2009; Williams, 2020). Bamboo coral (family Keratoisididae), the focus of this study, are a cosmopolitan group of deep-sea corals with endoskeletons containing alternating inorganic calcite “internodes” and organic “nodes” composed of a fibrillar structural protein called gorgonin (Ehrlich et al., 2006). The isotopic composition of bamboo coral proteinaceous nodes derives from dietary organic matter. The presence of radiocarbon signatures from mid-20th century atmospheric nuclear bomb testing indicates that the isotopic composition of gorgonin is linked to surface-derived exported particulate organic matter (POM), enabling reconstruction of euphotic zone processes back through time (Roark et al., 2005; Hill et al., 2014; Liu et al., 2023).

Stable isotopic ratios of organic carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) are powerful, commonly applied proxies in studies of present and past marine biogeochemistry, with potential to track shifts in ocean circulation, marine carbon and nitrogen cycles, ecosystem trophic structure, phytoplankton ecology, and primary productivity (Altabet and Francois, 1994; McMahon et al., 2013; Deutsch et al., 2014; Magozzi et al., 2017; Sigman and Fripiat, 2019). Bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses are rapid, inexpensive, and require only small amounts of material, enabling high-resolution reconstruction of past change from paleoarchives. In biological archives such as bamboo coral, bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($\delta^{13}\text{C}_{\text{bulk}}$ and $\delta^{15}\text{N}_{\text{bulk}}$) are influenced by multiple factors, including the isotopic composition of inorganic nutrient sources, fractionation during autotrophic inorganic nutrient uptake, and fractionation during trophic transfer (Ohkouchi et al., 2015; McMahon and Newsome, 2019). Despite widespread application of bulk stable isotope analysis, interpretation of $\delta^{13}\text{C}_{\text{bulk}}$ and $\delta^{15}\text{N}_{\text{bulk}}$ in paleoarchives is often challenging due to complex interplay between all these potential drivers of variability.

Compound-specific carbon and nitrogen isotope analysis of amino acids (CSI-AA) can address many of these challenges by deconvolving most of the underlying processes influencing the bulk isotopic composition of organic matter and animal tissues. The $\delta^{15}\text{N}$ values of “source” and $\delta^{13}\text{C}$ values of “essential” amino acid groupings pass relatively unaltered from autotrophs through food webs, whereas $\delta^{15}\text{N}$ of “trophic” and $\delta^{13}\text{C}$ of “non-essential” amino acids are sensitive to consumer metabolic processes (Chikaraishi et al., 2009; Larsen et al., 2013;

Ohkouchi et al., 2015). CSI-AA therefore provides separate proxies for the isotopic “baseline” (meaning $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of primary producers) and trophic dynamics in marine organisms and paleoarchives (Williams, 2020). Using paired sediment trap and coral skeletal samples, Shen et al. (2021) recently verified that the compound-specific isotopic composition of amino acids in bamboo coral skeletons faithfully records $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of export production in Monterey Bay. Earlier work also demonstrated the utility of CSI-AA in proteinaceous corals for revealing millennial-scale shifts in marine nitrogen cycling and primary producer community structure (Sherwood et al., 2011, 2014; McMahon et al., 2015). Although CSI-AA approaches are ideal for addressing several open questions about deep-sea coral feeding ecology and climate-driven planktic ecosystem dynamics, to date there has been only limited application of CSI-AA to deep-sea coral from California or any other upwelling system, with a focus primarily on proxy validation rather than paleoenvironmental reconstruction (Schiff et al., 2014; McMahon et al., 2018; Shen et al., 2021).

This work has two overarching goals. The first is to expand understanding of bamboo coral feeding ecology using CSI-AA and verify whether there is a direct linkage to export production. Although deep-sea corals are habitat-forming keystone species, little information is available about their feeding ecology due to unique difficulties with observation and aquarium culturing of deep-sea organisms. An initial euphotic zone source for deep-sea coral dietary organic matter is widely accepted based on radiocarbon evidence (Griffin and Druffel, 1989; Roark et al., 2005); however there has been some disagreement in the literature about the specific ecological connection between surface-derived sinking organic matter and bamboo coral diet. Some past work has variously proposed feeding on either degraded organic matter, the zooplankton component of sinking POM, or deep-sea zooplankton which first feed on sinking particles, as alternatives to direct feeding on surface-derived sinking organic matter (Sherwood et al., 2008, 2009; Hill et al., 2014; Liu et al., 2023). These inferences were based on relatively high $\delta^{15}\text{N}_{\text{bulk}}$ enrichment of gorgonin relative to sinking particles (~5–10 ‰), suggesting the possibility of multiple trophic transfers between sinking particles and deep-sea coral. Compound-specific nitrogen isotope analysis of amino acids is uniquely suited to test these hypotheses. Amino acid trophic position proxies do not rely on assumptions about autotrophic baseline $\delta^{15}\text{N}$ values (Chikaraishi et al., 2009), or bulk trophic enrichment factors, which vary depending on biomolecular composition and tissue type (Schmidt et al., 2004).

Our second major goal is to investigate the impact of past climate changes on central California margin biogeochemistry over the Anthropocene. Relationships between decadal-scale climate variability and ecological changes have been well-established (Hare and Mantua, 2000; Chavez, 2003); however, identifying causal links between physical forcing and ecosystem responses at higher trophic levels is often challenging. Information about shifts in biogeochemistry and plankton communities at the base of pelagic food webs can help establish these links, but such information is sparse and limited by the duration of modern monitoring efforts. CSI-AA measurements of deep-sea coral archives can provide centennial-length continuous proxy records of export production $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values and plankton trophic dynamics (Sherwood et al., 2014; Williams, 2020). Our second aim is therefore to examine both the long-term stability of plankton ecosystems since before the industrial revolution, as well as relationships between known ocean climate fluctuations and plankton ecosystem structure and productivity over the 20th century. We hypothesized that past periods of enhanced nutrient availability and upwelling on the central California margin during negative phases of the PDO would be associated with increased phytoplankton productivity due to greater nutrient availability and shorter, less complex trophic food webs.

To address these two major goals, we created high-resolution (~3 year) proteinaceous coral bulk isotope and CSI-AA records which span ~200 years of oceanographic history on the central California margin from c. 1810 to present. To our knowledge, this is the first CSI-AA work

on proteinaceous coral archives from an eastern boundary current upwelling ecosystem with a major emphasis on paleoenvironmental reconstruction instead of proxy development. Our study site is located at Sur Ridge, slightly south of Monterey Bay and offshore of a strong upwelling center at Point Sur. This site also lies within a unique oceanographic regime, where iron limitation due to an extremely narrow continental shelf results in relatively low productivity despite high macronutrient supply (Fig. 1; Biller et al. 2013). Leveraging recent CSI-AA findings for sediment trap samples from nearby Monterey Canyon (Shen et al., 2021) and marine organic matter endmembers (Doherty et al., 2021), we evaluated the fidelity of amino acid $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ proxies and examined bamboo coral trophic ecology. Finally, by comparing our reconstruction over the instrumental period with basin-scale climate and regional oceanographic variability, we examined linkages between climate forcing and planktic ecosystem response.

2. Materials and Methods

2.1. Specimen Collection, Storage and Sampling

The two cold-water bamboo coral skeletons (D621 #1B and D639 #1C) used in this work were live-collected between 1200 and 1300 m depth by ROV on the northern side of Sur Ridge (36.4° N, 122.3° W; Fig. 1), a rocky geologic feature located on the central California continental slope. Specimens were washed in freshwater and dried at sea, then stored dry at the University of California, Santa Cruz. From each coral specimen, one proteinaceous node selected from near the base of the skeleton was sectioned with a diamond saw, then mounted on a glass slide. Nodes were radially sampled at ~ 0.1 mm resolution using a New Wave micromill; this resolution yielded approximately 2–3 mg of gorgonin powder per sample. The node for D621 #1B had a radius of 8.46 mm, and the outer 5.85 mm were drilled, yielding 58 gorgonin samples. The node for D639 #1C had a radius of 9.4 mm from the center to the outside edge in the direction sampled, and the outer 6.85 mm were drilled, yielding 66 gorgonin samples.

2.2. Radiocarbon and Age-Model Development

Radiocarbon analysis was performed on a subset of samples ($n = 7$ from D621 #1B, $n = 6$ from D639 #1C). Detailed methods for bamboo

coral ^{14}C analysis have been described in previous work (Hill et al., 2014; Schiff et al., 2014). A linear age model was constructed using one tie point at or near the year of collection and two tie points estimated based on a California Current bomb radiocarbon reference chronology from petrale sole otoliths (Haltuch et al. 2013; Fig. S1). Our age modeling approach is similar to past work on proteinaceous deep-sea coral from the NE Pacific margin, but the use of the reference chronology developed by Haltuch et al. (2013) is unique to this study. One additional change from past work is the use of D^{14}C , instead of the more commonly reported parameter $\delta^{14}\text{C}$. We made this choice based on the best-practice recommendations of Reimer et al. (2004) for comparison of post-bomb reference chronologies to unknown-age samples like the bamboo coral skeletal samples. Calculation of $\Delta^{14}\text{C}$ requires knowledge of the growth year of the sample, which is not the case for our unknown age bamboo coral skeletal samples. Therefore, we converted the $\Delta^{14}\text{C}$ values reported by Haltuch et al. (2013) to D^{14}C to facilitate direct comparison with our samples of unknown age (Stuiver and Polach, 1977).

2.3. Bulk Stable Isotope Analysis

Bulk stable isotope analysis was performed on ~ 0.3 mg of dry powder from each sample ($n = 58$ from D621 #1B & $n = 65$ from D639 #1C) using a Carlo Erba 1108 elemental analyzer coupled to a Thermo Finnigan Delta Plus XP isotope ratio mass spectrometer following established procedures at the UC Santa Cruz Stable Isotope Lab (<https://websites.pmc.ucsc.edu/~silab/index.php>). Samples were not decarbonated prior to EA-IRMS analysis. Our micromill protocol sampled only the internal portion of the gorgonin node, which does not contact seawater or the calcite internodes and therefore is unlikely to contain carbonates. This assumption was tested on a small subset of samples ($n = 6$) by comparing $\delta^{13}\text{C}$ results from untreated subsamples and subsamples fumed in a desiccator with 12 N HCl for 16 h (Fig. S2). We find close agreement and no systematic $\delta^{13}\text{C}$ differences between the untreated and acid-fumed subsamples, with a small mean offset of 0.04 ‰, indicating no presence of carbonates in our samples. Isotope values are reported in per mil (‰) notation, relative to atmospheric nitrogen for $\delta^{15}\text{N}$ and Vienna PeeDee Belemnite for $\delta^{13}\text{C}$. Duplicate analyses of a subset of samples ($n = 8$) yielded average analytical standard deviations of 0.3‰ and 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

2.4. Compound-Specific Isotope Analysis of Amino Acids

A subset of samples selected for CSI-AA ($n = 13$ from D621 #1B; $n = 15$ from D639 #1C) were prepared following established McCarthy lab protocols that include acid hydrolysis, amino acid purification and TFA-derivatization procedures (e.g., McMahon et al. 2018). Approximately 1–2 mg of coral powder from each sample was hydrolyzed in 6 N HCl for 20 h at 110 °C then dried down under N_2 at 60 °C. To purify amino acids, hydrolysates were introduced to cation exchange columns (Dowex 50WX8-400) and rinsed in 0.01 N HCl, then eluted in 2 N NH_4OH (Metges and Petzke, 1997). After re-protonation with 0.2 N HCl and a two-step isopropyl-esterification and trifluoroacetic anhydride (TFA) derivatization procedure (Silfer et al., 1991), amino acid derivatives were further purified by solvent extraction with chloroform and phosphate buffer (Ueda et al., 1989). After solvent extraction, samples underwent a second TFA-derivatization. An aliquot (~0.1 mg of dry coral powder equivalent for carbon and ~ 0.2 mg of dry coral powder equivalent for nitrogen) was dried down under N_2 and brought up in approximately 20 μL ethyl acetate on the day of GC-IRMS analysis.

CSI-AA and molar abundance measurements were made in the shared UC Santa Cruz Stable Isotope Lab facility. Amino acid derivatives in ethyl acetate (~1 μL) were injected onto a Thermo Trace GC coupled to a Thermo-Finnigan Delta Plus XP isotope ratio mass spectrometer and GCC III (isoLink). Under our GC conditions, we were able to quantify 12 amino acids for both carbon and nitrogen: alanine (Ala), glycine (Gly),

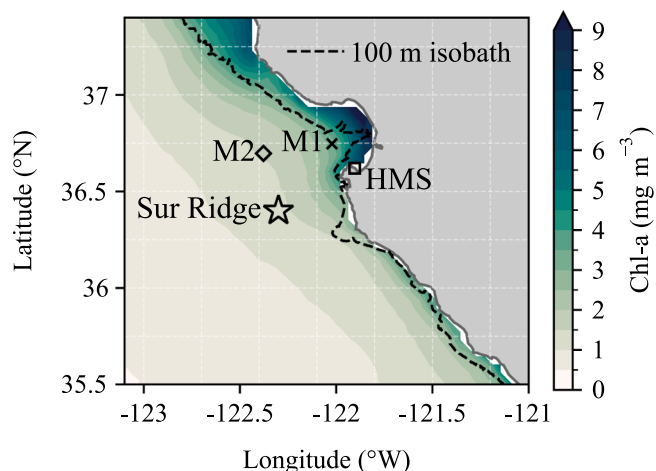


Fig. 1. The study site at Sur Ridge (star), along with MBARI Station M2 (diamond), Station M1 (x) and Hopkins Marine Station (HMS; square) shown in the context of regional mean chlorophyll-a concentrations between 1999–2021 from the monthly Copernicus-GlobColour satellite ocean color product and the 100 m isobath (GEOCO Compilation Group, 2022). Narrow continental shelf widths like those seen on the Big Sur Coast are associated with relatively low primary productivity due to low iron supply in the California Current System.

threonine (Thr), serine (Ser), valine (Val), leucine (Leu), isoleucine (Ile), Proline (Pro), aspartic acid (Asp), glutamic acid (Glu), phenylalanine (Phe) and lysine (Lys). During nitrogen isotope analysis, proline and hydroxyproline co-eluted, so their peaks were integrated together and reported as Pro. Methionine and tyrosine were also present in our samples; however, they were excluded from interpretation due to low concentrations and poor reproducibility, respectively. The $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for individual amino acids were standardized using pulses of N_2 or CO_2 reference gas and corrected based on bracketing injections of an amino acid mixed standard with known isotopic composition (Silfer et al., 1991). Data quality was monitored using an internal Norleucine amino acid standard and a D-amino acid standard with independently verified amino acid isotopic compositions, and a long-term laboratory algal standard. Each sample was analyzed in triplicate to determine analytical reproducibility, yielding mean analytical standard deviations of 0.3‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Finally, molar percent abundance (Mol %) of each amino acid was estimated from GC-IRMS peak areas generated during carbon isotope analysis, using response factors from bracketing measurements of the AA mixed standard. As expected, we found minimal Mol% variation between specimens or samples, with a mean between-sample standard deviation of 0.9%. As a result, for all calculations involving Mol% (Eq. (2) and Eq. (4) described below), we used mean Mol% values of all samples from both specimens.

2.5. CSI-AA Parameter Calculations

For $\delta^{13}\text{C}$ CSI-AA data analysis, we divided the amino acids into “essential” (EAA: Thr, Ile, Phe, Leu, Lys) and “nonessential” (NEAA: Gly, Ser, Asp, Glu, Pro, Ala) groupings. Val is classically grouped with the EAAs; however we excluded Val from EAA calculations for several reasons. In our records, Val displays high $\delta^{13}\text{C}$ variability and low correlations with other EAAs. Past work also noted incongruous results between Val and other EAAs in bamboo coral specifically (Shen et al., 2021). The $\delta^{13}\text{C}_{\text{EAA}}$ parameter, calculated as the mean $\delta^{13}\text{C}$ of the EAAs, is a proxy for $\delta^{13}\text{C}$ of primary production, because the carbon skeletons of essential amino acids are synthesized nearly exclusively by primary producers (Larsen et al., 2013). For $\delta^{15}\text{N}$, the amino acids were divided into four categories (McMahon and McCarthy, 2016): “source” (Phe, Lys), “trophic” (Glu, Asp, Ala, Ile, Leu, Pro, Val), “intermediate” (Gly, Ser) and “inverse-trophic” (Thr). The “intermediate” amino acids have traditionally been grouped with the “source” amino acids (McClelland and Montoya, 2002); however accumulated evidence from the literature shows trophic discrimination factors for Gly and Ser are typically intermediate between those of the source and trophic amino acids (McMahon and McCarthy, 2016; Shen et al., 2021). The inverse-trophic amino acid Thr has a negative trophic discrimination factor (McMahon and McCarthy, 2016). $\delta^{15}\text{N}_{\text{Phe}}$ is widely considered the most reliable source AA, and here is used as a proxy for $\delta^{15}\text{N}$ of phytoplankton at the base of the food web (i.e. baseline).

The CSI-AA trophic position (TP) was estimated from $\delta^{15}\text{N}_{\text{Glu}}$ and $\delta^{15}\text{N}_{\text{Phe}}$ using the trophic position calculation originally developed by Chikaraishi et al. (2009) and adapted for deep-sea coral skeletons by McMahon et al. (2018):

$$\text{Coral TP} = \frac{(\delta^{15}\text{N}_{\text{Glu}} + \partial) - \delta^{15}\text{N}_{\text{Phe}} - \beta}{\text{TDF}} + 1 \quad (1)$$

where ∂ is the $\delta^{15}\text{N}_{\text{Glu}}$ offset between coral polyp and skeletal tissue (3.4‰), β is the offset between $\delta^{15}\text{N}_{\text{Glu}}$ and $\delta^{15}\text{N}_{\text{Phe}}$ of primary producers at the base of the food web (3.4‰), and TDF is the trophic discrimination factor for $\delta^{15}\text{N}_{\text{Glu}}$ (7.6‰).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of total hydrolysable amino acid carbon and nitrogen ($\delta^{13}\text{C}_{\text{THAA-AT}}$ & $\delta^{15}\text{N}_{\text{THAA-AT}}$) were calculated using the following equations:

$$\text{C Wt}_i = \frac{\#C_i \times \text{Mol}\%_i}{\Sigma(\#C_i \times \text{Mol}\%_i)} \quad (2)$$

$$\delta^{13}\text{C}_{\text{THAA-AT}} = \Sigma(\text{C Wt}_i \times \delta^{13}\text{C}_i) \quad (3)$$

$$\text{N Wt}_i = \frac{\#N_i \times \text{Mol}\%_i}{\Sigma(\#N_i \times \text{Mol}\%_i)} \quad (4)$$

$$\delta^{15}\text{N}_{\text{THAA-AT}} = \Sigma(\text{N Wt}_i \times \delta^{15}\text{N}_i) \quad (5)$$

where i represents a given individual amino acid, and $\#C_i$ and $\#N_i$ represent the number of carbon and nitrogen atoms in a single molecule of the given amino acid i . We use the abbreviation THAA-AT, denoting “atomic THAA”, to differentiate from traditional THAA calculations, which weight based on Mol% but do not account for the variable number of carbon and nitrogen atoms in each amino acid. This distinction is largely unimportant for $\delta^{15}\text{N}$ because all the typically reported amino acids for CSI-AA except Lys contain just one N atom. However, variability in carbon content is much greater (ranging from 2 atoms in Gly to 9 in Phe), necessitating the atomic THAA approach for most applications. Error propagation equations for the atomic THAA and TP calculations are described in the [Supplementary Material](#).

Finally, ΣV , an indicator for microbial resynthesis of organic matter, was calculated using the equation developed by McCarthy et al. (2007):

$$\Sigma V = \frac{\Sigma|\delta^{15}\text{N}_i - \delta^{15}\text{N}_{\text{avg}}|}{n} \quad (6)$$

where i represents a given individual trophic amino acid (Glu, Asp, Ala, Ile, Leu, Pro, Val), $\delta^{15}\text{N}_{\text{avg}}$ represents the mean of all trophic amino acids, and n is the number of trophic amino acids ($n = 7$).

2.6. Statistical Data Analysis

Data analysis was completed primarily in Python. Data was processed using the open-source pandas library (McKinney, 2010). Plots were created using the Matplotlib, TrendVis and Cartopy plotting packages (Hunter, 2007; Cross, 2015; Elson et al., 2023). We tested for trends in the bulk isotope timeseries using Mann-Kendall tests adjusted for timeseries autocorrelation (Hamed and Ramachandra Rao, 1998) using the pyMannKendall package (Hussain and Mahmud, 2019). Spearman's ρ was computed using the Scipy statistics package (Virtanen et al., 2020). Corresponding probabilities were estimated based on the simulated probability distribution of Spearman's ρ from $n = 10,000$ randomly generated AR(1) process timeseries pairs with the same lag-1 autocorrelation coefficients as the variables of interest, using functionalities from the statsmodels, Pyleoclim and Scipy packages (Seabold and Perktold, 2010; Virtanen et al., 2020; Khider et al., 2022). Accounting for timeseries autocorrelation in probability estimation is necessary for accurate determinations of statistical significance in paleoenvironmental timeseries, which are often significantly autocorrelated (Hu et al., 2017).

We used commonality analysis and multiple linear regression to explore relationships between amino acid and bulk isotope proxies after methods described by Ray-Mukherjee et al. (2014). Amino acid isotope proxies such as trophic position and $\delta^{15}\text{N}_{\text{Phe}}$ are often correlated with one another, due to mechanistic links between proxies and/or spurious correlations due to non-independence. As a result of this collinearity, standardized regression (β) coefficients from multiple linear regression analysis cannot adequately describe the separate effects of different amino acid isotope proxies on a dependent variable such as $\delta^{15}\text{N}_{\text{bulk}}$. Commonality analysis permits decomposition of the unique and common effects of collinear predictor variables on a dependent variable. Unique effects describe what proportion of variance in the dependent variable is uniquely shared with a given predictor variable, whereas common effects describe what proportion of variance in the dependent variable results from common variance shared by multiple predictor variables.

2.7. Bayesian Mixing Model Coral Diet Analysis

The Bayesian mixing model R package MixSIAR (Stock et al., 2018) was used to estimate relative contributions of fecal pellets, zooplankton, phytoplankton and microbially-degraded organic matter endmembers to bamboo coral diet. We used the approach and endmember dataset developed by Doherty et al. (2021), who demonstrated that each of these four organic matter types have unique amino acid $\delta^{15}\text{N}$ signatures. In particular, the trophic amino acid Ala, which is trophically enriched by both microbial and metazoan metabolism, and the “inverse trophic” amino acid Thr, which is isotopically depleted only by animal and not microbial metabolism, together statistically separate the four endmembers (McMahon and McCarthy, 2016; Décima et al., 2017; Doherty et al., 2021). In the endmember dataset, $\delta^{15}\text{N}_{\text{Thr}}$ and $\delta^{15}\text{N}_{\text{Ala}}$ are normalized to $\delta^{15}\text{N}_{\text{Phe}}$ ($\delta^{15}\text{N}_{\text{Thr-Phe}}$ and $\delta^{15}\text{N}_{\text{Ala-Phe}}$). Normalization to $\delta^{15}\text{N}_{\text{Phe}}$ accounts for shifts in $\delta^{15}\text{N}$ baseline across space and time, permitting comparison between endmembers and consumer or mixture samples collected from different locations and time periods (Doherty et al., 2021). Zooplankton fecal pellet endmember data are from ship-board zooplankton incubation experiments ($n = 7$; Doherty et al., 2021), zooplankton endmember data are from field studies of size-fractionated zooplankton samples ($n = 49$; McClelland et al., 2003; Hannides et al., 2009, 2013; Romero-Romero et al., 2020; Doherty et al., 2021), phytoplankton endmember data are from laboratory cultures ($n = 11$; McCarthy et al., 2013), and the microbially degraded endmember data are from mesopelagic high molecular weight dissolved organic matter (DOM) and ultrafiltered particulate organic matter (UPOM; Yamaguchi and McCarthy, 2018).

The mixing model approach of Doherty et al. (2021) was initially developed for use with POM, and application to estimate consumer diet composition requires some corrections for isotopic offsets between diet and consumer tissue (in this case, gorgonin). Trophic discrimination factors for $\delta^{15}\text{N}_{\text{Thr-Phe}}$ and $\delta^{15}\text{N}_{\text{Ala-Phe}}$ were derived from expected $\delta^{15}\text{N}$ offsets between coral skeleton samples and dietary POM due to both trophic transfer (McMahon and McCarthy, 2016) and documented $\delta^{15}\text{N}$ differences between coral polyp and skeletal tissue (McMahon et al., 2018). The corresponding uncertainties in these parameters were propagated and input into the mixing model (further details provided in Table S1). The mixing model was parameterized using an uninformative prior estimate and the “very long” run setting in MixSIAR, which uses the following Markov Chain Monte Carlo parameters: chain length = 1,000,000, burn = 500,000, thin = 500, and chains = 3. Model convergence was confirmed using Gelman-Rubin and Geweke diagnostics.

As previously noted by Golombek et al. (2024), one limitation of this approach is that the microbially degraded endmember falls on the mixing line between the phytoplankton and zooplankton endmembers. This leads to difficulties in discriminating whether variation in $\delta^{15}\text{N}_{\text{Thr-Phe}}$ and $\delta^{15}\text{N}_{\text{Ala-Phe}}$ results from variable contributions of phytoplankton and zooplankton, or contributions from microbially degraded matter. Given that radiocarbon results clearly indicate an ultimate surface ocean source for deep-sea coral dietary organic matter (Griffin and Druffel, 1989; Roark et al., 2005; Sherwood et al., 2009; Hill et al., 2014), the older and more refractory UPOM and DOM sources represented by the microbially degraded endmember (Yamaguchi and McCarthy, 2018) are likely not an important component of bamboo coral diet. Therefore, in addition to an analysis using all four endmembers, we also performed diet estimations using only the phytoplankton, zooplankton and fecal pellets endmembers for comparison (contrast in results is presented below in Section 3.5). In this case, the mixing model converged using the MixSIAR “normal” run setting, which uses the following Markov Chain Monte Carlo parameters: chain length = 100,000, burn = 50,000, thin = 50, and chains = 3.

2.8. Ancillary climate and oceanographic datasets

To investigate relationships between the Sur Ridge bamboo coral proxy records and regional to basin-scale ocean climate variability, we examined correlations of isotope variables with the three year running mean PDO index from 1900 to 2014 (Mantua, 2017; downloaded from <https://research.jisao.washington.edu/pdo/PDO.latest>), and the original and detrended three-year running upwelling season mean SST at Hopkins Marine Station from 1919 to 2014 (Breaker and Miller, 2023). Three-year running means were selected to match the temporal resolution of the bamboo coral records. ENSO and NPGO variability were also considered, but exhibit variability on shorter timescales not adequately resolved by our records. Additionally, to aid in data interpretation and evaluate potential drivers of interannual ecosystem variation on the central California margin, we computed Spearman rank-based correlations of 1999–2021 annual means of monthly satellite chlorophyll-*a* concentrations (Chl-*a*) from the E.U. Copernicus Marine Service Information GlobColour data product (E.U. Copernicus Marine Service Information (CMEMS)) to annual means of monthly stream gauge data for the Salinas River (U.S. Geological Survey, 2016), upwelling season (April–August) SST means at Granite Canyon (Carter et al., 2022) and annual means between 35 and 37°N of the Biologically Effective Upwelling Transport Index (BEUTI), an index for the quantity of NO_3^- upwelled to the mixed layer depth (Jacox et al., 2018).

3. Results

3.1. Radiocarbon, Growth Rate and Age Modeling

D^{14}C results are similar across both specimens (Fig. S1), displaying low values (range -99‰ to -87‰) in gorgonin samples from the inner skeleton, and higher values (range 25‰ to 51‰) in the outer 2 mm of the skeleton. The abrupt increase in D^{14}C values in the outer portion of the skeletons reflects surface ocean uptake of atmospheric radiocarbon from nuclear bomb testing during the 1950s to 1960s (Broecker et al., 1985). Post-bomb values from our specimens closely align with a California Current radiocarbon reference chronology from petrale sole otoliths (Haltuch et al., 2013). We developed age models by matching D^{14}C observations from our specimens to tie points on this reference chronology and linearly interpolating between tie points (Fig. S1). Based on the resulting age model, we estimate an average radial growth rate of 0.03 mm/yr for specimen D621 #1B, and 0.04 mm/yr for specimen

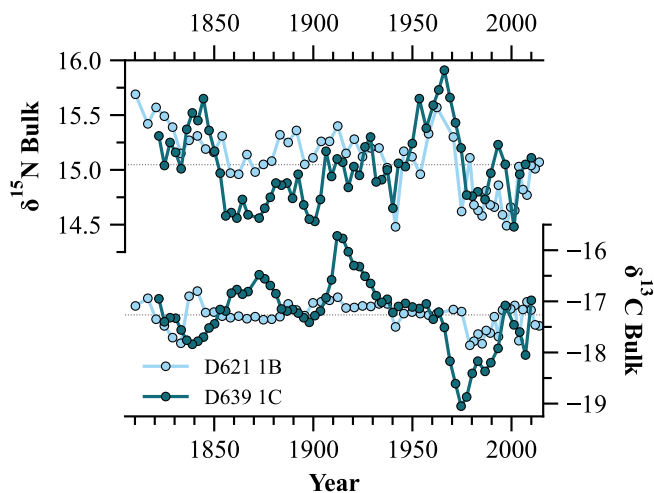


Fig. 2. Bulk $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ records from Sur Ridge bamboo coral specimens D639 #1C (green) and D621 #1B (blue), as well as mean values across both records (grey dashed lines), showing generally coherent patterns of decadal-scale variability overlain on overall ecosystem stability since c. 1810.

D639 #1C. Therefore, each of our drilled gorgonin samples represents approximately 2.5–3.5 years of time, yielding records with sub-decadal resolution.

3.2. Bulk Isotopes and C/N of Bamboo Coral Gorgonin Records

The Sur Ridge bamboo coral $\delta^{15}\text{N}_{\text{bulk}}$ and $\delta^{13}\text{C}_{\text{bulk}}$ records are characterized by multidecadal-scale fluctuations, with no evidence for long-term trends or permanent shifts in mean state between c. 1810–2014 (Fig. 2). $\delta^{15}\text{N}_{\text{bulk}}$ ranges between 14.5‰ to 15.9‰, with a mean value of 15.0 ± 0.3 ‰. $\delta^{13}\text{C}_{\text{bulk}}$ ranges between -19.1 ‰ and -15.7 ‰, with a mean value of -17.3 ± 0.5 ‰. Mann-Kendall tests for trend adjusted for timeseries autocorrelation (Hamed and Ramachandra Rao, 1998) indicate no significant trends in $\delta^{15}\text{N}_{\text{bulk}}$ ($Z = -1.47$, Theil-Sen slope = -0.002 , $p = 0.14$) or $\delta^{13}\text{C}_{\text{bulk}}$ ($Z = -0.69$, Theil-Sen slope = -0.002 , $p = 0.49$). In the records from both specimens, $\delta^{15}\text{N}_{\text{bulk}}$ values are elevated from approximately 1810–1850 and 1950–1975. $\delta^{15}\text{N}_{\text{bulk}}$ values are relatively low to average from approximately 1855–1950 and 1975–2014. A significant positive correlation between the two skeletal $\delta^{15}\text{N}_{\text{bulk}}$ records ($\rho = 0.40$, $p = 0.05$) indicates general inter-colony reproducibility of major multidecadal fluctuations. The $\delta^{13}\text{C}_{\text{bulk}}$ record also displays multidecadal-scale fluctuations, but they are less coherent. While intercolony $\delta^{13}\text{C}_{\text{bulk}}$ similarities are apparent over portions of the records, two positive excursions from 1860 to 1880 and 1905–1925 in specimen D639 #1C are notably absent from specimen D621 #1B, reducing overall reproducibility between specimens ($\rho = 0.38$, $p = 0.08$). Mean C/N of bamboo coral gorgonin is 2.8 ± 0.1 , with a range from 2.6 to 3.2. C/N values are higher in specimen D621 #1B (2.9 ± 0.07) than specimen D639 #1C (2.7 ± 0.04), with no overlap in values.

3.3. Bamboo coral amino acid $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ results

All amino acid groupings (trophic, source, transition and metabolic) display expected $\delta^{15}\text{N}$ patterns in the Sur Ridge bamboo coral samples (Fig. 3). The metabolic amino acid Thr has the lowest $\delta^{15}\text{N}$ values with a mean of -8.5 ‰, as expected based on its inverse trophic fractionation

behavior. $\delta^{15}\text{N}_{\text{Phe}}$ has a mean of 9.8 ± 0.7 ‰ and range from 8.3‰ to 11.1‰. Lys, the other source amino acid, has a mean $\delta^{15}\text{N}$ value of 11.5 ± 0.5 ‰ and range from 10.6‰ to 13.4‰. The two transition amino acids are slightly enriched relative to source amino acids, with mean $\delta^{15}\text{N}$ values of 13.6‰ for Gly and 14.3‰ for Ser. The trophic amino acids are the most enriched, with mean $\delta^{15}\text{N}$ values ranging from 18.3‰ for Asp to 24.9‰ for Val. Mean Coral TP is 2.5 ± 0.1 , with a range from 2.2 to 2.8. Mean $\delta^{15}\text{N}_{\text{THAA-AT}}$ is 15.4 ± 0.4 ‰, with a range from 14.7‰ to 16.5‰. Mean ΣV is 1.4 ± 0.2 ‰, with a range from 1.0‰ to 2.0‰.

For $\delta^{13}\text{C}$, the essential and nonessential amino acids have overlapping ranges, with overall higher mean values in the nonessential amino acids (Fig. 3). For the essential amino acids, mean $\delta^{13}\text{C}$ values range from -27.4 ‰ for Leu to -9.5 ‰ for Thr. For the nonessential amino acids, mean $\delta^{13}\text{C}$ values range from -19.3 ‰ for Pro and Ala to -7.1 ‰ for Thr. $\delta^{13}\text{C}_{\text{EAA}}$ has a mean of -19.3 ± 1.3 ‰, with a range from -21.3 ‰ to -16.9 ‰. $\delta^{13}\text{C}_{\text{THAA-AT}}$ has a mean of -15.9 ± 1.7 ‰, with a range from -18.2 ‰ to -12.6 ‰.

3.4. Comparison of bamboo coral and sediment trap $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$

Comparison of results from the Sur Ridge bamboo coral specimens to geographically adjacent outer Monterey Canyon sediment trap samples published by Shen et al. (2021; Fig. 3, Fig. S3) shows that $\delta^{15}\text{N}_{\text{bulk}}$ is lower in sinking particles than in coral skeletons, with a mean offset of 7.2‰. $\delta^{15}\text{N}_{\text{THAA-AT}}$ is also higher in bamboo coral than sinking particles, with a mean offset of 4.2‰. Sinking particles displayed a TP range from 1.3 to 1.9 with a mean of 1.6 ± 0.2 , approximately one trophic position below bamboo coral (mean Coral TP = 2.5 ± 0.1). Trophic amino acid $\delta^{15}\text{N}$ values are elevated in bamboo coral relative to sinking particles, with mean offsets ranging from 4.6‰ for Glu to 10.7‰ for Ile. $\delta^{15}\text{N}$ values of the intermediate amino acids are also elevated in coral relative to sinking particles, with offsets of 5.1‰ for Gly and 7.8‰ for Ser. For the inverse-trophic amino acid, mean $\delta^{15}\text{N}_{\text{Thr}}$ values are depleted in bamboo coral relative to sediment trap samples by 9.9‰. In contrast, $\delta^{15}\text{N}$ ranges for the source amino acids in coral overlap with the sediment trap data. Mean $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{15}\text{N}_{\text{Lys}}$ are enriched only 0.9‰, and 1.9‰, respectively, in coral relative to sinking particles. Additionally, all coral $\delta^{15}\text{N}_{\text{Phe}}$ values fall within the range observed in sinking particles. When bamboo coral amino acid $\delta^{15}\text{N}$ values are adjusted using documented polyp-skeleton offsets in bamboo coral (McMahon et al. 2018), the difference between coral and sinking particles increases for the trophic, intermediate and inverse-trophic amino acids, but remains very small (mean offsets < 1.6 ‰) for the source amino acids (Fig. S4).

In contrast to $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ ranges of individual amino acids in bamboo coral skeletal samples and sediment trap material all overlap, with relatively similar mean values (Fig. 3, Fig. S3). $\delta^{13}\text{C}_{\text{EAA}}$ and $\delta^{13}\text{C}_{\text{NEAA}}$ show small mean offsets between coral and sinking particles of 0.8‰ and 1.2‰, respectively. Coral and sinking particle $\delta^{13}\text{C}_{\text{THAA-AT}}$ values are also relatively close, with a mean offset of 1.8‰. In contrast to the overlap seen in the amino acid $\delta^{13}\text{C}$ results, $\delta^{13}\text{C}_{\text{bulk}}$ is lower in sinking particles than coral skeletons, with no overlap in range and a mean offset of 4.6‰. $\delta^{13}\text{C}_{\text{bulk}}$ in coral instead displays values similar to $\delta^{13}\text{C}_{\text{THAA-AT}}$ in sinking particles, with a mean offset of only 0.4‰.

3.5. Bayesian Coral Dietary Source Estimation from $\delta^{15}\text{N}$ of Amino Acids

We also used compound-specific nitrogen isotopes of amino acids to estimate the major dietary sources of organic matter to bamboo coral at Sur Ridge, based on a framework proposed by Doherty et al. (2021). When plotted with endmember $\delta^{15}\text{N}_{\text{Thr-Phe}}$ and $\delta^{15}\text{N}_{\text{Ala-Phe}}$ values for fecal pellets, microbially degraded matter, phytoplankton and zooplankton, estimated bamboo coral diet aligns closely with zooplankton fecal pellets (Fig. 4). From MixSIAR mixing model dietary source estimates using all four endmembers, the median (90% Bayesian credible interval) posterior density from coral skeletal samples is 0.71 (0.15–0.90) for fecal pellets, 0.09 (0.01–0.54) for microbially degraded

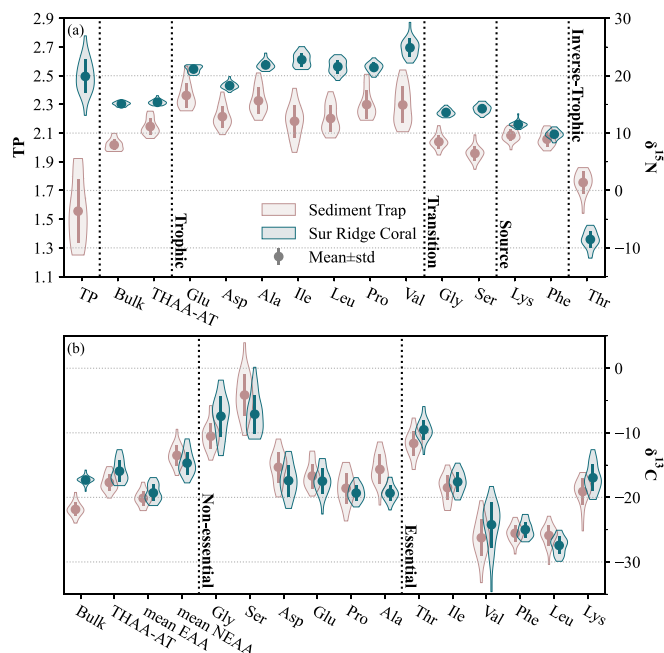


Fig. 3. Amino acid $\delta^{15}\text{N}$ (a) and $\delta^{13}\text{C}$ (b) results, including the mean $\pm$ std (round markers with error bars) and violin plots with lengths spanning the range of observed values and widths representing probability density (shaded areas) across all bamboo coral samples analyzed for this study (teal), and sediment trap samples from Station M2 (pink; Shen et al., 2021).

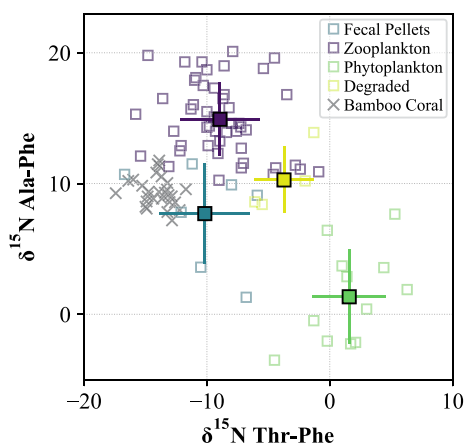


Fig. 4. Assessing bamboo coral food sources based on diagnostic amino acid $\delta^{15}\text{N}$ parameters (after Doherty et al., 2021). Individual observations (open squares) and mean $\pm$ std (solid squares with error bars) are shown for $\delta^{15}\text{N}_{\text{Thr-Phe}}$ vs $\delta^{15}\text{N}_{\text{Ala-Phe}}$ in zooplankton (purple), fecal pellets (blue), microbially degraded organic matter (yellow) & phytoplankton (green). Values from Sur Ridge coral (black x's) are corrected based on expected offsets between coral skeletal protein and dietary PON (McMahon and McCarthy, 2016; McMahon et al., 2018).

organic matter, 0.04 (0.00–0.17) for phytoplankton and 0.12 (0.01–0.32) for zooplankton. Using only the phytoplankton, zooplankton and fecal pellet endmembers, the median (90% Bayesian credible interval) posterior density from coral skeletal samples is 0.81

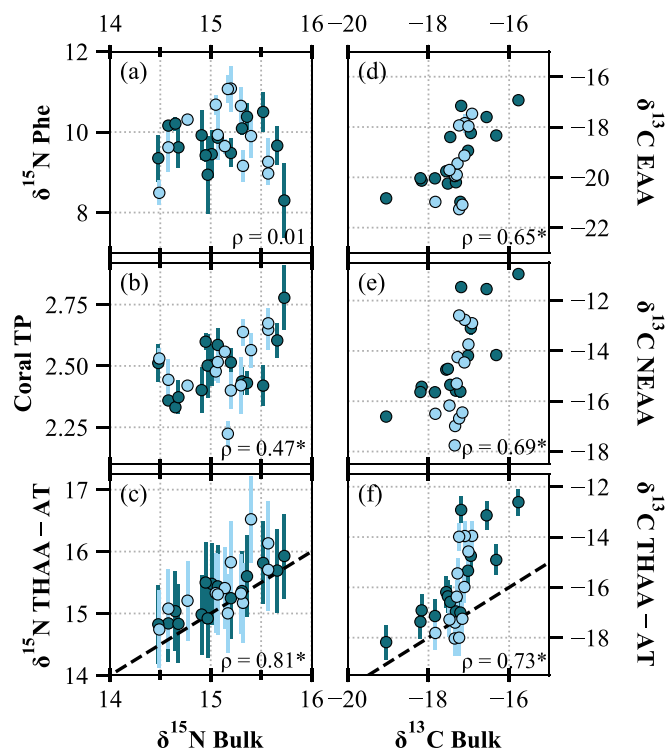


Fig. 5. Relationships between bulk isotopes and CSI-AA parameters from the two bamboo coral records, D621 #1B (light blue circles), and D639 #1C (dark teal circles). $\delta^{15}\text{N}_{\text{bulk}}$ is compared to $\delta^{15}\text{N}_{\text{Phe}}$ (a), Coral TP (b) and $\delta^{15}\text{N}_{\text{THAA-AT}}$ (c). $\delta^{13}\text{C}_{\text{bulk}}$ is compared to $\delta^{13}\text{C}_{\text{EAA}}$ (d), $\delta^{13}\text{C}_{\text{NEAA}}$ (e) and $\delta^{13}\text{C}_{\text{THAA-AT}}$ (f). Error bars denote analytical standard deviations from triplicate analyses. Spearman's ρ is listed on the bottom right of each biplot, asterisks denote statistical significance ($p < 0.05$). Dashed black lines on the bottom panels represent 1:1 lines.

(0.60–0.95) for fecal pellets, 0.04 (0.00–0.15) for phytoplankton and 0.14 (0.02–0.34) for zooplankton.

3.6. Relationships between bulk and amino acid $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ results

We investigated relationships between bamboo coral bulk isotope values and compound specific isotope proxies, seeking to understand major influences on variability in the high-resolution bulk records. We find strong positive Spearman correlations between $\delta^{13}\text{C}_{\text{bulk}}$ and $\delta^{13}\text{C}_{\text{EAA}}$ ($\rho = 0.64$, $p < 0.01$), $\delta^{13}\text{C}_{\text{NEAA}}$ ($\rho = 0.68$, $p < 0.01$) and $\delta^{13}\text{C}_{\text{THAA-AT}}$ ($\rho = 0.73$, $p < 0.01$) (Fig. 5). Compared to $\delta^{13}\text{C}_{\text{bulk}}$, values for $\delta^{13}\text{C}_{\text{THAA-AT}}$ (an estimate for $\delta^{13}\text{C}$ of total hydrolysable proteinaceous carbon) are elevated by 1.4‰ on average. Despite strong correlations, there are important discrepancies in the range of variability observed in $\delta^{13}\text{C}_{\text{bulk}}$ and amino acid proxies. $\delta^{13}\text{C}_{\text{THAA-AT}}$, $\delta^{13}\text{C}_{\text{EAA}}$ and $\delta^{13}\text{C}_{\text{NEAA}}$ exhibit wider ranges (5.6‰, 4.3‰ and 6.8‰ respectively), relative to $\delta^{13}\text{C}_{\text{bulk}}$ (3.3‰). One specimen (D621 #1B) specifically has a very narrow $\delta^{13}\text{C}_{\text{bulk}}$ range of 0.9‰, yet still displays near-identical amino acid $\delta^{13}\text{C}$ proxy ranges to specimen D639 #1C. Additionally, despite weak inter-colony reproducibility observed in portions of the $\delta^{13}\text{C}_{\text{bulk}}$ records, $\delta^{13}\text{C}_{\text{EAA}}$ fluctuations are coherent, showing stronger intercolony reproducibility of major multidecadal-scale variations (Fig. 6). In all cases, we find $\delta^{13}\text{C}_{\text{EAA}}$ agreement (typically within 1‰) between samples representing similar points in time (within ~ 5 years) from different specimens. Fluctuations in $\delta^{13}\text{C}_{\text{NEAA}}$ are less synchronized between specimens. In some cases samples representing similar time periods from different specimens show very large $\delta^{13}\text{C}_{\text{NEAA}}$ differences of 3–8‰ (Fig. 6).

In contrast with $\delta^{13}\text{C}$, mean $\delta^{15}\text{N}_{\text{THAA-AT}}$, the analogous estimate for $\delta^{15}\text{N}$ of total hydrolysable proteinaceous nitrogen, is nearly identical to

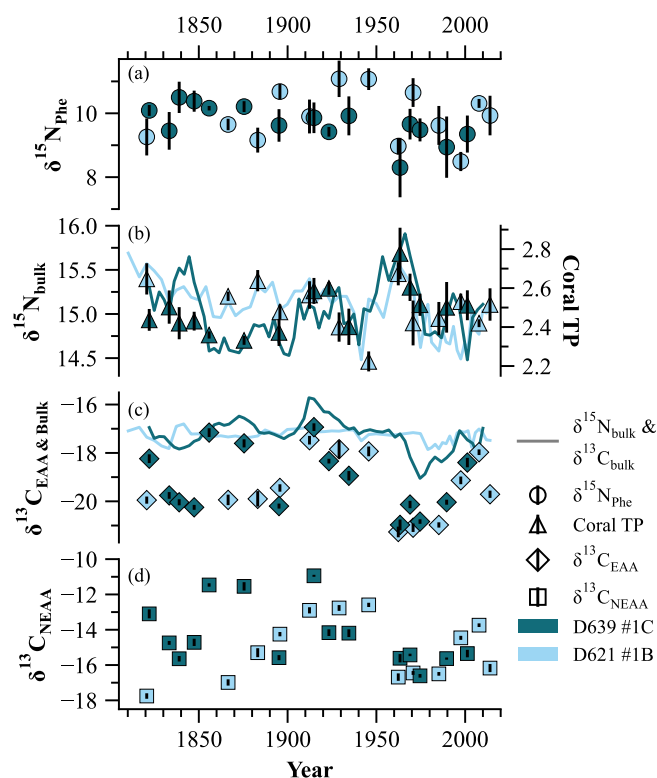


Fig. 6. Time series of (a) $\delta^{15}\text{N}_{\text{Phe}}$ (circles), (b) $\delta^{15}\text{N}_{\text{bulk}}$ (lines), Coral TP (triangles), (c) $\delta^{13}\text{C}_{\text{bulk}}$ (lines), $\delta^{13}\text{C}_{\text{EAA}}$ (diamonds) and (d) $\delta^{13}\text{C}_{\text{NEAA}}$ (squares), in Sur Ridge bamboo coral from c. 1815–2014. Blue symbols correspond with samples from specimen D621 #1B and green symbols with samples from specimen D639 #1C. Vertical bars represent analytical standard deviations from triplicate injections.

the mean $\delta^{15}\text{N}_{\text{bulk}}$ value ($15.6 \pm 0.4\%$ and $15.0 \pm 0.3\%$, respectively). All $\delta^{15}\text{N}_{\text{THAA-AT}}$ values except one fall within propagated 1σ analytical error of the 1:1 regression line with $\delta^{15}\text{N}_{\text{bulk}}$ (Fig. 5). Like $\delta^{15}\text{N}_{\text{bulk}}$, TP generally shows good intercolony reproducibility, with samples representing similar time periods from different specimens having values within the range of analytical error (Fig. 6). One notable exception occurs in our record between c. 1860–1900, when both TP and $\delta^{15}\text{N}_{\text{bulk}}$ are slightly elevated in specimen D621 #1B relative to specimen D639 #1C.

In contrast to many past studies, we find no correlation between $\delta^{15}\text{N}_{\text{phe}}$ and $\delta^{15}\text{N}_{\text{bulk}}$ ($\rho = 0.01$, $p > 0.9$), but instead a moderate positive correlation between coral trophic position (Coral TP) and $\delta^{15}\text{N}_{\text{bulk}}$ ($\rho = 0.47$, $p = 0.02$; Fig. 5). We used several multiple linear regression techniques including β coefficients, structure coefficients, and commonality analysis to better understand the respective influence of $\delta^{15}\text{N}_{\text{phe}}$ and Coral TP on $\delta^{15}\text{N}_{\text{bulk}}$. Multiple linear regression analysis with $\delta^{15}\text{N}_{\text{phe}}$ and Coral TP as predictor variables and $\delta^{15}\text{N}_{\text{bulk}}$ as the dependent variable yielded a model with $R^2 = 0.51$. β coefficients for TP and $\delta^{15}\text{N}_{\text{phe}}$ in the linear regression model, which represent the expected number of standard deviations change in $\delta^{15}\text{N}_{\text{bulk}}$ per standard deviation increase in each predictor variable, were 1.1 and 0.8, respectively. Despite its high β coefficient, the structure coefficient for $\delta^{15}\text{N}_{\text{phe}}$ was 0.0, suggesting a possible suppression effect, based on criteria described by Ray-Mukherjee et al. (2014). Commonality analysis reveals unique predictive effects of $\delta^{15}\text{N}_{\text{phe}}$ and Coral TP on $\delta^{15}\text{N}_{\text{bulk}}$ of 0.27 and 0.51 respectively, indicating that 27% of variance in $\delta^{15}\text{N}_{\text{bulk}}$ is driven by changes in $\delta^{15}\text{N}$ of primary production recorded by $\delta^{15}\text{N}_{\text{phe}}$, and 51% of variance is attributable to changes in Coral TP. The common effect for $\delta^{15}\text{N}_{\text{phe}}$ and Coral TP is -0.27 , indicating the predictive effect of $\delta^{15}\text{N}_{\text{phe}}$ on $\delta^{15}\text{N}_{\text{bulk}}$ is explained by a suppression effect arising from collinearity of Coral TP and $\delta^{15}\text{N}_{\text{phe}}$. These findings are consistent with Coral TP as the main driver of $\delta^{15}\text{N}_{\text{bulk}}$ variability.

3.7. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Relationships with Climate and Oceanographic Variables

To assess relationships between our records and documented climate and oceanographic variability, we examined Spearman correlations

(Fig. 7) of bulk and amino acid $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ proxies with three year running means of the PDO index (1900–2014), and original and detrended upwelling season SST at Hopkins Marine Station (1919–2014). For $\delta^{15}\text{N}$ variables, $\delta^{15}\text{N}_{\text{bulk}}$, $\delta^{15}\text{N}_{\text{THAA-AT}}$ and Coral TP show weak to moderate negative correlations with the PDO index, and both original and detrended upwelling season SST at Hopkins Marine Station (Fig. 7). Correlations between $\delta^{15}\text{N}_{\text{bulk}}$ and PDO ($\rho = 0.43$, $p = 0.02$), $\delta^{15}\text{N}_{\text{bulk}}$ and SST ($\rho = -0.54$, $p = 0.02$), $\delta^{15}\text{N}_{\text{THAA-AT}}$ and SST ($\rho = -0.63$, $p = 0.04$) and $\delta^{15}\text{N}_{\text{THAA-AT}}$ and detrended SST ($\rho = -0.74$, $p < 0.01$) are statistically significant using a 90% significance threshold. For $\delta^{13}\text{C}$ variables, SST is moderately negatively correlated with $\delta^{13}\text{C}_{\text{bulk}}$ ($\rho = -0.48$, $p = 0.01$), but not statistically significantly related to any amino acid $\delta^{13}\text{C}$ variables. $\delta^{13}\text{C}_{\text{THAA-AT}}$, $\delta^{13}\text{C}_{\text{EAA}}$ and $\delta^{13}\text{C}_{\text{NEAA}}$ are moderately positively correlated with the PDO index, but only the correlation with $\delta^{13}\text{C}_{\text{EAA}}$ is significant using a 90% significance threshold ($\rho = 0.46$, $p = 0.10$).

4. Discussion

4.1. Bamboo Coral Feeding Ecology and Fidelity as Living Archives

Deep-sea proteinaceous corals have sometimes been called “living sediment traps” (Sherwood et al., 2011) because they record the isotope signatures of POM from their diet; however, some questions remain about whether bamboo coral feed directly on surface-derived sinking particles. As noted above, some previous work using bulk isotopes hypothesized feeding on isotopically enriched microbially degraded particles or directly on deep-water zooplankton that feed on surface-derived particulate matter. These studies inferred multiple trophic steps based on 5–10‰ enrichment in bamboo coral $\delta^{15}\text{N}_{\text{bulk}}$ values relative to bulk sinking particles (Sherwood et al., 2008, 2009; Hill et al., 2014; Liu et al., 2023). This distinction matters when considering whether bamboo coral paleoceanographic records directly reflect changes in properties of exported surface-derived POM, or other sources of variability such as deep-sea zooplankton trophic dynamics or sediment resuspension and transport.

We addressed these questions using two approaches. First, we compared CSI-AA results from the Sur Ridge bamboo coral records and sediment trap data from Station M2 in Monterey Canyon (36.7°N , 122.4°W ; Fig. 1). The sediment trap was moored at ~ 1200 m depth, and samples were collected at two-week intervals between 1999–2004. Our findings are complementary to those described by Shen et al. (2021), who published the sediment trap data and performed a more detailed comparison to a bamboo coral specimen from Station M1 in Monterey Bay. However, we note that Sur Ridge is a similar distance offshore with a similar oceanographic regime to Station M2 and therefore may be more directly geographically comparable to M2 than the more nearshore Station M1 (Fig. 1). Second, we used the new Bayesian mixing model approach for estimating contributions from marine organic matter endmembers developed by Doherty et al. (2021). The results from both these approaches clearly indicate that bamboo corals from Sur Ridge feed directly on surface-derived exported sinking particles, which are composed primarily of zooplankton fecal pellets.

Amino acid isotope trophic position estimates from our new bamboo coral records and sediment trap samples from Station M2 are consistent with bamboo corals at Sur Ridge feeding directly on local sinking particles. The mean and range of TP in bamboo coral gorgonin is shifted up almost exactly one trophic position from outer Monterey Canyon sinking particles (Fig. 3), exactly as expected if sinking POM was the direct food source. In contrast, for $\delta^{15}\text{N}_{\text{bulk}}$ we observe a relatively large $\sim 7\%$ enrichment in bamboo coral gorgonin relative to sinking particles. This latter finding is similar to $\delta^{15}\text{N}_{\text{bulk}}$ offsets observed in past work, which led to the suggestion that bamboo corals feed on zooplankton or degraded organic matter (Sherwood et al., 2008, 2009; Hill et al., 2014; Liu et al., 2023). However, our new CSI-AA TP data seem to rule out this possibility, and therefore an explanation for discrepancies between

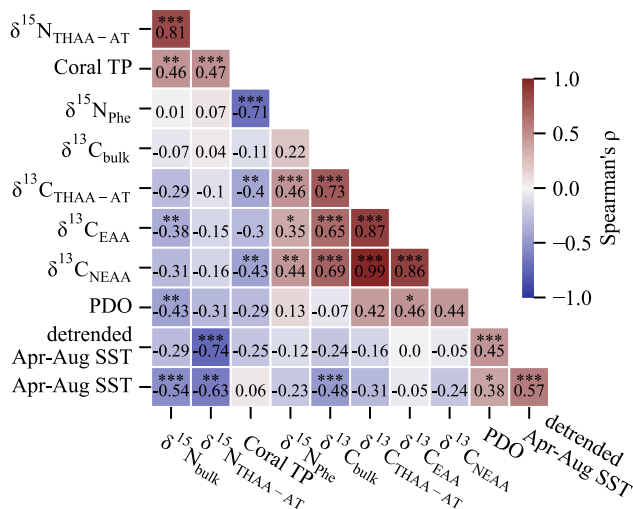


Fig. 7. Spearman rank correlation matrix including the major bulk and amino acid isotope variables considered for this study and three-year running means of the PDO index, and original and detrended upwelling season SST at Hopkins Marine Station. Statistically significant correlations at the 90%, 95% and 99% levels are noted with asterisks: * $p \leq 0.1$, ** $p \leq 0.05$, *** $p \leq 0.01$. We used a numerical approach to account for timeseries autocorrelation in probability estimation (described in Section 2.6).

trophic position estimates from $\delta^{15}\text{N}_{\text{bulk}}$ and CSI-AA is needed.

We hypothesize that discrepancies between deep-sea coral trophic position estimates from bulk and compound-specific nitrogen isotope approaches likely result from selective assimilation of the relatively bioavailable hydrolysable amino acid fraction from particulate organic nitrogen. In support of this explanation, both $\delta^{15}\text{N}_{\text{bulk}}$ and $\delta^{15}\text{N}_{\text{THAA-AT}}$ of gorgonin are elevated by $\sim 4\%$ relative to $\delta^{15}\text{N}_{\text{THAA-AT}}$ in sinking particles, consistent with the canonical $3.4 \pm 1.1\%$ $\delta^{15}\text{N}_{\text{bulk}}$ trophic enrichment factor first proposed by Minagawa & Wada (1984; Fig. S5). Sinking particulate organic nitrogen is a heterogeneous mixture comprised of $\sim 15\text{--}60\%$ hydrolysable amino acids, mixed with variable proportions of other organic nitrogen compounds, a large proportion of which are uncharacterized (Gupta and Kawahata, 2000; Ingalls et al., 2003; Shen et al., 2023). Amino acids are among the most labile of all organic nitrogen forms, with hydrolysable yields decreasing dramatically with degradation across multiple types of marine organic matter (Cowie and Hedges, 1994). THAA represents the most bioavailable amino acids, and is widely considered an indicator for overall lability of organic matter (Cowie and Hedges, 1994; Benner and Amon, 2015). Selective assimilation of nitrogen from bioavailable hydrolysable amino acids would therefore be expected, and could explain $\delta^{15}\text{N}_{\text{bulk}}$ values that appear approximately one trophic step above $\delta^{15}\text{N}_{\text{THAA-AT}}$ in sinking particles. Additionally, routing of nitrogen directly from dietary hydrolysable amino acids into the proteinaceous gorgonin skeleton may also play a role. Based on these considerations, and the potentially highly misleading TP estimates that are possible from bulk $\delta^{15}\text{N}$ data, we suggest that the amino acid trophic position proxy is likely a more accurate and robust indicator of deep-sea coral trophic ecology than $\delta^{15}\text{N}_{\text{bulk}}$. More broadly, we suggest caution should always be applied when inferring trophic relationships via direct comparison of $\delta^{15}\text{N}_{\text{bulk}}$ in animal tissues to complex heterogeneous mixtures like particulate organic nitrogen.

The second line of evidence that bamboo coral from Sur Ridge feed directly on sinking particles is Bayesian endmember-mixing analysis based on amino acid $\delta^{15}\text{N}$ patterns in gorgonin (Fig. 4). Zooplankton fecal pellets likely comprise a majority of bamboo coral diet, based on high median posterior estimates for fecal pellet dietary contributions (71% using all four endmembers, 81% if the microbially degraded endmember is excluded from analysis). It is important to note that although our data cannot rule out the possibility of selective feeding on zooplankton fecal pellets, the amino acid $\delta^{15}\text{N}$ data provides no direct evidence indicating selectivity. Previous work identified fecal pellets as a major component of sinking particulate flux, and one of the primary vehicles for export of fresh organic matter to depth in the northeast Pacific and California margin (Pilska et al., 1996; Wilson et al., 2013; Dagg et al., 2014; Morrow et al., 2018; Wojtal et al., 2023). Notably, our estimates of fecal pellet contributions to bamboo coral diet are very similar to recent estimates for fecal pellets contributions to sediment traps from the Northeast Pacific ($\sim 70\text{--}90\%$; Wojtal et al., 2023). Together with the trophic position results discussed above, our findings suggest bamboo coral likely feed directly on large sinking particles, which are primarily composed of zooplankton fecal pellets.

We cannot rule out microbially degraded organic matter as a potential additional component of bamboo coral diet based on endmember mixing analysis alone (median estimate = 9%, 90% Bayesian credible interval = 1–54% using all four endmembers). Importantly, we note that a minor dietary contribution from microbial organic matter is not inherently inconsistent with feeding on recently exported sinking particles, based on recent findings by Shen et al. (2023), who showed that deep sinking POM from Station M2 contains a non-negligible detrital bacterial organic nitrogen component. Previous work based on AA fingerprinting with deep-sea coral and bivalves also demonstrated that heterotrophic bacteria can have small but non-negligible contributions to filter feeder dietary organic matter (Vokshoori et al., 2022; McMahon et al., 2015). The low ΣV values in our bamboo coral samples ($<2\%$) are consistent with the low median posterior estimate for the

microbially degraded endmember, suggesting that a major contribution from highly degraded, microbially resynthesized organic matter sources is unlikely (McCarthy et al., 2007). Further, the modern ^{14}C signatures observed in our coral specimens and previous studies of proteinaceous coral (Roark et al., 2005; Sherwood et al., 2009; Hill et al., 2014) definitively rule out a major dietary component specifically from highly degraded, ^{14}C depleted organic matter sources like the mesopelagic DOM and UPOM endmembers.

Finally, the agreement of primary production “baseline” isotope proxies ($\delta^{15}\text{N}_{\text{phe}}$ and $\delta^{13}\text{C}_{\text{EAA}}$) between our new bamboo coral records and sinking particles from Station M2 lends support for bamboo coral gorgonin as a high-fidelity archive for export production. The near-identical $\delta^{15}\text{N}_{\text{phe}}$ ranges observed in the coral and sediment trap datasets validate it as an excellent proxy for $\delta^{15}\text{N}$ of primary production, minimally altered by the effects of trophic transfer (Fig. 3). Similarly, $\delta^{13}\text{C}$ ranges for individual essential amino acids (which are synthesized only by primary producers) are highly overlapping with ranges observed in sinking particles. The mean and range for $\delta^{13}\text{C}_{\text{EAA}}$, a proxy for $\delta^{13}\text{C}$ of phytoplankton production, is nearly identical in sinking particles and gorgonin (Fig. 3). By comparison, Shen et al. (2021) found a slightly higher $\delta^{13}\text{C}_{\text{EAA}}$ offset of $\sim 2\%$ in bamboo coral collected near Station M1, a site closer to shore, relative to the same sinking particle samples. This is not surprising, as $\delta^{13}\text{C}$ values are typically higher in productive coastal environments and lower offshore in oligotrophic environments, as previously observed in krill from Monterey Bay, deep-sea coral collected on the California margin and northern California Current zooplankton and POM (Miller et al., 2008, 2010; Hill et al., 2014; Bernstein et al., 2021). Closer $\delta^{13}\text{C}_{\text{EAA}}$ agreement between sediment trap samples from Station M2 and our Sur Ridge coral specimens (relative to coral specimens from the more nearshore Station M1) is therefore consistent with expectations, and further validates $\delta^{13}\text{C}_{\text{EAA}}$ as a proxy for $\delta^{13}\text{C}$ of primary production.

Together, comparison to nearby sediment trap samples and end-member mixing model results validate bamboo coral gorgonin as an archive of surface ocean biogeochemical and food web processes on the central California margin. Strong agreement between sediment trap and coral samples suggests $\delta^{15}\text{N}_{\text{phe}}$ and $\delta^{13}\text{C}_{\text{EAA}}$ signals recorded in bamboo coral paleoarchives derive from export production. Our trophic ecology analyses indicate bamboo coral likely feed directly on exported sinking particles, based on Coral TP estimates shifted up one trophic position relative to local sediment trap samples (Shen et al., 2021) and similar estimates for fecal pellet contributions to coral diet and large sinking particles (Wojtal et al., 2023). We also find no support for feeding primarily on isotopically enriched deep-sea zooplankton or highly degraded resuspended organic matter. One caveat is that the coral data reflect a longer time scale that only overlaps partially with the sediment trap time series. Further, each gorgonin sample integrates over multiple years of bamboo coral growth, whereas the sediment trap samples capture higher-frequency variability. However, the Bayesian endmember mixing model approach also tells the same story as the sediment trap comparison, increasing confidence in these interpretations.

4.2. Potential issues with $\delta^{13}\text{C}_{\text{bulk}}$ as a proxy for $\delta^{13}\text{C}$ of export production

Our results imply that deep-sea coral $\delta^{13}\text{C}_{\text{bulk}}$ records may not accurately reflect variability in $\delta^{13}\text{C}$ of export production. As expected, $\delta^{13}\text{C}$ of primary production is a major driver of gorgonin $\delta^{13}\text{C}_{\text{bulk}}$ in our record, based on the strong positive correlation of $\delta^{13}\text{C}_{\text{bulk}}$ with $\delta^{13}\text{C}_{\text{EAA}}$, a proxy for $\delta^{13}\text{C}$ of phytoplankton production (Fig. 5). However, fairly large discrepancies in reproducibility and the magnitude of variability in $\delta^{13}\text{C}_{\text{bulk}}$ compared to $\delta^{13}\text{C}_{\text{EAA}}$ raise questions about the validity of $\delta^{13}\text{C}_{\text{bulk}}$ as a proxy for $\delta^{13}\text{C}$ of primary production. Discrepancies between $\delta^{13}\text{C}_{\text{bulk}}$ and CSI-AA proxies include a $1.4 \pm 1.3\%$ mean enrichment in $\delta^{13}\text{C}_{\text{THAA-AT}}$ relative to $\delta^{13}\text{C}_{\text{bulk}}$, and strongly attenuated variability in $\delta^{13}\text{C}_{\text{bulk}}$ relative to $\delta^{13}\text{C}_{\text{THAA-AT}}$, $\delta^{13}\text{C}_{\text{NEAA}}$ and $\delta^{13}\text{C}_{\text{EAA}}$

(Fig. 3; Fig. 6). Previous work on bamboo coral from the California margin and proteinaceous gold coral from Hawaii similarly reported dramatically attenuated variability in $\delta^{13}\text{C}_{\text{bulk}}$ relative to $\delta^{13}\text{C}_{\text{EAA}}$ (Schiff et al., 2014; McMahon et al., 2015). Finally, we find strong intercolony reproducibility of $\delta^{13}\text{C}_{\text{EAA}}$, but only moderate intercolony reproducibility of $\delta^{13}\text{C}_{\text{bulk}}$.

Our findings concur with past work which proposed that $\delta^{13}\text{C}_{\text{EAA}}$ is more accurate than $\delta^{13}\text{C}_{\text{bulk}}$ as a proxy for $\delta^{13}\text{C}$ of primary production (Schiff et al., 2014; McMahon et al., 2015, 2018). Strong intercolony reproducibility of $\delta^{13}\text{C}_{\text{EAA}}$ is consistent with expectations if $\delta^{13}\text{C}$ of the essential amino acids derive uniquely from phytoplankton primary production, unaltered by intercolony differences in skeletal composition, diet quality or physiology. The strong observed agreement between our two co-located records (Fig. 6) therefore provides validation that gorgonin $\delta^{13}\text{C}_{\text{EAA}}$ is likely an accurate proxy for $\delta^{13}\text{C}_{\text{EAA}}$ of export production. These findings together with past work showing a strong linear relationship between $\delta^{13}\text{C}_{\text{EAA}}$ and $\delta^{13}\text{C}_{\text{bulk}}$ in sinking particles from Monterey Bay (Shen et al. 2021) suggest that $\delta^{13}\text{C}_{\text{EAA}}$ likely reflects the true range of variability in primary producer $\delta^{13}\text{C}$ better than $\delta^{13}\text{C}_{\text{bulk}}$. In our records, both the magnitude and timing of major fluctuations differ between $\delta^{13}\text{C}_{\text{EAA}}$ and $\delta^{13}\text{C}_{\text{bulk}}$ (Fig. 7). This implies that relying solely on interpretation of $\delta^{13}\text{C}_{\text{bulk}}$ could therefore result in incorrect inferences about past shifts in $\delta^{13}\text{C}$ of primary production.

Overall, we suggest caution should be applied when interpreting $\delta^{13}\text{C}_{\text{bulk}}$ records from deep-sea coral archives, without access to additional information from CSI-AA data. Further work is needed to fully characterize gorgonin composition and understand drivers of $\delta^{13}\text{C}_{\text{bulk}}$ variability. Understanding underlying drivers of discrepancies between $\delta^{13}\text{C}_{\text{bulk}}$ and amino acid $\delta^{13}\text{C}$ proxies is important for robust interpretation of $\delta^{13}\text{C}_{\text{bulk}}$ records. While the data presented here cannot indicate any single explanation, a more detailed discussion of the three types of discrepancy observed in our records (the absolute value offset between $\delta^{13}\text{C}_{\text{THAA-AT}}$ and $\delta^{13}\text{C}_{\text{bulk}}$, strongly attenuated variability in $\delta^{13}\text{C}_{\text{bulk}}$ relative to amino acid proxies, and reduced intercolony reproducibility of $\delta^{13}\text{C}_{\text{bulk}}$ relative to $\delta^{13}\text{C}_{\text{EAA}}$) is included in the [Supplementary Material](#).

4.3. Drivers of coral skeletal $\delta^{15}\text{N}_{\text{bulk}}$ variability

One major finding of this work is that Coral TP, not “baseline” $\delta^{15}\text{N}$ of primary production, is the primary driver of $\delta^{15}\text{N}_{\text{bulk}}$ variability in bamboo coral archives from Sur Ridge. This interpretation is confirmed by the results of correlation and commonality analysis. TP is positively correlated with $\delta^{15}\text{N}_{\text{bulk}}$ (Fig. 5), and commonality analysis reveals that TP uniquely predicts 51% of variability in $\delta^{15}\text{N}_{\text{bulk}}$. In contrast, $\delta^{15}\text{N}_{\text{Phe}}$ is uncorrelated with $\delta^{15}\text{N}_{\text{bulk}}$, and in commonality analysis was found to explain just 27% of variance in $\delta^{15}\text{N}_{\text{bulk}}$, and only via the suppression effect caused by a negative correlation between Coral TP and $\delta^{15}\text{N}_{\text{Phe}}$. The potential influence of TP on $\delta^{15}\text{N}_{\text{bulk}}$ is often invoked as an important motivation for applying CSI-AA to paleoarchives, since $\delta^{15}\text{N}_{\text{bulk}}$ integrates signals from both baseline and trophic processes (Sherwood et al., 2011, 2014; Batista et al., 2014). However, previous work in deep-sea coral archives largely found that $\delta^{15}\text{N}$ of source amino acids is the strongest predictor of $\delta^{15}\text{N}_{\text{bulk}}$ (Sherwood et al., 2014; Shen et al., 2021; Guilderson et al., 2024), consistent with common usage of $\delta^{15}\text{N}_{\text{bulk}}$ in paleoarchives to reconstruct “baseline” fluctuations (i.e., changes in $\delta^{15}\text{N}$ of the nitrate supply or primary production). Our finding that $\delta^{15}\text{N}_{\text{bulk}}$ is driven primarily by Coral TP at Sur Ridge is the first direct demonstration that ecosystem structure changes, not baseline $\delta^{15}\text{N}$ values, may drive $\delta^{15}\text{N}_{\text{bulk}}$ in some deep-sea coral records. This finding likely extends to other paleoarchives from some regions; for example, Batista et al. (2014) similarly suggested that TP may influence $\delta^{15}\text{N}_{\text{bulk}}$ in sediments, based on work in the well-preserved Santa Barbara Basin sedimentary record.

Together, these results suggest caution may be required when interpreting $\delta^{15}\text{N}_{\text{bulk}}$ from paleoarchives, as the trophic structure of the

planktic food web may play an underappreciated but central role in some regions. In some cases, $\delta^{15}\text{N}_{\text{bulk}}$ clearly reflects baseline $\delta^{15}\text{N}$ of phytoplankton exported from the euphotic zone, as is very often assumed (Sherwood et al., 2011, 2014; Guilderson et al., 2024). However, the Sur Ridge data clearly shows that $\delta^{15}\text{N}_{\text{bulk}}$ can also be driven primarily by changes in planktic ecosystem trophic structure. It is important to stress that it is not possible to determine which process is most important from $\delta^{15}\text{N}_{\text{bulk}}$ alone, so additional information from TP and source amino acid proxies is needed for high-confidence interpretation of deep-sea coral records. Similar basic considerations likely apply to at least some well-preserved sedimentary $\delta^{15}\text{N}_{\text{bulk}}$ records as well, despite the fact that interpretation of such trends in sediments could be complicated by the far more complex matrix, and the influence of resuspension and microbial alteration (Batista et al., 2014; Choi et al., 2022; Golombek et al., 2024).

Finally, it is not immediately clear why a relationship between TP and $\delta^{15}\text{N}_{\text{bulk}}$ is observed at our study site on the Big Sur Coast, but not in other coral records. One possibility is that the relationship at Sur Ridge may be attributable to incomplete utilization of inorganic nitrogen sources due to iron-limitation of primary productivity or spatial decoupling of new and export production (Plattner et al., 2005; Walker and McCarthy, 2012; Biller et al., 2013). When dissolved inorganic nitrogen utilization is incomplete, typical mass-balance assumptions dictating that $\delta^{15}\text{N}$ of upwelled nitrate must equal $\delta^{15}\text{N}$ of sinking particles are violated. Therefore, under conditions of incomplete nitrogen utilization, other factors besides $\delta^{15}\text{N}$ of the nitrate supply, like degree of nutrient utilization (Altabet and Francois, 1994) and trophic structure

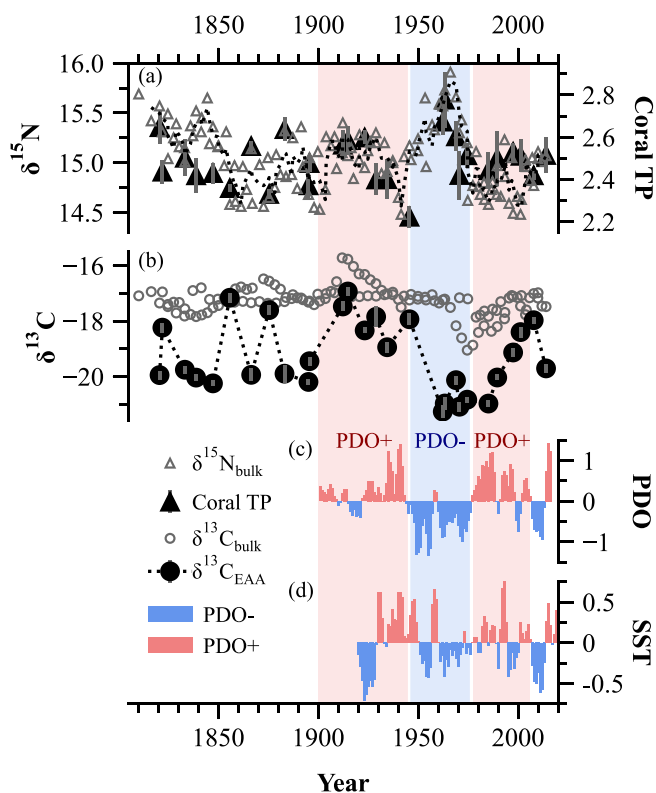


Fig. 8. Bamboo coral isotope records in relation to historical basin-scale climate and local oceanographic variability. (a) $\delta^{15}\text{N}$ of bulk coral skeleton (open grey triangles) and Coral TP (black triangles), (b) $\delta^{13}\text{C}$ of bulk coral skeleton (open grey circles) and $\delta^{13}\text{C}_{\text{EAA}}$ (black circles and dotted line), (c) 3-year running mean Pacific Decadal Oscillation Index, and (d) detrended 3-year running mean sea surface temperature at Hopkins Marine Station. Red (blue) shaded areas represent multidecadal periods when the PDO index was predominantly positive (negative).

variation may exert an influence on $\delta^{15}\text{N}$ of exported sinking particles. While there is conclusive literature establishing the importance of nutrient utilization in such environments (Altabet and Francois, 1994, 2001), the potential influence of ecosystem trophic structure on $\delta^{15}\text{N}$ of exported organic matter has not been extensively investigated. We suggest future CSI-AA work in paleoarchives should continue examining the prevalence of trophic effects on $\delta^{15}\text{N}_{\text{bulk}}$, and identify mechanisms that determine whether variations in $\delta^{15}\text{N}$ of primary production or trophic dynamics are more important for driving $\delta^{15}\text{N}_{\text{bulk}}$ in different types of marine ecosystems.

4.4. Climate-Driven Plankton Ecosystem Change

One primary aim of this work was to examine the influence of centennial to multidecadal-scale climate variability on “baseline” $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of primary production and planktic ecosystem trophic structure on the California margin. The Sur Ridge bulk and compound-specific $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ records contain a series of multidecadal-scale fluctuations in ecosystem trophic structure and $\delta^{13}\text{C}$ of primary productivity, but no apparent long-term trends or systematic shifts since onset of the industrial era (Fig. 8). These results suggest overall long-term planktic ecosystem stability despite significant anthropogenic warming and environmental change over the past century. This finding is consistent with previous work in the California Current System that found resilience of pelagic ecosystem structure on the California margin to environmental perturbations (Rebstock, 2003; Ohman et al., 2012; Lindegren et al., 2016).

It is no surprise that bamboo coral archives from the central California margin record decadal-scale fluctuations in plankton trophic dynamics and $\delta^{13}\text{C}$ of primary production. In the California Current, negative phases of the PDO (PDO-) are associated with stronger southward transport of subarctic waters, cooler temperatures, higher nutrient concentrations and greater nearshore upwelling intensity than positive phases of the PDO (PDO+; Macias et al. 2012; Di Lorenzo et al. 2013; Jacox et al. 2014). Planktic ecosystems are sensitive to these environmental perturbations. Increased nutrient availability is generally associated with higher primary productivity and shorter planktic food webs with lower average trophic positions (Chavez et al., 2011; Décima et al., 2013). Low trophic position values in sinking fecal pellets may also co-occur with high productivity due to low digestion efficiency of zooplankton grazers when prey availability is high (Doherty et al., 2021). $\delta^{13}\text{C}$ of primary production, as indicated by $\delta^{13}\text{C}_{\text{EAA}}$, is also responsive to climate-driven shifts in phytoplankton ecology because light-limited, large-celled, fast-growing phytoplankton are typically $\delta^{13}\text{C}$ enriched relative to nutrient-limited, small-celled, slow-growing taxa (Pancost et al., 1997; Popp et al., 1998; Rau et al., 2001; Woodworth et al., 2004; Wilkes and Pearson, 2019). The result is higher organic matter $\delta^{13}\text{C}$ values in productive coastal environments and lower $\delta^{13}\text{C}$ values offshore in less productive environments, as mentioned previously in Section 4.1 (Miller et al., 2008, 2010; El-Sabaawi et al., 2012; Hill et al., 2014; Bernstein et al., 2021). Based on this framework, we initially expected to find higher $\delta^{13}\text{C}_{\text{EAA}}$ and lower Coral TP values during past PDO- conditions and periods of increased upwelling, consistent with increased phytoplankton productivity due to increased macronutrient availability.

Surprisingly, the correlations of PDO to $\delta^{15}\text{N}_{\text{bulk}}$, Coral TP and $\delta^{13}\text{C}_{\text{EAA}}$ we find in the Sur Ridge bamboo coral records are largely the opposite of expectations, indicating higher TP of sinking particles and lower $\delta^{13}\text{C}$ of primary production occurred during PDO- phases (Fig. 7; Fig. 8). Higher TP and $\delta^{15}\text{N}_{\text{bulk}}$ values also occurred during periods of low detrended sea surface temperatures, which correspond with intensified coastal upwelling. Lower $\delta^{13}\text{C}$ values likely reflect a shift to a slower-growing, less productive plankton ecosystem at Sur Ridge during PDO- phases. Higher TP values suggest a longer, more complex planktic food web developed during past PDO- conditions. These TP findings are broadly consistent with the findings of Rau et al. (2003), who found

increased $\delta^{15}\text{N}_{\text{bulk}}$ in specimens of the copepod *Eucalanus californicus* collected offshore of Monterey Bay during PDO- conditions (Rau et al., 2003), although this past work was unable to distinguish the effects of trophic dynamics from baseline $\delta^{15}\text{N}$ variability. Based on the TP and $\delta^{13}\text{C}_{\text{EAA}}$ results, lower primary productivity may occur in our study region on the nearshore central California coast during PDO- periods characterized by enhanced macronutrient availability and upwelling. Typically, upwelling of macronutrients is assumed to drive high productivity in eastern boundary currents, but another explanation is needed to explain our results.

Our findings align with a growing body of evidence that although coastal upwelling of macronutrients enhances the productivity of eastern boundary upwelling systems relative to other regions of the world oceans, factors besides upwelling-driven macronutrient supply are also important drivers of temporal variability (Gruber et al., 2011; Messié and Chavez, 2015). Our data cannot conclusively explain the mechanisms linking the PDO to decadal-scale ecosystem variability, but we will explore two possible explanations: (1) Climate-driven changes in fluvial sediment discharge on the central California coast may regulate iron availability, and/or (2) Climate-driven changes in the intensity of eddies and currents may influence offshore transport and subduction of nutrients and phytoplankton biomass. Messié and Chavez (2015) found that both iron limitation and subduction/offshore transport regulate seasonal patterns of primary productivity on the central California margin, and we hypothesize that one or both processes may also operate on interannual to decadal scales.

We suggest a precipitation-mediated link between iron supply and the PDO could explain the observed TP and $\delta^{13}\text{C}$ fluctuations at Sur Ridge from our records. Trace metal limitation due to narrow continental shelf width and low river discharge on the Big Sur Coast results in relatively low primary productivity despite persistent year-round high surface nitrate and ammonium concentrations (Hutchins et al., 1998; Chase et al., 2007; Walker and McCarthy, 2012; Biller et al., 2013). Variability in nitrate availability is therefore likely not the dominant control on ecosystem structure and productivity on this portion of the central California coast (Messié and Chavez, 2015). Experimental iron addition results in substantial macronutrient drawdown, increasing primary productivity and favoring community shifts towards fast-growing large diatoms (Hutchins et al., 1998). In central California, surface concentrations of bioavailable iron are largely controlled by annual spring upwelling of particulate iron from a fine-grained sedimentary “fluff” bottom boundary layer on the continental shelf. This boundary layer is replenished by fluvial sediments during episodes of high river discharge in winter and depleted by upwelling (Elrod et al., 2008). During PDO+ and El Niño conditions, which commonly co-occur, storm track trajectories shift, increasing the frequency and intensity of rainfall events in coastal central California (Guirguis et al., 2019; Cheng et al., 2021). Suspended sediment discharge to the continental shelf from the Salinas River, the main source of fluvial sediment to the central California coast, is tenfold higher during El Niño years than neutral or La Niña years (Farnsworth and Milliman, 2003; Gray et al., 2015), likely increasing the supply of bioavailable particulate iron upwelled during spring and summer. Consequently, the low TP values and higher $\delta^{13}\text{C}_{\text{EAA}}$ values we observe during PDO+ conditions may reflect increased primary productivity due to precipitation-mediated amelioration of iron limitation.

Subduction or offshore transport of nutrients and phytoplankton may also suppress nearshore phytoplankton production on the central California coast during PDO- phases. Physical circulation processes can affect phytoplankton production in several ways. Strong offshore Ekman transport reduces the residence time of water masses in the nearshore region, potentially reducing nearshore primary production by transporting phytoplankton offshore before they can fully utilize available nutrients (Messié and Chavez, 2015). Eddy-driven subduction of upwelled nutrients and particles below the euphotic zone along isopycnal surfaces can also significantly dampen primary production. This effect is

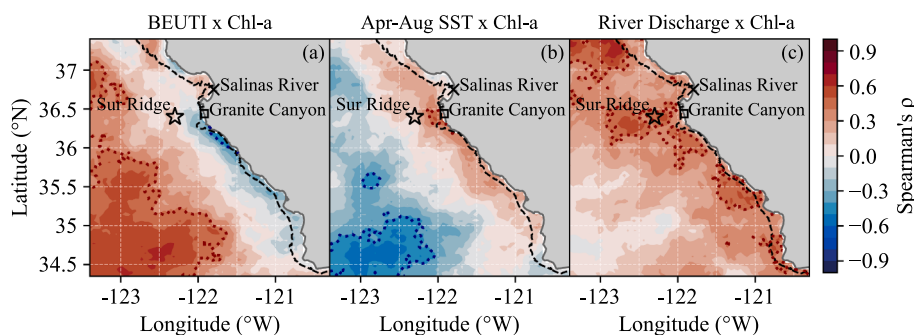


Fig. 9. Spearman rank correlations between mean annual satellite chlorophyll-*a* from the Copernicus Marine Environment Monitoring Service GlobColour monthly data product and (a) annual mean BEUTI between 35 and 37°N, an index for nitrate upwelled to the mixed layer depth, (b) mean sea surface temperature at Granite Canyon during the April–August upwelling season and (c) Salinas River mean water year discharge. Areas with statistically significant positive (negative) correlations are outlined with red (blue) dotted lines.

especially pronounced in nearshore regions of eastern-boundary current systems, where isopycnals slope steeply upwards towards the coastline during coastal upwelling (Gruber et al., 2011; Renault et al., 2016; Kessouri et al., 2020). Currently, this is an ongoing area of research and only limited information is available about interannual to interdecadal variability in submesoscale and mesoscale mixing on the central California coast. However, Giddings et al. (2022) found evidence for strengthened mesoscale activity and offshore transport in the California Current System during PDO- phases and La Niña conditions. While we acknowledge that this hypothesis is somewhat speculative, evidence in our proxy records for a less productive planktic ecosystem at Sur Ridge during PDO- phases may be attributable to enhanced eddy-driven subduction and offshore transport of nutrients and phytoplankton, suppressing nearshore productivity. Finally, we also note that our iron supply and offshore transport/subduction hypotheses are also not mutually exclusive.

4.5. Modern observations corroborate deep-sea coral isotope records

The modern satellite chlorophyll-*a* record provides independent corroboration of the findings from our Sur Ridge bamboo coral records. We examined Spearman correlations of interannual mean satellite chlorophyll-*a* variability with Salinas River discharge, sea surface temperatures and a nutrient upwelling index over the past two decades (Fig. 9). Within approximately 60 km from shore on the Big Sur Coast, Chl-*a* is negatively or very weakly correlated with BEUTI, an index for the quantity of NO_3^- upwelled to the mixed layer depth (Jacox et al., 2018). Further offshore, correlations between Chl-*a* and BEUTI are positive. We also find a positive correlation in the nearshore region between Chl-*a* and sea surface temperature at Granite Canyon, a shore station near the upwelling center at Point Sur. These correlations suggest an inverse relationship exists between interannual upwelling-driven macronutrient availability and phytoplankton biomass along the Big Sur Coast, in agreement with our bamboo coral isotope records. Decoupling of primary production from upwelled nitrate is consistent with expectations if other factors besides macronutrient availability drive interannual variability.

Although the correlations of BEUTI and SST to satellite Chl-*a* are relatively weak at our specific study site (Fig. 9), we expect that sinking POM supplied to the benthic community at Sur Ridge likely originates in the nearshore Big Sur Coast region rather than in the surface ocean directly overlying Sur Ridge. The prevailing current direction in the overlying water column is strongly offshore towards the west-northwest (Collins et al., 2000). We performed a rough calculation to generally estimate where particles reaching the coral at our study site may originate. Assuming a sinking velocity of 100 m/day, based on work by Dagg et al. (2014) in the Monterey Bay and Point Sur regions that estimated sinking velocities for large zooplankton fecal pellets on the order of

50–250 m/day, it would take around 12 days for fecal pellets to reach 1200 m depth, where the coral specimens were collected. Assuming a horizontal velocity of approximately 3.5 km per day (Collins et al., 2000), this corresponds to approximately 40 km of horizontal transport. Considering the location of our study site approximately 35 km offshore of Point Sur and prevailing current direction towards the west-northwest (Collins et al., 2000), this estimate indicates a likely origin for coral dietary organic matter in the nearshore region of the Big Sur Coast.

The relationships of satellite Chl-*a* to river discharge and BEUTI provide tentative support for iron availability and/or physical mixing processes as drivers of ecosystem dynamics in our study region. Over broad areas of the Big Sur Coast extending out to approximately 100 km offshore, we find positive correlations between Salinas River discharge and annual mean Chl-*a* (Fig. 9). This suggests a link between primary production and fluvial sedimentary iron discharge is plausible. While we did not examine a direct proxy for physical mixing, the onshore-offshore dipole we observe in correlations of BEUTI and SST to Chl-*a* points toward the possible influence of offshore nutrient advection during physical mixing. Submesoscale to mesoscale mixing suppresses nearshore production while simultaneously enhancing offshore production via cross-shelf transport of nutrients and particles (Gruber et al., 2011; Kessouri et al., 2020). Although this simple correlation analysis certainly has limitations, our findings support the feasibility of the two mechanisms we proposed to explain the link between PDO and isotopic variations in our records.

4.6. Broader implications for ecosystem change in eastern boundary current regions

Our findings have a number of broader implications, which will be important for future work focused on biogeochemical dynamics in eastern boundary current upwelling ecosystems. Whatever the ultimate driving mechanism(s), our finding that interannual to multidecadal planktic ecosystem variability is inversely related to or decoupled from upwelling on portions of the nearshore California margin has several important consequences. First, recognition that upwelling-driven nutrient supply is not the only potential driver of ecosystem change in eastern boundary upwelling systems is important for both paleoceanography and projections of future change due to anthropogenic climate change. Without ancillary information about 20th century ocean climate, we might have incorrectly interpreted increases in Coral TP and lower values of $\delta^{13}\text{C}_{\text{EAA}}$ in our record as evidence of reduced upwelling or positive phases of the PDO, when in fact the opposite appears to be true. This result therefore underscores that interpretation of paleoceanographic records from complex and spatially heterogeneous eastern boundary current upwelling ecosystems requires careful consideration of modern oceanographic dynamics at a given study site. In terms of predicting future ecosystem change, our results imply that ecosystem

projections based solely on upwelling or macronutrient supply may be incomplete both in the California System and eastern boundary current systems more broadly (Messié and Chavez, 2015). Other factors including iron limitation, cross-shelf transport and intensity of meso-scale to submesoscale mixing may be as or more important than macronutrient supply in some locations. We suggest that detailed understanding of links between climate, precipitation, iron supply, physical mixing processes and plankton ecosystem dynamics will be crucial for predicting future change in the California Current and other eastern-boundary current ecosystems.

5. Synthesis and Conclusions

Our new findings advance understanding of proteinaceous deep-sea coral as paleoceanographic archives, with important implications for future work both in the California Current System and globally. First, our analysis of bamboo coral trophic ecology confirms that bamboo coral feed directly on exported sinking particles, with a single trophic position enrichment relative to local sediment trap samples. This finding validates that bamboo coral, which have a widespread distribution on ocean margins globally (Li and Wang, 2019), can provide valuable high-fidelity archives of euphotic zone plankton ecosystem change through time. Notably, this finding based on CSI-AA approaches contrasts with some past work based only on bulk $\delta^{15}\text{N}$ values, which called into question the direct link to export production. This finding highlights potential pitfalls for trophic position estimation in food webs based on complex detrital mixtures where the molecular identity, bioavailability and isotopic composition of major organic matter fractions is unknown. We therefore suggest that amino acid-based approaches are likely more appropriate for trophic position estimation in proteinaceous corals. These findings may also be significant for trophic position estimation in other suspension or deposit feeding organisms such as sponges and bivalves that also feed on complex mixtures of detrital organic matter.

Our results also demonstrate that amino acid isotope proxies like Coral TP, $\delta^{15}\text{N}_{\text{Phe}}$ and $\delta^{13}\text{C}_{\text{EAA}}$ can provide key additional information required for accurate interpretation of bulk $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. In particular, our record provides the first direct demonstration that bulk $\delta^{15}\text{N}$ in deep-sea coral skeletal records from some ocean regions is driven predominantly by shifts in the trophic structure of the overlying plankton community, not by shifts in $\delta^{15}\text{N}$ of nitrate or primary production. One major implication of this finding is that trophic position may play a currently underrecognized role in driving $\delta^{15}\text{N}$ of proteinaceous coral and potentially other paleoarchives from some regions, and should be considered during interpretation of $\delta^{15}\text{N}_{\text{bulk}}$ records. Finally, comparison of bulk bamboo coral $\delta^{13}\text{C}$ to amino acid isotope proxies reveals several additional limitations of bulk isotope records for reconstructing biogeochemical change. In particular, reduced intercolony reproducibility and dramatically dampened variability in $\delta^{13}\text{C}_{\text{bulk}}$ of skeletal protein relative to $\delta^{13}\text{C}_{\text{EAA}}$, a proxy for “baseline” $\delta^{13}\text{C}$ of primary production, suggests the need for cautious interpretation of $\delta^{13}\text{C}_{\text{bulk}}$ in proteinaceous coral records.

In terms of oceanographic processes, our results also provide new insight into the response of planktic ecosystem dynamics in a globally significant upwelling system to centennial and decadal-scale climate forcing. Our reconstruction of sinking particle trophic position and $\delta^{13}\text{C}$ of primary production shows overall long-term ecosystem stability on the central California margin since c. 1810, punctuated by multidecadal fluctuations linked to the PDO. This long-term stability in the face of intensifying anthropogenic change over the 20th century indicates resilience to environmental perturbation. Our findings are consistent with past work suggesting eastern boundary current upwelling ecosystems may be especially resilient to climate changes due to high naturally-occurring environmental variability (Rebstock, 2003; Ohman et al., 2012; García-Reyes et al., 2015; Lindegren et al., 2016). Perhaps our most surprising finding, $\delta^{13}\text{C}_{\text{EAA}}$ and trophic position proxies indicate phytoplankton productivity was likely higher and the planktic food

web was shorter/less complex at our study site during positive phases of the PDO over the 20th century. This result indicates an unexpected negative correlation between primary production and upwelling-driven macronutrient supply in this region. Modern satellite Chl-a observations for the Big Sur Coast corroborate this conclusion. We hypothesize that shifts in iron supply from fluvial sediments and/or subduction and offshore transport of nutrients due to physical mixing may be linked to the PDO, explaining our results. This finding has important implications for understanding paleoceanographic records from dynamic upwelling margin regions, indicating that the direct coupling often assumed between upwelled nutrients and primary production must be examined more closely, and that site-specific modern observations can provide useful context for interpretations.

Data availability

All new data generated for this work are publicly available through the NOAA NCEI Paleoclimatology archive (<https://doi.org/10.25921/6m4e-n944>). All datasets and code required to reproduce the data analyses and generate the main text and supplementary figures in Python and R are publicly available through a GitHub repository (<https://github.com/evepug/SurRidgeBambooCoral>), and archived using Zenodo (<https://doi.org/10.5281/zenodo.13743543>).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

The supplementary material file contains all Supplemental Tables and Figures (Table S1, Figures S1–S5) referenced in the main text. Specifically, Table S1 details the error propagation procedure used to account for amino acid $\delta^{15}\text{N}$ offsets between coral skeletal material and diet for mixing model analysis. Figure S1 illustrates the radiocarbon and age model results, Figure S2 shows the results from a test of the effects of acid fuming on gorgonin bulk $\delta^{13}\text{C}$, and Figures S3–S5 show further detail about isotopic offsets between the Sur Ridge deep-sea coral and Station M2 sediment trap samples. A Supplemental Text section is also included, with information on error propagation, as referenced in Section 2.5 in the main text, and further discussion of our deep-sea bamboo coral amino acid and bulk $\delta^{13}\text{C}$ results, as referenced in Section 4.2 in the main text. Supplementary material to this article can be found online at <https://doi.org/10.1016/j.gca.2025.02.018>.

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