

Ecological and environmental stability in offshore Southern California Marine Basins through the Holocene

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Key Points:

- In the Southern California Borderlands, oxygenation below 1400 m was stable and reduced relative to modern from 11.0-4.7 ka
- San Nicolas Basin experienced an oxygenation episode from 4.7-4.3 ka and oxygenation in Tanner Basin increased at 1.7 ka relative to 5.4-1.7 ka
- Variance in reconstructed Holocene dissolved oxygen concentration is similar to decadal scale variance in modern dissolved oxygen

Abstract

In the face of ongoing marine deoxygenation, understanding timescales and drivers of past oxygenation change is of critical importance. Marine sediment cores from tiered silled basins provide a natural laboratory to constrain timing and implications of oxygenation changes across multiple depths. Here, we reconstruct oxygenation and environmental change over time using benthic foraminiferal assemblages from sediment cores from three basins across the Southern California Borderlands: Tanner Basin (EW9504-09PC, 1194 m water depth), San Nicolas Basin (EW9504-08PC, 1442 m), and San Clemente Basin (EW9504-05PC, 1818 m). We utilize indicator taxa, community ecology, and an oxygenation transfer function to reconstruct past oxygenation, and we directly compare reconstructed dissolved oxygen to modern measured dissolved oxygen. We generate new, higher resolution carbon and oxygen isotope records from planktic (*Globigerina bulloides*) and benthic foraminifera (*Cibicides mckennai*) from Tanner Basin. Geochemical and assemblage data indicate limited ecological and environmental change through time in each basin across the intervals studied. Early to mid-Holocene (11.0-4.7 ka) oxygenation below 1400 m (San Clemente and San Nicolas) was relatively stable and reduced relative to modern. San Nicolas Basin experienced a multi-centennial oxygenation episode from 4.7-4.3 ka and oxygenation increased in Tanner Basin gradually from 1.7-0.8 ka. Yet across all three depths and time intervals studied, dissolved oxygen is consistently within a range of intermediate hypoxia (0.5-1.5 ml L⁻¹ [O₂]). Variance in reconstructed dissolved oxygen was similar to decadal variance in modern dissolved oxygen and reduced relative to Holocene-scale changes in shallower basins.

Plain Language Summary

Globally, marine oxygenation is declining with detrimental impacts to ecosystems and economies. To better understand the drivers and consequences of ocean oxygen change, we can examine the fossil record to identify how oxygenation changed in the past. Specifically, we use the relative abundance and chemistry of microfossils (i.e., foraminifera) to reconstruct past oxygenation. Here, we examined microfossils from three sediment cores in three basins (Tanner, San Nicolas, San Clemente) off the coast of Southern California. Marine dissolved oxygen (below 1400 m water depth) was relatively stable and lower than modern from 11,000 to 4,700 years before present. San Nicolas Basin experienced a multi-centennial oxygenation episode from 4,700-4,300 years before present and oxygenation increased in Tanner Basin gradually from 2,000-800 years before present. When compared to modern, the range of values of reconstructed oxygen through the entire time studied (thousands of years) is similar to the range of values of modern oxygen at the same depths, indicating that the changes in the last ten thousand years were similar to the amount of change occurring on annual and decadal timescales in the modern ocean.

1 Introduction

1.1 Marine oxygenation in the past and present

At present, global marine oxygenation is declining due to anthropogenic climate change, with important implications for benthic and pelagic ecosystems (Breitburg et al., 2018; Oschlies et al., 2018; Schmidtko et al., 2017). Ocean oxygenation, particularly at depth, is an important driver of ecosystem zonation, and expansion of oxygen minimum zones (OMZ) is a current threat to global marine ecosystems (Breitburg et al., 2018; Helly & Levin, 2004; Stramma, Schmidtko, et al., 2010). Deoxygenation at depth can be driven by several processes: increased export of organic matter from surface to depth leading to increased respiration below the photic zone, increased stratification (often due to surface warming) reducing ventilation at depth, warming surface temperatures reducing rates of diffusion of atmospheric oxygen into surface waters, and changes in the source, current velocity, or oxygenation of intermediate waters (Levin et al., 2009; Oschlies et al., 2018; Stramma, Schmidtko, et al., 2010).

Understanding drivers of changes to marine oxygenation in the past is critical for understanding and predicting future change (Jaccard et al., 2014). Paleorecords provide an important archive to investigate temporal and spatial scales of changes to marine oxygenation. In general, warm intervals during the late Quaternary were associated with decreased global ocean oxygenation and cool intervals were associated with increased oxygenation (Cannariato & Kennett, 1999; Cardich et al., 2019; Erdem et al., 2019; Jaccard et al., 2014; Praetorius et al., 2015). The Holocene is an ideal epoch to investigate marine oxygenation because it has well documented intervals of oceanographic change and provides an opportunity to investigate ecological response to stress, including changes to temperature, oxygenation, carbon cycling and ocean circulation (Addison et al., 2017; Barron et al., 2003; Fisler & Hendy, 2008; Moffitt et al., 2015; Praetorius et al., 2015). Over millennial timescales, significant work along the California margin has documented paleoceanographic changes in coastal basins and within the bounds of the modern OMZ (Balestra et al., 2018; Cannariato & Kennett, 1999; Moffitt et al., 2014; Taylor et al., 2015). However, additional work is needed to constrain the timing and extent of oxygenation change below 1000 m, the relative impacts of surface processes and source waters on seafloor oxygenation, and how oxygenation at these depths responds to global and regional environmental change.

1.2 Southern California modern and paleoceanography

In the modern California Current eastern boundary upwelling system, an OMZ exists at approximately 500 – 1000 m water depth and is an important driver of ecosystem zonation, impacting species distributions in pelagic and seafloor communities (Helly & Levin, 2004; Stramma, Johnson, et al., 2010). The combination of high productivity, high export of organic matter, and age of water masses entering the

North Pacific at depth make this a particularly thick and laterally extensive OMZ (Bograd et al., 2008, 2019; Evans et al., 2020). The California Margin OMZ is expanding in intensity (decreasing dissolved oxygen), horizontal extent, and vertical thickness (shoaling) (Schmidtko et al., 2017; Stramma, Johnson, et al., 2010). Changes to the OMZ are caused by reductions in the oxygenation of source water and reduced ventilation due to surface warming and stratification (Bograd et al., 2008; Evans et al., 2020). Off the coast of California, dissolved oxygen decreased at a rate of up to 0.047 ml/L/year from 1984-2006 in the upper 500 m of the water column (Bograd et al., 2008, 2015). In the Southern California Current System, 81% of observed change in oxygenation in the upper 400 m of the water column from 1993-2018 can be attributed to changes in oxygenation of source waters (Evans et al., 2020).

In the modern system, Southern California Borderlands surface water flow is counterclockwise (Southern California Eddy), with the western margin dominated by the southward flowing California Current and the eastern margin driven by the northward-flowing California Countercurrent and Davidson Current. At depth, the California Undercurrent flows south to north and is comprised of a mix of Southern Component Intermediate Water from the eastern tropical Pacific and northerly sourced North Pacific Intermediate Water (Balestra et al., 2018; Bograd et al., 2019; Checkley & Barth, 2009; Stott et al., 2000; Talley, 1993). Offshore Southern California, a series of submarine basins, generally deepening from north to south, structure intermediate and deep-water flow (Berelson, 1991; Berelson & Stott, 2003). Oxygenation in basinal environments is impacted by the export of organic matter from overlying surface waters, advection of intermediate and deep waters that spill into the basin, and within basin processes, including sediment and pelagic biogeochemical cycles. By examining the environments of multiple silled basins, the effects of water advection can be separated from surface processes and the depths of significant biogeochemical change can be determined.

The California margin OMZ fluctuated throughout the Holocene (Balestra et al., 2018; Christensen et al., 1994; McGann, 2011; Moffitt et al., 2014; Palmer et al., 2020). Previous analyses of marine sediment cores from the Santa Barbara Basin (SBB) document intervals of hypoxia in the early Holocene (11.5-10 ka) followed by oscillations in the strength of the OMZ from 10-6 ka with several intervals of hypoxia (less than 0.5 ml L⁻¹ [O₂]) and an increase in oxygenation in the last 6 ka within SBB, yet the OMZ persists throughout the Holocene (Moffitt et al., 2014; Ohkushi et al., 2013; Wang et al., 2020). In Santa Monica Basin (SMB), severe hypoxia (less than 0.3 ml L⁻¹ [O₂]) was present from the start of the Holocene to 9 ka, and the mid to late Holocene (9-0 ka) had weaker hypoxia (0.3-1.5 ml L⁻¹ [O₂]) than the early Holocene (Balestra et al., 2018). The modern OMZ, with oxygen levels at 0-1.5 ml L⁻¹ [O₂], developed in the mid to late Holocene (by 6-4 ka) across the broader North Pacific (Addison et al., 2017;

McGann, 2011; Ohkushi et al., 2013; Praetorius et al., 2015). Over the past several centuries the SMB experienced variable degrees of dysoxia at interannual to interdecadal time scales (Christensen et al., 1994). These changes are attributable to variable biological carbon flux and respiration at depth (Berelson and Stott, 2003; Stott et al., 2000), underscoring how sensitive the shallow-silled basins are to small changes in biological productivity. Previous analysis of ecosystem responses (benthic foraminiferal and invertebrate) to oxygenation change through the Holocene from the SBB indicate that intervals within the Holocene exhibit distinct phases of ecosystems that do not repeat or overlap, as the oxygen minimum zone and carbon maximum zone fluctuate (Moffitt et al., 2015; Myhre et al., 2017).

Here, we utilize records from three offshore basins to constrain changes in ocean oxygenation through the Holocene and resultant impacts on benthic ecosystems. Silled basins provide a unique opportunity to examine both local changes within each basin and to compare oxygenation history across depths when records overlap temporally. Combining a series of silled basins allows for the examination of change through time at multiple water depths and sill depths to investigate the relative impact of surface processes and intermediate water changes in determining oxygenation at depth (Balestra et al., 2018; Moffitt et al., 2014; Wang et al., 2020).

1.3 Benthic foraminiferal assemblages as a metric of past oxygenation and organic matter export

Benthic foraminiferal assemblages are an effective and established metric to quantify past changes in marine oxygenation (Balestra et al., 2018; Belanger et al., 2020; Bernhard et al., 1997, 2003; Bernhard & Gupta, 1999; Cardich et al., 2015, 2019; Caille et al., 2014; De & Gupta, 2010; Kaiho, 1994; Moffitt et al., 2014; Murgese & De Deckker, 2005; Ohkushi et al., 2013; Praetorius et al., 2015). Benthic foraminiferal assemblages are sensitive to small changes in oxygenation in the North Pacific, even in suboxic environments, not exclusively across large biological thresholds of anoxic or sulfidic conditions (Sharon et al., 2021). Multiple methodologies are used to interpret past environmental change from benthic foraminiferal assemblages, which we introduce and review below.

Quantifying absolute and relative abundance of benthic foraminiferal species is an established and foundational method; typically, studies quantify species downcore and interpret trends through time using observational or statistical approaches (e.g. Moffitt et al., 2014; McGann, 2011; Gardner et al., 1988). Studies of modern benthic foraminifera from multiple depositional environments and oxygenation regimes have identified oxygenation affinity of benthic foraminiferal species that can be used as indicator species of change through time; this method is most useful to reconstruct relative oxygenation or to

identify past oxygenation thresholds (e.g. Cannariato and Kennett, 1999; Palmer et al., 2020; Balestra et al., 2018; Bernhard and Gupta, 1999).

While these approaches provide relative oxygenation history, transfer functions are used to translate whole or partial benthic species assemblages into absolute oxygenation values (Behl & Kennett, 1996; Kaiho, 1994, 1999; McGann, 2011; Moffitt et al., 2014; Ohkushi et al., 2013; Sharon et al., 2021). Multi-species transfer functions including the Kaiho Benthic Foraminiferal Oxygenation Index, Schmiedl Dissolved Oxygen Index, and Behl Dissolved Oxygen Index are used to generate absolute values of past oxygenation by transforming the relative abundance of species into $\text{ml L}^{-1} [\text{O}_2]$ (Kaiho, 1994; Ohkushi et al., 2013; Sharon et al., 2021). Transfer functions have typically been constructed using case studies from very low oxygen environments (such as Santa Barbara Basin) or by using the lowest known oxygen tolerance for a species; as such, this approach generates inherently conservative (lower) predictions of oxygenation, with the exception of the analysis by Sharon et al., 2021 which utilized multivariate statistical analysis to group species by oxygenation (Kaiho, 1994; Ohkushi et al., 2013; Sharon et al., 2021). Categorization of species into oxic, intermediate hypoxic, and anoxic environments used in multiple transfer functions and as indicator species varies by author (Bernhard et al., 1997; Bernhard & Gupta, 1999; Cannariato & Kennett, 1999; Kaiho, 1994; Moffitt et al., 2014; Palmer et al., 2020; Praetorius et al., 2015). Here we follow the convention: weakly suboxic/oxic ($[\text{O}_2] > 1.5 \text{ ml L}^{-1}$), intermediate hypoxic/suboxic ($[\text{O}_2] 1.5\text{-}0.5 \text{ ml L}^{-1}$), and severe hypoxic/dysoxic ($[\text{O}_2] < 0.5 \text{ ml L}^{-1}$) (Moffitt et al., 2014; Palmer et al., 2020; Sharon et al., 2021; Tetard et al., 2021).

Recent work on paleoecological assemblages, including benthic foraminifera, utilizing analysis of diversity, richness, and multidimensional statistical analysis has expanded our breadth of understanding of how oxygenation impacts seafloor ecosystems (Belanger et al., 2020; Myhre et al., 2017; Sharon et al., 2021). Ecological analysis provides community-scale assessments of environmental change over time and often complements analysis of indicator taxa or transfer function calculations (Belanger et al., 2020; Myhre et al., 2017; Sharon et al., 2021). In addition to taxonomic evaluation of benthic foraminifera, studies are increasingly relying on morphometrics to assess past environments. These studies are predicated on morphological response or adaptation to oxygenation such as pore density, size, and shape (i.e., roundedness) and are used in both taxon-specific and taxon-independent analyses (Keating-Bitonti & Payne, 2016, 2018; Keating-Bitonti & Payne, 2017; Rathburn et al., 2018; Tetard et al., 2021). Typically, smaller, thin-walled, elongate species are indicative of low oxygen environments in which high-surface area to volume ratio is advantageous, to maximize oxygen absorption, while in well oxygenated

environments, larger, thick-walled and porcelaneous taxa with rounded shapes are dominant (Tetard et al., 2021).

Importantly though, oxygenation is not the only driver of benthic foraminiferal assemblages. Food availability, driven by the timing (pulsed vs. constant) and amount of export of organic matter, water depth, sediment grain size, and water temperature play an important role in structuring seafloor ecosystems, including benthic foraminiferal assemblages (Belanger et al., 2012, 2020; Kaiho, 1999; Venturelli et al., 2018). Here we employ stable isotope and benthic foraminiferal assemblage analyses to investigate cores from three silled basins in the Southern California Borderlands. By combining multiple approaches to assemblage analysis as listed above, we quantify changes in oxygenation below 1000 m, deconstruct surface vs. advective processes as drivers of change, and investigate changes in source waters. This multi-site, multi-faceted approach allows us to reconstruct change over time in each basin and to assess regional scale oxygenation history and environmental change in the Southern California Borderlands through the Holocene.

2 Methods

2.1 Study site

Cores were collected from three silled basins within the Southern California Borderlands (Figure 1). Tanner Basin is located west of the Channel Islands and is the farthest offshore. The basin has a sill depth of 1160 m and a bottom depth of approximately 1500 m (Figure 1). San Nicolas Basin is located south of San Nicolas Island and west of San Clemente Island. The basin has a sill depth of 1100 m and a bottom depth of approximately 1800 m (Figure 1). San Clemente Basin is located south of San Clemente Island and is the deepest site explored here. The basin has a sill depth of 1815 m and a bottom depth of approximately 1950 m (Figure 1). The water depth of each core was assessed at time of core collection and bottom depths of each basin were measured using GeoMapApp.

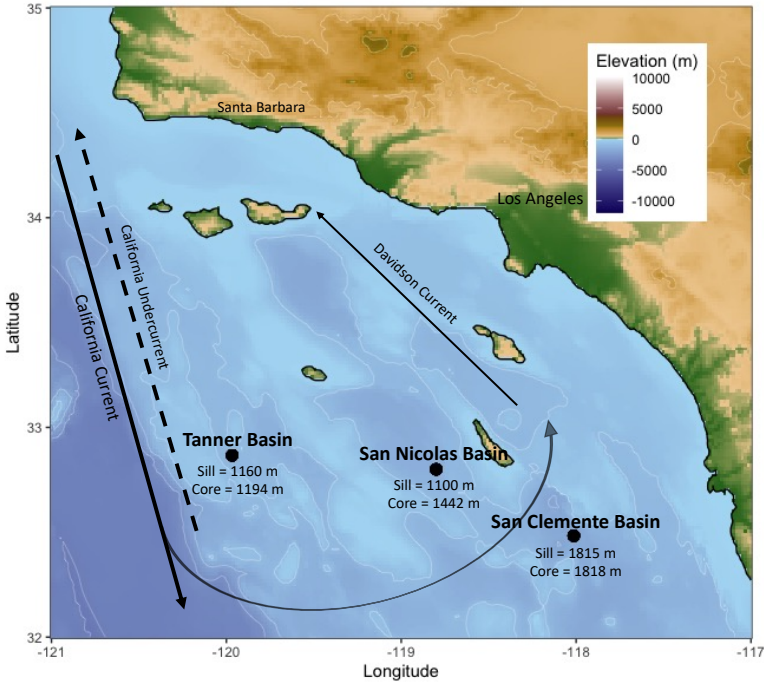


Figure 1: Map of the locations of the three cores used in this study. Schematic of current locations and directions included, solid lines indicate surface currents (California Current and Davidson Current), dashed line indicates subsurface current (California Undercurrent). The sill depth and core collection depth for each core is reported in meters.

2.2 Sediment cores

We investigate three piston cores collected from the Southern California Borderlands on the Maurice Ewing Cruise 9504 in May - June 1995: EW 9504-09PC from Tanner Basin at 1194 m water depth, EW 9504-08PC from San Nicolas Basin at 1442 m water depth, and EW 9504-05 from San Clemente Basin at 1818 m water depth. All cores have 10.16 cm inner diameter and were split and sampled at 2 cm intervals aboard the ship (initial volume of all samples was 162.15 cm³). Sediments from the working half of the core were disaggregated in sodium hexametaphosphate washed over a 63 μ m sieve (see Stott et al. 2000). Sediments were dried and stored in glass vials at the University of Southern California until they were processed for this study. The core from Tanner Basin (EW 9504-09PC) was examined from 0-40 cm at 2 cm intervals; intervals below 40 cm were not available for analysis (total of 19 intervals examined). The core from San Nicolas Basin (EW 9504-08PC) was examined at 2 cm intervals from 0-22 cm and every 6 cm from 24-64 cm (due to sample availability, total of 19 intervals examined). The core from San Clemente Basin (EW 9504-05) was examined at 2 cm intervals from 30-52 cm; intervals from 0-30 cm in EW9504-05 did not have sufficient foraminifera for robust analysis (see below) and were thus excluded from analysis (total of 11 intervals examined). Analysis was conducted at the resolution available to the

authors and all intervals with sufficient sediment volume and foraminifera (see below) were used in the study.

2.3 Radiocarbon dating and age model development

Radiocarbon based age models were developed for each core using a combination of previously published and newly generated planktic radiocarbon ages (Table S1, Figure S1). Five age dates within the Holocene (1 San Clemente, 1 Tanner, 2 San Nicolas) were previously measured (Stott et al., 2000). These AMS ^{14}C ages were completed using bulk planktonic foraminifera (weight ~3-5 mg) analyzed at the Lawrence Livermore National Laboratory (Stott et al., 2000). Three additional radiocarbon dates (1 San Clemente, 2 Tanner, 1 San Nicolas) from bulk planktic foraminifera were analyzed in this study. All samples for radiocarbon analysis were prepared by picking shell material from the >150 μm fraction, rinsing shells in methanol, sonicating in methanol for 5-10 seconds, and rinsing twice with deionized water. Shells were then dried in a 60°C drying oven. Radiocarbon analysis was completed at the Lawrence Livermore National Laboratory using $\delta^{13}\text{C}$ assumed values following the convention of Stuiver and Polach (1977). The reported age is given in radiocarbon years using the Libby half-life of 5568 years. Accelerator mass spectrometry ages were converted to calendar ages before present (BP) by calibration against the Marine20 curve using the open-source software “R” package Bchron (Haslett & Parnell, 2008; Heaton et al., 2020). Calibration included correction for reservoir ages for the Southern California Coast of 220.0 ± 40.0 years (Ingram & Southon, 1996; Stuiver & Polach, 1977). Age/depth models for each core were generated using the Bayesian age-depth modeling functionality of Bchron (Table S1, Figure S1).

2.4 Stable Isotope Analysis

Stable isotope analyses from planktic and benthic foraminifera from EW9504-09 (Tanner Basin) were conducted on *Globigerina bulloides* planktic foraminifera and *Cibicides mckannai* benthic foraminifera from 0-40 cm at 2 cm intervals. Samples were prepared by picking from the >150 μm size fraction (2-5 individual *C. mckannai* per interval, 15-25 *G. bulloides* per interval) and cleaned using the same methodology as above. Planktic foraminifera were analyzed at the UC Davis Stable Isotope Laboratory and benthic foraminifera were analyzed at the UC Santa Cruz Stable Isotope Laboratory.

Planktic carbon and oxygen isotope samples were analyzed using a GasBench II system interfaced with a Delta V Plus Isotope Ratio Mass Spectrometer at the UC Davis Stable Isotope Laboratory using standard UCD-SM92 (-1.94 for $\delta^{18}\text{O}$ and 2.08‰ $\delta^{13}\text{C}$) (Ostermann 2000). Values for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are expressed in per mil (‰) relative to Vienna Pee Dee Belemnite, and values are corrected for changes in linearity and instrumental drift. Benthic carbon and oxygen isotope samples were analyzed at the UC Santa Cruz Stable

Isotope Laboratory by acid digestion using an individual vial acid drop Thermo Scientific Kiel IV carbonate device interfaced to Thermo Scientific MAT 253 dual-inlet isotope ratio mass spectrometer. All samples were measured with several replicates of the externally calibrated Carrera Marble in-house standard reference material 'CM12' and the NBS-18 limestone international standard reference material. Values for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ are expressed in per mil (‰) relative to Vienna Pee Dee Belemnite, and values are corrected for changes in linearity and instrumental drift. Data were combined with previously published records of planktic oxygen isotopes and benthic oxygen and carbon isotopes from the same core examined here (EW9504-09) to increase replicates in the late Holocene and to extend the record through the entire Holocene (Stott et al., 2000). As such, isotope records reflect analyses from three different laboratories. Instrument precision from all labs for $\delta^{13}\text{C}$ calcite was 0.05-0.06‰ and for $\delta^{18}\text{O}$ calcite was 0.06-0.10‰. Thus, we report the maximum uncertainty of 0.06‰ for $\delta^{13}\text{C}$ calcite and 0.10‰ for $\delta^{18}\text{O}$ calcite (Figure 3).

2.5 Benthic Foraminiferal Assemblages

Samples were dry sieved over a 150 μm sieve and picked for benthic foraminifera. Foraminifera greater than 150 μm have been documented to capture the range of environmental variability in paleoceanographic reconstructions as well as assemblages containing smaller foraminifera and the use of larger specimens results in reduced error in identification (Cannariato & Kennett, 1999; Caille et al., 2014; Fenton et al., 2018; Palmer et al., 2020). Foraminifera in the size fraction below 150 μm were excluded from this analysis which may have excluded some smaller taxa or smaller individuals of the taxa identified here. Individual foraminifera were picked and identified from each interval to obtain >90 individuals per sample (Kemp et al., 2020), as sample sizes as low as 58 have been shown to have stable assemblages (Belanger et al., 2020; Forcino et al., 2015). The average number of individual foraminifera identified in each interval was 230, with a range of 90-665. Samples were mounted on micropaleontology slides using gum tragacanth at time of identification and are archived in the Ocean Climate Laboratory at the UC Davis Bodega Marine Laboratory. Cores were not laminated; thus, bioturbation is expected and may have had an averaging effect on assemblages.

2.6 Foraminiferal morphometrics

Morphometrics of benthic foraminifera, including length, width, and surface area were measured using ImageJ software. Length and width of each individual was measured to the longest and widest margins of the shell. Three species were selected for analysis to represent a gradient of oxygenation affinity: *Quinqueloculina* sp. is weakly suboxic/oxic and *B. spissa* and *U. peregrina* are categorized as suboxic (Table S2). Measurements of *Quinqueloculina* sp. and *B. spissa* were quantified in Tanner Basin at 2 cm

intervals from 0-40 cm, measurements of *Quinqueloculina* sp. and *U. peregrina* were quantified in San Clemente Basin at 2 cm intervals from 30-44 cm. From each interval, 3-30 individual shells of each species were measured (based on availability of taxa). Results of morphometric analysis were compared to morphometric data (collected using the same methodology) from five open coastal margin sites (300-1175m) near San Diego (see Palmer et al., 2020 for further explanation of the open margin study site, all morphometric data is available on Dryad, see Palmer et al., 2022).

2.7 Metazoan microfossil assemblages

In addition to picking and identifying benthic foraminifera, ostracods (Arthropoda - Ostracoda) and urchin spines (Echinodermata) were picked from the 150 µm sediment fraction at all intervals examined. Samples were mounted on micropaleontology slides using gum tragacanth at time of identification and are archived in the Ocean Climate Laboratory at the UC Davis Bodega Marine Laboratory. Due to low abundances, presence/absence is recorded, rather than relative abundance.

2.8 Benthic foraminiferal oxygenation index

Oxygenation was reconstructed using two modified benthic foraminiferal oxygenation indices: Behl and Schmiedl (Schmiedl et al., 2003; Sharon et al., 2021). Data were analyzed using both indices in order to compare the results; the Schmiedl Index uses diversity as a input, but does not include suboxic taxa, while the Behl Index does not include diversity, but includes oxic, suboxic, and weakly suboxic/dysoxic taxa (Ohkushi et al., 2013; Schmiedl et al., 2004). Using a combination of paleo and modern samples, Sharon et al., 2021 used detrended correspondence analysis (DCA) to expand the list of species that can be used as inputs to the Behl Index, thus allowing for its application in a broader range of seafloor environments (Sharon et al., 2021). Here we utilize the Behl dissolved oxygen index following Ohkushi et al., 2013, but expand the list of species included in the assessment following the work of Sharon et al., 2021. We further modified the list of species used in the Behl and Schmiedl indices by adding ten additional species using previously published oxygenation affiliations and morphometric or taxonomic similarities (Table S2). We included all species that made up at least 2% of the total foraminifera identified across all time intervals and cores examined. Oxygenation reconstructions were calculated using two equations:
Behl DO index = $((\text{dysoxic \%} * 0.1) + (\text{suboxic \%} * 0.5) + (\text{weakly suboxic/oxic \%} * 1.5)) / 100$ and
Schmiedl index = $((\text{weakly suboxic/oxic \%}) / (\text{weakly suboxic/oxic \%} + \text{hypoxic \%}) + \text{diversity (H')}) * 0.5$ (Ohkushi et al., 2013).

2.9 Statistical analysis

Diversity of each interval was calculated using Shannon Index (H). Richness was calculated by tabulating the number of distinct species present in an interval. Non-metric multidimensional scaling (NMDS) ordination, using square root transformation of assemblage species counts and Bray-Curtis similarities and detrended correspondence analysis were conducted and compared (Figure S2, Table S3, S4). We used a single factor ANOVA to determine if there were significant differences among mean morphometrics (length, width, surface area), diversity between basins, diversity through time, and values of reconstructed vs. modern oxygenation. If the results of ANOVA were significant, we performed Tukey's Test to determine where differences in the means occurred. All statistical analyses were completed using the Vegan R package (nmds function, decorana function) or base R functions (tukeyHSD function and res.aov function) (Oksanen et al., 2013; R Core Team, 2021).

2.10 Modern oxygenation data

Modern oxygen data were sourced from the California Cooperative Oceanic Fisheries Investigations (CalCOFI) for the years 1949-2019. Data were included from all sites in the CalCOFI sampling grid bounded by -116° – -121° W longitude and 32° – 34.5° N latitude (Point Conception is northern boundary)) and depths 1000-2000 m to maximize data availability. Oxygenation was calculated using Winkler Titration of bottle samples at the Scripps Institution of Oceanography (Bograd et al., 2003; Bograd & Lynn, 2003). Flagged data from CalCOFI and property-property and time series analysis excluded 19 data points. The CalCOFI data set used here includes a total of 272 modern oxygen measurements.

3 Results

3.1 Age Model Development

Age models produced a median age and probability distribution (at a range of 95.0% uncertainty, 2σ) at each depth (Figure S1). Age model uncertainty is reported in Table S2. Coherence of age model within each core and between cores supports use of this age model (Figure S1). Mean sedimentation rates for the entire Holocene are similar for all three cores: Tanner has a mean sedimentation rate of $10.8 (\pm 1\sigma = 5.3 \text{ cm/ka})$, San Nicolas has a mean sedimentation rate of $9.9 (\pm 1\sigma = 1.8 \text{ cm/ka})$, and San Clemente has a mean sedimentation rate of $12.0 (\pm 1\sigma = 4.8 \text{ cm/ka})$. Sedimentation rates reported here are similar to those observed offshore Central California through the Holocene (McGann, 2011). All following results are discussed as age in thousands of years before present (ka).

3.2 Benthic foraminiferal assemblages

Benthic foraminiferal assemblages were quantified down core for each core in which sufficient benthic foraminifera were present (Tanner Basin 0-40 cm at 2 cm intervals, San Nicolas Basin 0-22 cm at 2 cm intervals, 24-66 at 6 cm intervals, San Clemente Basin 30-54 cm at 2 cm intervals). The total number of species (richness) in each sample ranged from 15 to 24 (Figure S4) and species diversity (Shannon Index, H) ranged from 2.12 to 2.68, with a mean of 2.40 ($\pm 1\sigma = 0.15$) across all three basins (Figure S4). Species diversity (H) is significantly higher in Tanner Basin (mean=2.51, $\pm 1\sigma = 0.11$), relative to San Nicolas Basin (mean=2.30, $\pm 1\sigma = 0.11$) and San Clemente Basin (mean=2.37, $\pm 1\sigma = 0.10$) (ANOVA, Tukey Test $p < 0.05$) (Figure 3). Comparison of diversity through time in individual basins using 0.5 or 1 ka time bins shows that diversity (H) is not statistically different through time in Tanner, San Nicolas, and San Clemente basins (ANOVA, Tukey Test $p < 0.05$ for all sites). Multivariate statistical analysis using nonmetric multidimensional scaling (NMDS) and detrended correspondence analysis (DCA) of down-core assemblages shows that, through time, assemblage similarity within sites exceeds similarity to assemblages at any other site (Figure S2). Comparison of results of DCA and NMDS with previously published benthic foraminiferal species categorization by oxygenation do not clearly indicate that oxygenation is the dominant factor in controlling species assemblage at the community level.

In Tanner Basin, the most common species (in descending order) are *B. spissa*, *G. subglobosa*, *H. soldanii*, *Quinqueloculina* sp., and *P. murrhina* (Figure 2). Species diversity (H) ranged from 2.32-2.68 with a mean of 2.51 ($\pm 1\sigma = 0.11$) (Figure 3). Benthic foraminiferal assemblage gradually changed from 5.5 – 1.9 ka; this shift is largely driven by a gradual increase in *Hansenisca soldanii* (previously *Gyroidina soldanii*) and decrease in *B. spissa* and *U. peregrina* (Figure 2). *G. subglobosa* and *Quinqueloculina* sp consistently make up 10-20% of the assemblage through time (Figure 2). In San Nicolas Basin, the most common species (in descending order) are *U. peregrina*, *E. pacifica*, *C. mckannai*, *B. spissa*, and *Uvigerina* sp (Figure 2). Species diversity (H) ranges from 2.12-2.56 with a mean of 2.30 (± 0.11) (Figure 3). The assemblage in San Nicolas Basin exhibits little change through time from 10.1-4.7 ka when *U. peregrina* makes up 15-45% of the assemblage. From 4.7-4.2 ka, there is a sharp decline in *U. peregrina* and a sharp increase in *C. mckannai* (Figure 2). From 4.0-1.9 ka, the trend reverses, and the assemblage is very similar to the assemblage from 10.1-4.7 ka. In San Clemente Basin, the most common species (in descending order) are *U. peregrina*, *C. mckannai*, *E. pacifica*, *Quinqueloculina* sp., and *Uvigerina* sp (Figure 2). Species diversity (H) ranges from 2.17-2.51 with a mean of 2.37 (± 0.10) (Figure 3). In San Clemente Basin, relative abundance of benthic foraminifera exhibits little change over time from 11.2-7.1 ka as shown by both individual species analysis and DCA (Figure S2).

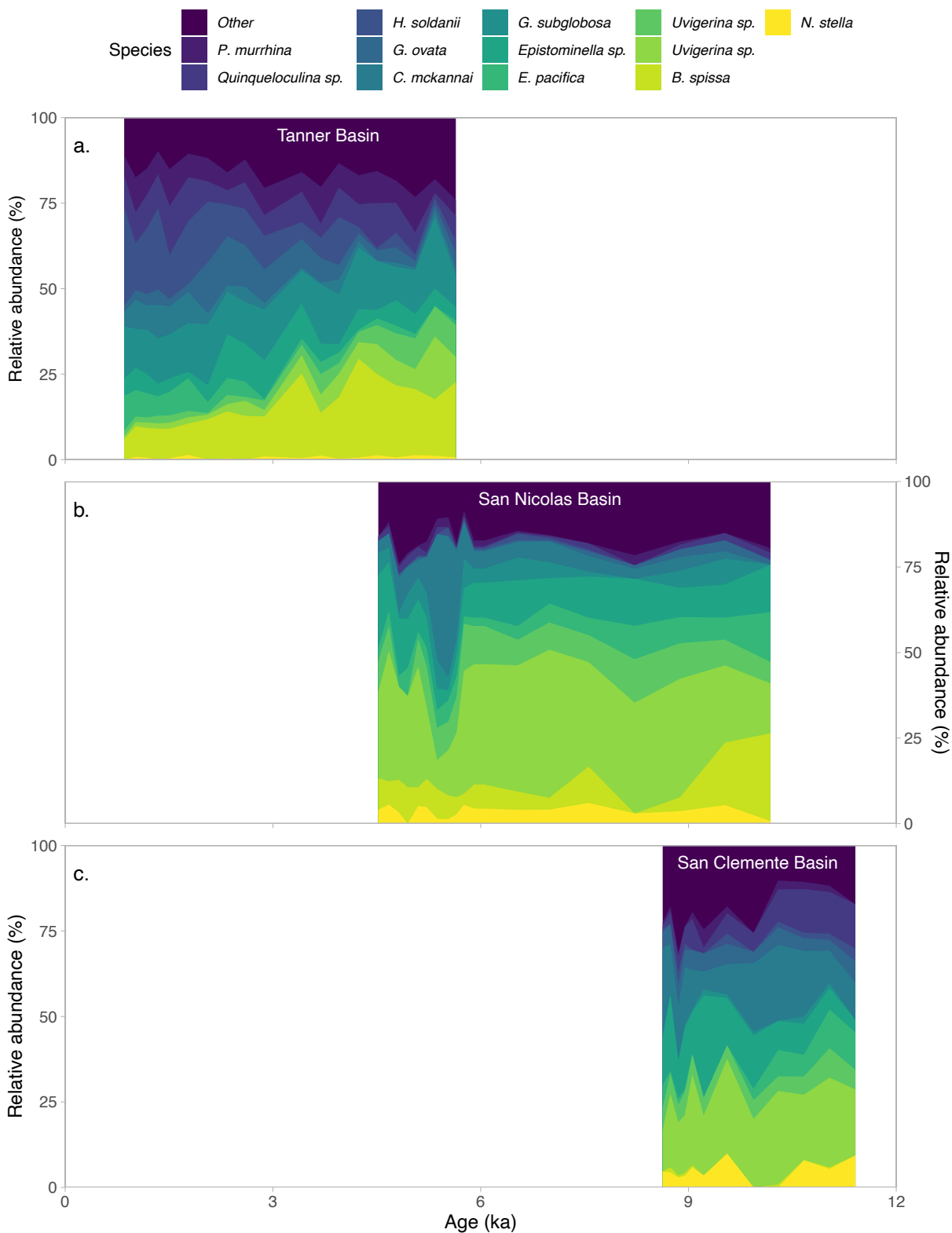


Figure 2: Relative abundance of benthic foraminifera vs. age in thousands of years before present for three cores examined here: Tanner (a.), San Nicolas (b.), and San Clemente (c.). Ten most abundant

species are shown; all other species grouped as “other.” Each color represents a taxonomic group (species, genus, or other). See legend at top of plot for color of each. Taxa colors are ordered from dysoxic indicator taxa (yellow/bottom of plot) to oxic indicator taxa (blue/top of plot).

3.3 Shell morphometrics

Shell size was quantified to examine sub-lethal impacts of environmental change on benthic fauna. Shell size, measured as length, width, and surface area of three taxa (*U. peregrina*, *Quinqueloculina* sp., and *B. spissa*) was compared across the three cores examined here and to size data from a suite of cores from the San Diego Margin (Palmer et al., 2020). Shell size of *U. peregrina* is statistically significantly larger in coastal sites ($p < 0.05$) relative to San Clemente basin (Figure S3a). Shell size of *B. spissa* is statistically significantly larger in coastal sites ($p < 0.05$) relative to Tanner Basin (Figure S3a). Shell size of *B. spissa* and *Quinqueloculina* from Tanner Basin show relatively little variability through time (5.5-1.9 ka) (Figure S3b, c). As all metrics of shell size (length, width, and surface area) show the same trends, further discussion uses only shell surface area as a metric of whole shell size.

3.4 Reconstructed oxygenation using transfer functions

Reconstructed dissolved oxygen using the Behl Index ranges from 0.56-1.12 ml L⁻¹ with a mean of 0.79 ml L⁻¹ (Figure S4) and varies across basins: Tanner Basin mean is 0.86 ml L⁻¹ and ranges from 0.59-1.12 ml L⁻¹, San Nicolas Basin mean is 0.67 ml L⁻¹ and ranges from 0.56-1.02 ml L⁻¹, and San Clemente Basin mean is 0.84 ml L⁻¹ and ranges from 0.68-0.96 ml L⁻¹. Reconstructed dissolved oxygen using the Schmiedl Index ranges from 1.36-1.81 ml L⁻¹ for all three cores, with a mean of 1.62 ml L⁻¹ (Figure S4). Schmiedl Index reconstructed oxygenation varies across basins: Tanner Basin mean is 1.73 ml L⁻¹ and ranges from 1.59-1.81 ml L⁻¹, San Nicolas Basin mean is 1.50 ml L⁻¹ and ranges from 1.36-1.66 ml L⁻¹, and San Clemente Basin mean is 1.60 ml L⁻¹ and ranges from 1.48-1.71 ml L⁻¹. Importantly, the number of individual foraminifera identified did not impact the outcomes of the Behl or Schmiedl indices (Figure S4). Species richness is not correlated with outputs of the Behl Index, but is positively correlated with the Schmiedl Index (Figure S4).

3.5 Stable isotope record

Stable isotope records from Tanner Basin varied slightly through time (Figure 3). Analysis of planktic oxygen and carbon isotopes from *G. bulloides* yielded the following: $\delta^{13}\text{C}$ mean is $-0.59 (\pm 1\sigma = 0.25)$, range is -0.92 to -0.05 , $\delta^{18}\text{O}$ mean is $0.22 (\pm 1\sigma = 0.31)$, range is -0.15 to 1.08 (Figure 3). Analysis of benthic oxygen and carbon isotopes from *C. mckannai* yielded the following: $\delta^{13}\text{C}$ mean is $-0.03 (\pm 1\sigma = 0.07)$, range is -0.13 to 0.10 , $\delta^{18}\text{O}$ mean is $2.53 (\pm 1\sigma = 0.17)$, range is 2.29 to 2.73 (Figure 3).

3.6 Metazoan microfossil analysis

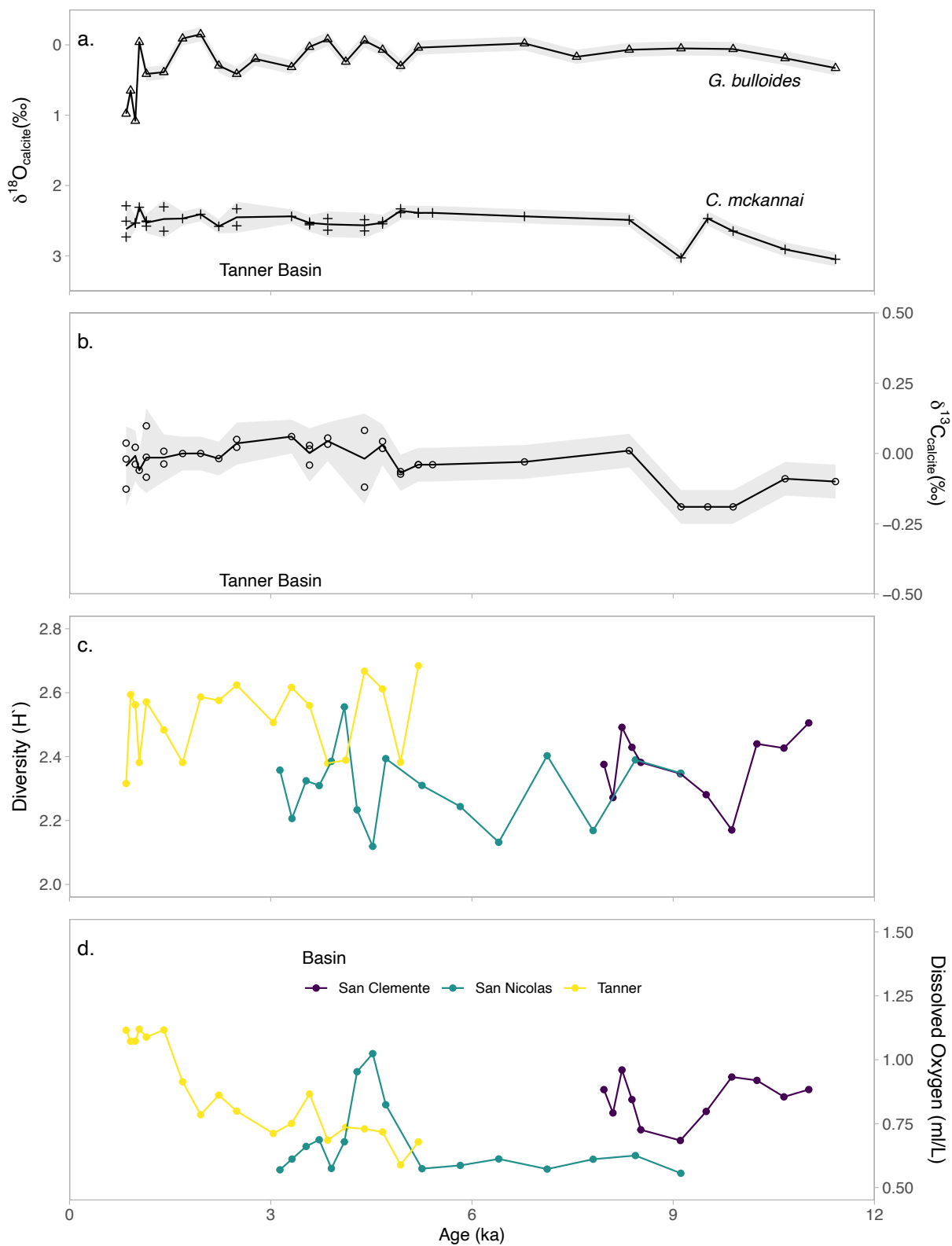
Urchin spines and ostracods were present in the Tanner Basin core, but do not present a coeval trend; urchins are present in 13 of 19 intervals, ostracods are present in 5 of 19 samples. Urchin spines and ostracods were scarce in sediments from San Nicolas Basin: urchin spines are present in 6 of 17 and ostracods are present in 2 of 17 intervals. Ostracods and urchin spines were nearly ubiquitous (present in every interval except one) in San Clemente Basin (Figure S5).

3.7 Modern oxygenation in the Southern California Borderlands

Modern oxygenation decreases linearly with depth from 1000 to 2000 m in this region, and ranges from 0.15-1.67 ml L⁻¹ and has a mean of 0.78 ml L⁻¹ across all depths (1000-2000m). Modern oxygenation in the 50 m above and below the Tanner Basin site (1144-1244 m) has a mean of 0.77 ± 0.18 ml L⁻¹. Modern oxygenation in the 50 m above and below the San Nicolas Basin site (1392-1492 m) has a mean of 0.88 ± 0.37 ml L⁻¹. Modern oxygenation in the 50 m above and below the San Nicolas Basin site (1392-1492 m) has a mean of 1.51 ± 0.09 ml L⁻¹.

	Tanner Basin		San Nicolas Basin		San Clemente Basin	
	Mean	Range	Mean	Range	Mean	Range
Behl Index reconstructed oxygen (ml L ⁻¹)	0.86	0.59-1.12	0.67	0.56-1.02	0.84	0.68-0.96
Schmiedl Index reconstructed oxygen (ml L ⁻¹)	1.73	1.59-1.81	1.50	1.36-1.66	1.60	1.48-1.71
Modern dissolved oxygen (ml L ⁻¹)	0.77	0.31-1.45	0.88	0.28-1.39	1.51	1.39-1.61

Table 1: Reconstructed and modern dissolved oxygen values for Tanner, San Nicolas, and San Clemente Basins. Modern oxygenation is from CalCOFI data from 50 m above and below the water depth of core collection for each basin.



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Figure 3: Stable isotope record from Tanner Basin (a., b.), benthic foraminiferal diversity (c.), and reconstructed oxygenation (d.) for all three sites using Behl Dissolved Oxygen Index. Oxygen isotopes of planktic foraminifera *G. bulloides* from this study and Stott et al., 2000 indicated as triangles (a.). Oxygen and carbon isotopes of benthic foraminifera *C. mckannai* from this study and Stott et al., 2000 indicated as + (b.). Analytical uncertainty for stable isotopes is shown as gray bar ($\delta^{13}\text{C} \pm 0.06\text{‰}$ and $\delta^{18}\text{O} \pm 0.10\text{‰}$). In the isotope figures, data from 3.8-0.8 ka includes both data from Stott et al., 2000 and this study, data from 11.4-3.8 ka is from Stott et al., 2000. For diversity and reconstructed dissolved oxygen yellow indicates Tanner, green indicates San Nicolas, and purple indicated San Clemente). Oxygen is reported in ml L^{-1} . **Discussion**

4.1 Paleo-oxygenation reconstruction

By analyzing the complete assemblage from each basin, we interpret a gradual shift in relative abundance of taxa in Tanner Basin, multi-centennial shifts in the assemblage at San Nicolas Basin, and stability in the assemblage in San Clemente Basin. Examining indicator taxa, we identify a decrease in suboxic taxon *B. spissa* and a decrease in *U. peregrina* coeval with an increase in oxidic indicator *Hansenisca* sp. in Tanner Basin from 1.7 to 0.8 ka. In San Nicolas Basin, we observe a short period of divergence from the mean assemblage driven by an increase in the oxidic-associated taxon *C. mckannai* and a sharp decline in *U. peregrina* from 4.7-4.3 ka. We observe little change over time in the relative abundance of these indicator taxa in San Clemente Basin. We do not identify a relationship between NMDS and DCA species scores and previously published categories of oxygenation indicating that oxygenation may not be the dominant factor in determining the full assemblage. Other parameters such as proximity to the margin of the OMZ, sediment grain size, and organic matter availability also play important roles in structuring foraminiferal diversity and assemblage (e.g., Bernhard et al., 1997; Sharon et al., 2021; Venturelli et al., 2018).

Reconstructed oxygen concentration differs between the two transfer functions compared here. Reconstructed dissolved oxygen using Behl Index for all three cores yields values ($0.56\text{--}1.12 \text{ ml L}^{-1}$) within “intermediate hypoxia” as defined by Moffitt et al., and “suboxic” as defined by Cannariato and Kennett and Kaiho (Cannariato & Kennett, 1999; Kaiho, 1994; Moffitt et al., 2014). Reconstructed values using the Behl Index are similar to the range of modern values for bottom water oxygenation with notable exceptions discussed below (Figure 3d, 4). In comparison, the Schmiedl Index output is higher ($1.36\text{--}1.81 \text{ ml L}^{-1}$) than the Behl Index by approximately 0.5 ml L^{-1} (Figure S4). We posit that this is due to the fact that diversity and oxygenation are not necessarily inversely correlated, particularly in intermediate hypoxic environments, yet the Schmiedl Index is based on diversity. Oxygenation plays a more dominant role in structuring diversity across biological thresholds (such as below $0.5 \text{ ml L}^{-1} [\text{O}_2]$) than across

oxygen gradients that do not cross biological thresholds (McGann, 2011; Palmer et al., 2020; Sharon et al., 2021; Venturelli et al., 2018). Additionally, the Schmiedl index only considers the end member groups: hypoxic and weakly suboxic/oxic, and does not include the relative abundance of suboxic taxa, taxa which may be important community members and oxygenation indicators at this water depth. Thus, we utilize the Behl Index to reconstruct absolute values of paleo-oxygenation (Figure 3).

4.2 Ecological and environmental change through the Holocene in the Southern California Borderlands

Geochemical and faunal records from Tanner, San Nicolas, and San Clemente Basins indicate environmental and ecological stability in water below 1000m through the Holocene in the Southern California Borderlands. Planktic $\delta^{18}\text{O}$ records from Tanner Basin indicate constant sea surface conditions (salinity/temperature) through most of the Holocene (11.75 – 2.3 ka) and a decrease in sea surface temperature or increase in salinity from 1.0-0.8 ka relative to the rest of the Holocene (Figure 3). Benthic $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of the epibenthic foraminifera *C. makannai* exhibit little change through the Holocene (Figure 4). Reconstructed seafloor oxygenation using the Behl Index is within the range of intermediate hypoxia (0.5 – 1.5 ml L⁻¹) and are similar to the range of modern values for bottom water oxygenation with notable exceptions discussed below (Figure 3d, 4).

Ecological and environmental change over time as measured by diversity and multi-dimensional community metrics also indicate stability through the Holocene. Diversity varied little between basins and through time within each basin. Shannon Index of diversity (H) ranged from 2.12 to 2.68 across all sites and points in time, and diversity did not significantly change through time at any site across this interval (ANOVA, $p>0.05$) (Figure 3, S4). Results of NMDS and DCA show species assemblages are distinct in each basin; at any time point, assemblages are more similar to other time points from the same basin than to any other time point from an adjacent basin (Figure S2). This demonstrates that each basinal environment is unique and the analysis of benthic foraminifera as environmental indicators must consider local factors. We hypothesize that the stability in diversity and community-scale ecology indicates that environmental conditions were also relatively stable through this interval. This evidence aligns with results of oxygenation reconstruction from the Behl Index and stable isotope analysis (Figure 3).

Changes in benthic foraminifera morphology can reflect environmental variations that are missed by community-based analyses. Comparison of two species (*U. peregrina*, *B. spissa*) between basins (studied here) and open margin sediments (San Diego Margin, 300-1200 m water depth see Palmer et al., 2020) shows that both species are larger in the nearshore environment relative to offshore basins (Tanner, San

Clemente Basin, see Figure S3). At this scale, we interpret the size difference to be representative of higher relative organic matter input at coastal margin sites or warmer bottom water temperatures at shallower coastal margin sites in comparison to offshore basins (Keating-Bitonti & Payne, 2016, 2018). Importantly though, in comparison to changes between coastal margins and offshore basins, there is relatively little change in shell size of *Quinqueloculina* sp. (oxic indicator species) or *B. spissa* (suboxic indicator species) over time (5.4-0.8 ka) in Tanner Basin (Figure S3). Thus, benthic foraminiferal $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$, reconstructed dissolved oxygen (Behl Index), community scale ecology, and morphology all indicate relative stability in environmental conditions at water depths 1194-1818 m through the studied time interval with few notable exceptions discussed below.

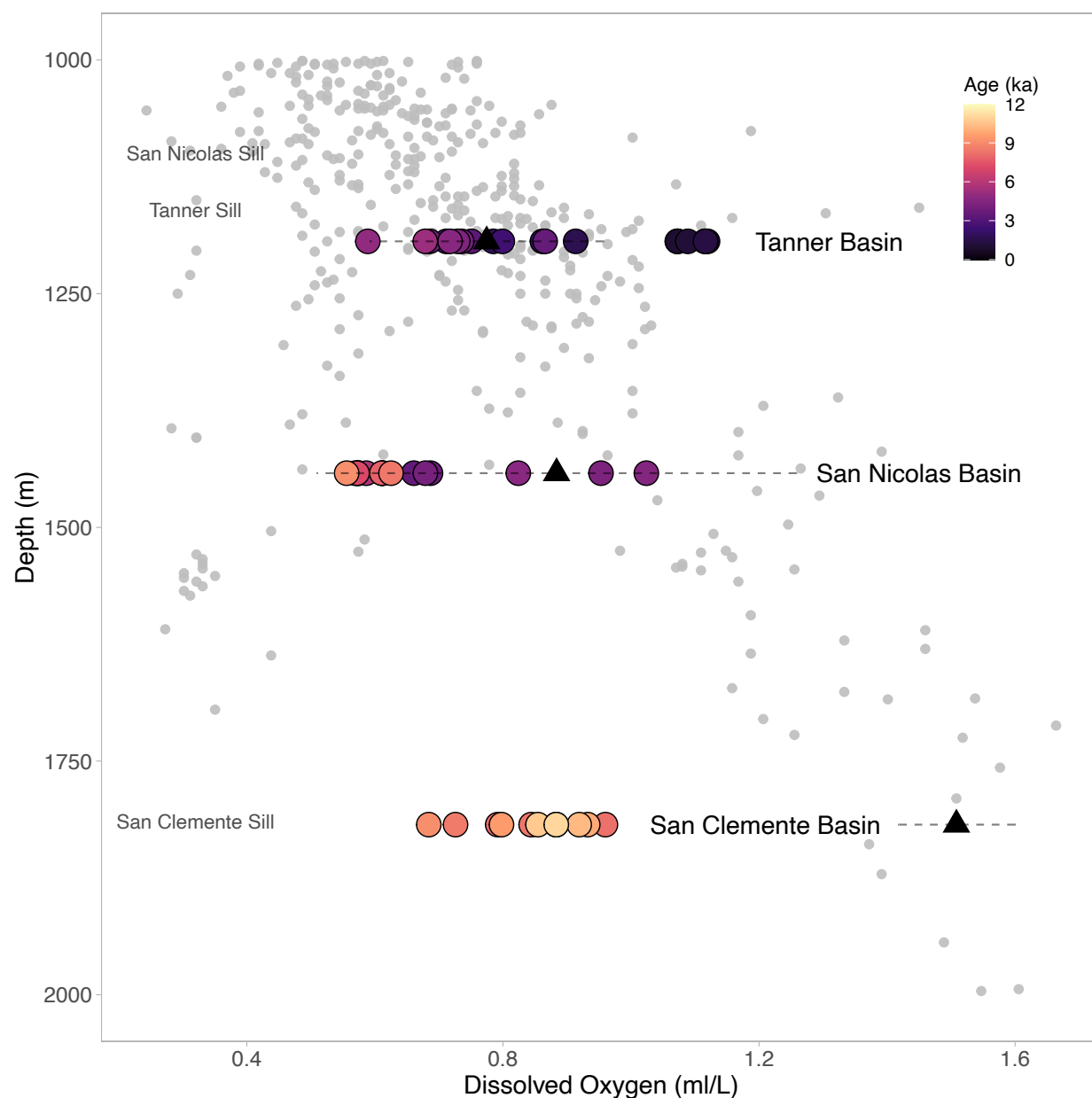
4.2.1 Ecological and environmental change through time in Tanner Basin

In Tanner Basin, the benthic foraminiferal assemblage shifts from more hypoxic taxa at 5.4-1.7 ka to more oxic associated taxa from 1.7-0.8 ka (Figures 2, 3). This shift is largely driven by the increase in *Hansenisca soldanii* (previously *Gyroidina soldanii*) and decrease in *B. spissa* and *U. peregrina* (Figure 2). *Hansenisca soldanii* has been documented in well oxygenated, oligotrophic, cold deep water with pulsed food supply (De & Gupta, 2010), and both *B. spissa* and *U. peregrina* are well documented indicators of low oxygen. Using the modified Behl Index, reconstructed oxygenation increases from 0.58 to 1.12 ml L⁻¹ across this interval (Figure 3). Thus, we interpret this assemblage shift as an indication of a increase of approximately 0.4 ml L⁻¹ in Tanner Basin occurring around 1.7 ka.

Downcore morphometric analysis shows that neither relative abundance nor surface area of *Quinqueloculina* sp. (an oxic indicator species) changes through time. Although *B. spissa* decreases in relative abundance from 5.4-0.8 ka, shell size (surface area) does not change through time (Figure S3). Stability in shell size concurrent with changes in relative abundance may indicate an interaction of factors including oxygen and organic matter influx in determining lethal vs. sublethal effects on *B. spissa*. Further, the lack of changes in shell size of *B. spissa* and *Quinqueloculina* across this interval may indicate a consistent supply of surface-exported organic matter, the main food resource for these benthic foraminifera. Ostracod and echinoderm presence are not correlated with increase in dissolved oxygen at this site (Figure S5). We hypothesize that the shift identified in the benthic foraminiferal assemblage is in response to a relatively small change in oxygenation (less than 1 ml L⁻¹) and does not represent fluctuations across biologically important thresholds for metazoan taxa, as dissolved oxygen was never below 0.4 ml L⁻¹ (Figure 3).

When compared to modern CalCOFI data, reconstructed oxygenation (using the Behl Index) is within 1σ of modern mean oxygenation (Figure 4), except for the interval from 1.7 – 0.8 ka in which reconstructed oxygen is higher than modern by 0.3 ml L^{-1} (Figure 4). There is no significant difference (ANOVA, Tukey, $p=0.51$) between reconstructed oxygenation values (mean= 0.86 ml L^{-1}) and all modern oxygenation values (mean= 0.77 ml L^{-1}) within waters 50 m above and below the Tanner Basin site (Figure 4). Combining assemblage, oxygenation index, and isotopic records of Tanner Basin, we identify increased dissolved oxygen in the basin from 1.7-0.8 ka relative to 5.4-1.7 ka that is not correlated with changes in either the oxygen or carbon isotope records and remains within the modern range of dissolved oxygen variability. The changes in Tanner Basin dissolved oxygen are minor when compared to changes in oxygenation in nearby more shallow basins within the OMZ (Balestra et al., 2018; Moffitt et al., 2014; Palmer et al., 2020; Wang et al., 2020).

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580 **Figure 4:** Reconstructed dissolved oxygen concentration (ml L^{-1}) from Tanner, San Nicolas, and San
 581 Clemente Basin (large dots colored by age) compared with modern dissolved oxygen concentration (ml L^{-1})
 582 from CalCOFI bottle sampling (1986-2019) (shown in small gray dots). Depth of sill of each basin is
 583 labeled. Black triangles show mean modern dissolved oxygen concentration from 50 m above and below
 584 each site and dashed gray line shows 1σ range in modern dissolved oxygen concentration from 50 m
 585 above and below each site.

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587 **4.2.2 Ecological and environmental change through time in San Nicolas Basin**

In San Nicolas Basin, low oxygen-associated benthic foraminiferal taxa dominate from 9.8 to 4.7 ka. A short period of anomalous assemblage driven by an increase in *C. mckannai*, an oxic-associated taxon, and a sharp decline in *U. peregrina*, an intermediate hypoxia-associated taxon, occurs at 4.7-4.3 ka and is interpreted as an interval of increased oxygenation. Using the modified Behl Index, reconstructed oxygenation increases from 0.59 ml L⁻¹ before the interval to a maximum of 1.03 ml L⁻¹ during the oxygenation interval (Figure 3). Oxygenation returned to pre-event levels of dissolved oxygen after 4.3 ka and pre and post event assemblages are similar, indicating an absence of a legacy effect of the event on the community (Figure 2). Metazoan invertebrate microfossils (ostracods and urchin spines) are scarce in this core and changes in presence/absence of metazoans do not correlate with shifts in benthic foraminiferal assemblages (Figure S5). Modern studies of circulation in San Nicolas Basin indicate that residence time for bottom waters in the basin are 9 ± 2 months (Berelson, 1991). As such, we hypothesize that the assemblage response recorded here represents persistent oxygenation or repeated ventilation on a decadal-to centennial scale, rather than a single episode of ventilation. Yet, the absolute change in oxygenation is relatively minor and still within a threshold of intermediate hypoxia and within the range of modern values (Figure 3, 4).

When compared to modern CalCOFI data, reconstructed oxygenation in San Nicolas Basin is slightly lower than modern mean dissolved oxygen yet remains within 1 σ of the modern mean at all points throughout the Holocene (Figure 4). Reconstructed oxygenation (mean=0.67 ml L⁻¹) is statistically lower than modern oxygenation from waters 50 m above and below the depth of the San Nicolas site (ANOVA, Tukey $p < 0.05$) (Figure 4). Further, the variance in reconstructed dissolved oxygen is similar to variance in modern oxygenation at the sill depth of San Nicolas Basin (1100m, see Figure 4). The scale of change in reconstructed dissolved oxygen, relative abundance of species, and species diversity in San Nicolas Basin across this interval of change is minor when compared to intervals of change in nearby basins across the deglacial and in comparison to Holocene changes within basins that experienced shifts between anoxic and oxic conditions, such as the Macoma Event in the Santa Barbara Basin (Balestra et al., 2018; Cannariato & Kennett, 1999; Moffitt et al., 2015; Praetorius et al., 2015; Schimmelmann et al., 2013).

4.2.3 Ecological and environmental change through time in San Clemente Basin

Environmental conditions remained relatively constant in San Clemente Basin from 11.0-8.0 ka as demonstrated by the lack of variability in the benthic foraminiferal assemblages. Species diversity does not change significantly through time (Figure 3, S4). Reconstructed oxygenation from the modified Behl Index ranges from 0.67 to 0.96 ml L⁻¹ across this interval; this variability is reduced relative to Tanner and San Nicolas Basins (Figure 3). The assemblage at this depth is distinct from coastal margin environments

and other, shallower basins (Balestra et al., 2018; Moffitt et al., 2014; Palmer et al., 2020). Ostracods and urchin spines are present in every interval (except one) examined here, indicating a well-oxygenated seafloor environment that supported metazoan life and motile organisms (Figure S5) (Moffitt et al., 2015). Ecological differences between the shallow sill basins (San Nicolas and Tanner) vs. the deep sill basin (San Clemente) documented here are mirrored in previously documented seafloor metazoan assemblages (France, 1994). We hypothesize that at 1815 m water depth, this site was not impacted by changes in the oxygen minimum zone during the Holocene and that intermediate and deep water reaching this site had a consistent source from 11.0-8.0 ka.

In comparison to modern CalCOFI data, reconstructed dissolved oxygen (mean=0.84 ml L⁻¹) in the early and mid-Holocene is statistically lower than modern dissolved oxygen (mean=1.50 ml L⁻¹) within 50 m above and below the depth of the San Clemente Site (p<0.05) (Figure 4). We propose three potentially overlapping hypotheses for this difference. First, this may be an artifact of categorizations of some species used in the Behl Index that use lowest known thresholds of oxygenation and thus may predict the minima of dissolved oxygen concentrations. Second, in the early Holocene, sea level was lower than modern (by approximately 70 m), thus, the sites sampled here may have been less well oxygenated simply due to being at a shallower depth, but this would not entirely explain the difference from modern (Figure 4) (Fleming et al., 1998; Moffitt et al., 2014). Finally, the preformed oxygenation of the incoming water masses may have been lower than modern, a pattern that is reflected in Santa Monica and Santa Barbara Basins at this time (Balestra et al., 2018; Wang et al., 2020).

4.3 Environmental stability in Southern California Borderlands through the Holocene and comparison to modern ocean conditions

Environmental conditions in Tanner, San Nicolas, and San Clemente Basins remained relatively stable across the time intervals examined. In the early to mid-Holocene (11.0-4.7 ka), seafloor oxygenation and environmental conditions more broadly below 1400 m were stable in the Southern CA Borderlands, evidenced by stability in assemblage records from San Clemente Basin (1815 m) and San Nicolas Basin (1442 m), and was likely driven by consistent source and composition of intermediate waters. Benthic foraminiferal assemblage records from the Santa Lucia Slope (ODP 1017, 955 m) offshore Point Conception indicate a stable suboxic environment (reconstructed [O₂] 1.5-0.5 ml L⁻¹) through the early and mid-Holocene and are similar in taxonomic composition to the records presented here from San Nicolas and San Clemente Basins (Cannariato & Kennett, 1999; Sharon & Belanger, 2022). Synchrony in stability and assemblages across San Nicolas Basin (1442 m), San Clemente Basin (1818 m), and the Santa Lucia Slope (955 m) contrasts with evidence of fluctuations in age of North Pacific Intermediate

Water entering SBB (as recorded by benthic-planktic radiocarbon age differences) at 9 ka (Roark et al., 2003), expansion of the OMZ in SBB in the early Holocene (Wang et al., 2020), and a turning point from hypoxic to suboxic conditions at 9 ka in Santa Monica Basin (indicated by benthic foraminiferal assemblages and geochemical records) (Balestra et al., 2018). Differences in oxygenation between sites may be explained by differences across water depth; we propose that changes in the source and strength of NPIW impacted sites at 400-1000m water depth (SBB, SMB) (Balestra et al., 2018; Roark et al., 2003; Wang et al., 2020), but had less of an effect on the water column below 1000 m. Similar patterns of stable suboxic conditions below the depth of the OMZ and variability in dissolved oxygen at shallower, OMZ-impacted depths through the Holocene were observed further north, offshore British Columbia, and have been attributed to changes in the strength of NPIW (Sharon & Belanger, 2022). In the mid to late Holocene, San Nicolas Basin experienced a multi-centennial oxygenation interval from 4.7-4.3 ka and oxygenation increased in Tanner Basin beginning at 1.0 ka, yet all changes were within $1 \text{ ml L}^{-1} [\text{O}_2]$. Drivers of oxygenation in each basin may have been due to “indirect” ventilation through diffusion of dissolved oxygen from overlying waters, rather than “direct” ventilation due to advection (Talley, 1993), a change in oxygenation of source waters, or basinal processes related to the shape, depth, and overlying surface water productivity in each basin.

Although oxygenation does vary across the Holocene in Tanner, San Nicolas, and San Clemente basins, all variability was within $1 \text{ ml L}^{-1} [\text{O}_2]$ and does not cross critical biological thresholds below 0.5 ml L^{-1} or above 1.5 ml L^{-1} in any basin. As such, variability in oxygenation and ventilation of San Nicolas, Tanner, and San Clemente basins is reduced relative to shallower sites, including Santa Barbara Basin and Santa Monica Basin, across the entire Holocene (Balestra et al., 2018; Moffitt et al., 2014; Ohkushi et al., 2013). Additionally, Holocene-scale oxygenation changes (presented here) are reduced relative to glacial/interglacial changes in oxygenation in the basins examined here and in the nearby Santa Lucia Slope (Cannariato & Kennett, 1999; Stott et al., 2000). This indicates that Holocene-scale climate changes driving oxygenation change shallower than 1000 m are not impacting waters below 1000 m and that climate changes within the Holocene do not significantly impact oxygenation below 1000 m, despite changes in the intensity and extent of the OMZ shallower than 1000 m. As such, we hypothesize that deoxygenation due to anthropogenic climate change will also have a greater impact on the water column above 1000 m, relative to below 1000m.

Direct comparison of reconstructed dissolved oxygen with modern measured dissolved oxygen indicates that the variance across millennia is similar to decadal-scale variance in the modern ocean (Figure 4). Variance in dissolved oxygen occurring on centennial to millennial timescales does not exceed the

variance observed in this modern ocean, indicating stability in intermediate waters and oxygenation below 1100 m in the Southern California Borderlands. We hypothesize that if there are significant changes to oxygenation below 1000m due to anthropogenic climate change, these changes may have large impacts on benthic ecosystems as they have not experienced significant changes in dissolved oxygen over the last 11 ka.

5 Conclusion

Reconstruction of past oxygenation using analysis of benthic microfaunal communities (foraminiferal and metazoan) is optimized by combining multiple approaches including analysis of indicator taxa, reconstruction of oxygenation using multi-taxa indices, and community scale-analysis such as multidimensional analysis and diversity. Here we demonstrate the utility of combined approaches, and we expand the use of the Behl Index for paleo-oxygenation reconstruction. Analysis of benthic foraminiferal assemblages from three silled basins (Tanner, San Nicolas, San Clemente) in the Southern California Borderlands combined with benthic and planktic stable isotope analysis from Tanner Basin show largely stable oxygenation except for a gradual increase (approximately $0.4 \text{ ml L}^{-1} [\text{O}_2]$) in oxygenation in Tanner Basin occurring at 1.7 ka and multi-centennial variability in oxygenation (approximately $0.5 \text{ ml L}^{-1} [\text{O}_2]$) in San Nicolas Basin. The seafloor environment is stable in San Clemente Basin from 11.0-8.0 ka, yet reconstructed oxygenation is lower than modern at this site. Holocene scale climate changes did not drive significant changes ($> 1 \text{ ml L}^{-1}$) in marine oxygenation below 1000 m in the Southern California Borderlands. In the context of modern oxygenation changes, findings from this analysis show that seafloor oxygenation of the Southern California Borderlands through the Holocene below 1000 m remained relatively stable and variance in oxygenation across millennia is similar to decadal-scale variance in the modern ocean. As such, we expect that future changes to marine oxygenation will be greater at depths above 1000 m relative to deeper waters and note that if anthropogenic climate change induced changes in oxygenation do cause shifts in dissolved oxygen greater than $> 1 \text{ ml L}^{-1}$ below 1000 m, it will represent a divergence from scales of variability over the last 11 ka.

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Open Research

The benthic foraminiferal assemblage data, radiocarbon age model data, carbon and oxygen stable isotope data, and morphometric data used for environmental reconstruction in the study are available at Dryad via Palmer et al. (2022).

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