A database of Holocene nearshore marine mollusc shell geochemistry from the Northeast Pacific

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Abstract

The shells of marine invertebrates can serve as high-resolution records of oceanographic and atmospheric change through time. In particular, oxygen and carbon isotope analyses of nearshore marine calcifiers that grow by accretion over their lifespans provide seasonal records of environmental and oceanographic conditions. Archaeological shell middens generated by Indigenous communities along the Northeast Pacific coast contain shells harvested over multiple seasons for millennia. These shell middens, as well as analyses of archival and modern shells, have the potential to provide multi-site, seasonal archives of nearshore conditions throughout the Holocene. A significant volume of oxygen and carbon isotope data from archaeological shells exists, yet is separately published in archaeological, geochemical, and paleoceanographic journals and has not been comprehensively analyzed to examine oceanographic change over time. Here, we compiled a database of previously published oxygen and carbon isotope data from archaeological, archival, and modern marine molluscs from the North American coast of the Northeast Pacific (32ºN to 50ºN). This database includes oxygen and carbon isotope data from over 550 modern, archaeological, and sub-fossil shells from 8880 years before present (BP) to the present, from which there are 4,845 total δ^{13}C and 5,071 total δ^{18}O measurements. Shell dating and sampling strategies vary among studies (1-118 samples per shell) and vary significantly by journal discipline. Data are from various bivalves and gastropod species, with *Mytilus* spp. being the most commonly analyzed taxon. This novel database can be used to investigate changes in nearshore sea surface conditions including warm-cool oscillations, heat waves, and upwelling intensity, and provides nearshore calcite δ^{13}C and δ^{18}O values that can be compared to the vast collections of offshore foraminifera calcite δ^{13}C and δ^{18}O data from marine sediment cores. By utilizing previously published geochemical data from midden and museum shells rather than sampling new specimens, future scientific research can reduce or omit the alteration or destruction of culturally valued specimens and sites. The data set is publicly available through PANGAEA at https://doi.org/10.1594/PANGAEA.932671 (Palmer et al., 2021).

1 Introduction

1.1 Nearshore records of environmental change

Analysis of past climatic and oceanographic change is critical for understanding scales of natural variability in marine systems and is thus essential to predict outcomes of modern climate change. Paleoceanographic studies largely focus on offshore marine sediment archives because they provide long-term, continuous archives of ocean and climate change over time (e.g. Hendy et al., 2002; Lisiecki and Raymo, 2005). Yet, we lack similar continuous records of nearshore environments, preventing quantification of past oceanographic changes in these systems. Shell material from nearshore marine molluscs are archives of the environment in which these organisms lived, and shifts in oxygen and carbon isotope ratios indicate changes in sea surface temperature, salinity, and upwelling (Andrus, 2011). Additionally, such archives can provide insight into the role of nearshore marine molluscs in ecosystems and as resources for human communities. In the coastal Northeast Pacific, an abundance of sub-fossil marine mollusc shells are found in archaeological middens, which have been analyzed to provide environmental proxies and to understand historical food sources and trading routes (Rick et al., 2006a; Braje et al., 2012; Eerkens et al., 2013). Nearshore shell archives typically represent snapshots of paleoceanographic history due to the limited lifespan of these organisms and inconsistencies in the preservation of these archaeological and geologic records compared to long-term offshore marine records (Kennett and Kennett, 2000; Rick et al., 2006a; Robbins and Rick, 2006; Andrus, 2011). Here we synthesize previously published records of oxygen and carbon isotopes in nearshore marine molluscs in order to provide an archive that allows researchers to ask questions across broader spatial and temporal scales. We address the following questions in this paper to provide context for our database:

1) What are the spatial, temporal, and taxonomic distributions of previously collected geochemical data from nearshore marine molluscs from the Northeast Pacific?
2) What metadata exists for these shell geochemistry records (taxa, age, latitude and longitude)?
3) What strategies are used to sample individual shells? How do sampling strategies differ between studies that collected data for archaeological vs. oceanographic research?

1.2 Oxygen and carbon isotopes as proxies for oceanographic reconstruction

Oxygen and carbon isotopes from molluscan biocalcite are established proxies for past environmental and oceanographic change. In an oceanographic context, oxygen isotopes of shell carbonate are used as a proxy for changes in sea surface temperature, salinity, and ice volume. In archaeological research, oxygen isotopes analyses of the outermost growth edge of shells (the most recent growth before death) are often used to infer sea surface temperatures that reflect seasonal human foraging patterns (Butler et al., 2019). Shell carbon isotopes are a proxy for the isotopic signature of dissolved inorganic carbon, which is largely dependent on biological productivity and respiration (Butler et al., 2019). *Vital effects,* or offsets from expected isotopic equilibria due to biological processes of each individual species and organism, confound interpretations of oxygen and carbon isotopes as oceanographic proxies (Gröcke and Gillikin, 2008). Here, we do not attempt to adjust values for the vital effects of each species or to convert carbonate oxygen or carbon isotope values into environmental variables (e.g. sea surface temperature), rather we compile the raw values as reported in each study to maintain consistency within the database.

1.2 Archaeological shells as environmental archives

Shell middens - the remnants of harvesting by Indigenous humans - are common along the west coast of North America. These middens are composed of diverse assemblages of intertidal and subtidal invertebrate taxa, including arthropods, bivalves, echinoderms, and gastropods. Along the western North American coast, evidence for human occupation and human-environment interactions in the nearshore environment extends back to the late Pleistocene (Rick et al., 2006a; Andrus, 2011; Becerra-Valdivia and Higham, 2020). Well preserved archaeological records from the California Channel Islands show evidence of human communities that relied heavily on marine hunting, fishing, and foraging throughout the Holocene (Rick et al., 2005). Marine molluscs were an important dietary and cultural resource for many Native peoples living along the North American coast through the Holocene (Jones and Richman 1995, Braje et al., 2012, Vellanoweth et al., 2006, Jones and Richman 2012). Archaeological shells are ideal candidates for paleoceanographic analysis in this region because they are relatively abundant along the North American west coast and many shells have been isotopically analyzed for environmental reconstruction in past studies.

Synthesizing previous work conducted by both archeologists and paleoceanographers in the context of environmental reconstruction will allow for the examination of a substantial amount of existing nearshore data while minimizing future destructive sampling. Shell middens remain important cultural sites for many Indigenous tribes today; as such, reducing or eliminating the use of additional destructive testing (including isotopic analysis) for scientific analysis maintains the cultural value of middens and respects cultural practices and traditions of tribes. Further, specimens maintained in museum collections are often not available for destructive analysis. Thus, by synthesizing previously published work and by increasing collaboration and conversations between archeologists, geochemists, and paleoceanographers, we can gain further insight across all fields without conducting additional destructive sampling.

1.4 Shell Sampling Strategies

Paleoceanographers and archaeologists target different questions, and thus utilize divergent sampling strategies when analyzing the geochemistry of nearshore mollusc shells. Small, often powdered, samples of calcium carbonate are extracted from the whole shell for analysis. Subsampling, here defined as taking more than one measurement from the same shell, can be achieved through drilling with a micromill or handheld drilling device (such as Dremel tool). The number of subsamples collected from a given shell and the location of the subsampling varies broadly across disciplines and individual researchers. Archeologists who seek to determine the seasonality of shell collection to better understand human history often conduct isotopic analyses only of the outermost edge of a shell (Eerkens et al., 2013; Jazwa and Kennett, 2016). This may involve a single sample or multiple subsamples from an individual shell (Andrus, 2011). Alternatively, researchers seeking to use shells as an archive of oceanographic change through time or to understand the life history of the mollusc may use higher resolution sequential sampling in order to generate a record of isotopic changes over time (Takesue and van Geen, 2004; Ferguson et al., 2013;

Robbins et al., 2013). For this approach, a micromill or other drilling tool is typically used to sequentially sample a
110   shell at multiple points along a growth (time) axis (Andrus, 2011). The new database presented here provides
opportunities to examine the variation in shell sampling protocols used among researchers from different disciplines
and explore how these methods may limit or enhance the usefulness of sampling at different resolutions for
paleoceanographic interpretations.

115   **2 Methodology**

Here, we assembled a database of oxygen and carbon isotope values from nearshore marine molluscs extracted from
peer-reviewed publications in archaeological, geochemical, and oceanographic journals. The database is structured
with each entry (row) representing a unique geochemical measurement; multiple subsamples were often collected
from individual shells; therefore a single shell may have multiple entries (rows) for each subsample drilled along the
120   shell. Detailed metadata were recorded for each individual data point including, when available: paper of original
publication, publication year, sample number (given by original authors), subsample number (given by original
authors), age in years before present, species, source (midden or modern), latitude, longitude, calculated sea surface
temperature (only if published by original authors), archaeological trinomial (when applicable). For every entry in
the database, we added a unique shell identification number for each individual and a unique subsample
125   identification number (when applicable). We also recorded the number of subsamples per shell, which is the number
of calcium carbonate samples extracted from and analyzed for oxygen or carbon isotopes for each given shell.

Additionally, we compiled the following metadata about the species represented in the database: tidal height
(intertidal, subtidal), life mode (infaunal, epifaunal), and habitat (estuary, open coast). Life mode represents the
130   faunal niche of the species, either infaunal or epifaunal (Table 1). Habitat indicates the marine environment as
determined by geographic location, proximity to coast, species, and reported environment in the original publication
(Table 1).

Species	Common Name	Tidal Height	Life Mode	Citations
Chione fluctifraga		intertidal	infaunal	(Keen, 1971)
Chione cortezi		intertidal	infaunal	(Keen, 1971)
Haliotis cracherodii	Black abalone	intertidal	epifaunal	(Tissot, 1988; Light et al., 2007)
Haliotis rufescens	Red abalone	intertidal, subtidal	epifaunal	(Díaz et al., 2000; Light et al., 2007)
Macoma sp.		intertidal	infaunal	(Light et al., 2007)
Crassostrea gigas	Pacific oyster (Magallana gigas)	intertidal	epifaunal	(Light et al., 2007)
Mytilus californianus	California mussel	intertidal	epifaunal	(Suchanek, 1978, 1981; Light et al., 2007)
Mytilus edulis	Blue mussel	intertidal	epifaunal	(Suchanek, 1978, 1981; Light et al.,

				2007)
Mytilus sp.	Mussel	intertidal	epifaunal	(Seed and Suchanek, 1992; Light et al., 2007)
Mytilus trossulus	Bay mussel	intertidal	epifaunal	(Seed and Suchanek, 1992; Light et al., 2007)
Olivella biplicata	Purple olivella	intertidal, subtidal	infaunal	(Light et al., 2007)
Panopea abrupta	Geoduck	intertidal	infaunal	(Light et al., 2007)
Protothaca staminea	Littleneck clam	intertidal	infaunal	(Fraser and Smith, 1928; Takesue and van Geen, 2004; Light et al., 2007)

Table 1: Common name, tidal height, and life mode for all taxonomic groups included in the database.

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Age model type varied across publications. If the age of a shell was reported as an age range of a midden section, the age range is included in the database and the midpoint of the reported age range is included in the database as the age in years before present. For all archaeological shells, age in years before present designates 1950 as present, following the convention of radiocarbon dating and most archaeological studies. For modern samples, age in years

140 before present represents age in years before 2020. Thus, for users of the database, a 70-year correction must be applied to align all ages to the same timescale. We adhere to this dual system to maintain the ages as they were presented in each publication and to prevent negative values for age in years before present. All oxygen and carbon isotope data published in the original papers are included. Oxygen and carbon isotope values are reported in per mil (‰) relative to Vienna Pee Dee Belemnite (VPDB). In one instance, we included data in the database that the author

145 reports as unreliable (see Flores 2017 for full explanation of data quality).

After compilation of the database, we quantified the geographic distribution of the data, temporal distribution of the data, number of taxa, relative abundance of taxa represented in the database, range of subsamples within an individual shell, and range of $\delta^{13}C$ and $\delta^{18}O$ values. Differences in $\delta^{18}O$ and $\delta13C$ among species and in the

150 subsamples per shell by journal disciplines were quantified using ANOVA and Tukey's Test using R (R Core Team, 2021). The database is publicly available through PANGEA at https://doi.org/10.1594/PANGAEA.932671 (Palmer et al., 2021). Data publication adheres to FAIR Principles.

3 Results and discussion

155 **3.1 Data Sources**
We identified and included 24 previously published studies in the database. Out aim was to create a database that could be used for paleoenvironmental reconstruction at various temporal scales, as such, we included published datasets that reported isotopic data within the context of shell growth, i.e., the directionality and therefore seasonality of isotopic patterns in time could be determined. For this reason, isotopic analyses of fragments or

160 broken shells, often for archaeological studies, are not included in the database. Studies included in the database were largely published in archaeological journals (13) rather than geochemical (4) or paleoclimate and paleoceanography journals (7). The database includes 554 shells including 4732 carbon isotope values and 5068

oxygen isotope values. Data was published from 1994-2017; the number of papers published increases towards the

present. Data was largely sourced from midden specimens (487) and to a lesser extent from modern collected

165 specimens (66).

3.2 Spatial distribution of data

The database includes analyses of shells collected from 30ºN to 52ºN along the western coast of North America. The

spatial distribution of data is not continuous, due to the nature of human settlement and differences in the

170 preservation and sampling of middens across space (Fig. 1). More data are available from California relative to

Oregon, Washington, or British Columbia (Fig. 1). A significant portion of the available data are from midden shells

collected on the northern Channel Islands, California due to exceptional preservation in a semi-arid climate (Fig. 1)

(Rick et al., 2006b). Most studies (19) analyzed shells collected from open coast sites and a few studies (5) analyzed

specimens from estuarine environments (Fig. 4E, F).

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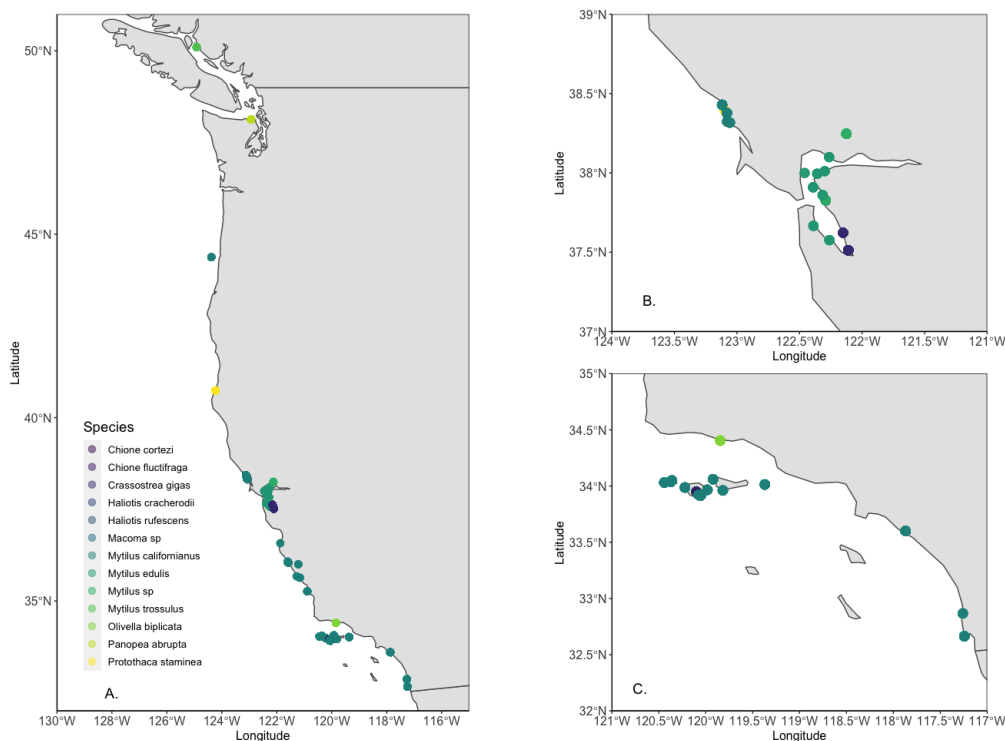


Figure 1: Maps of location of collection (for modern) and midden sites (for midden) of all specimens included in
database. All specimens included in map (A.), zoom in on northern California (B.) and southern California (C.).

180 ### 3.3 Temporal distribution of data

The age range of the shells in the database is 8800 - 0 BP (Fig. 2). The methodology for age control on individual shells varied among studies; some provide age ranges defined by radiocarbon dating of material that was co-collected with shells from stratigraphic sections of the midden, some studies provide radiocarbon dates from individual shells, and some shells in the database were collected live. Nine papers reported age ranges: Eerkens et
185 al., 2005, Eerkens et al., 2013, Eerkens et al., 2016, Glassow et al., 1994, Glassow et al., 2012, Jazwa and Kennett 2016, Jones and Kennett 1999, Rick et al., 2006, and Robbins and Rick 2006. In cases when age was reported as a range, the range is listed in the database (age_range column) and the midpoint of the range is recorded as the age of shell (age_ybp). The majority of entries in the database are from midden shells (3470) compared to modern shells (1621). The data are biased towards the present; more data are available from 0-3000 BP (3399 entries) relative to
190 3000-9000 BP (1636 entries).

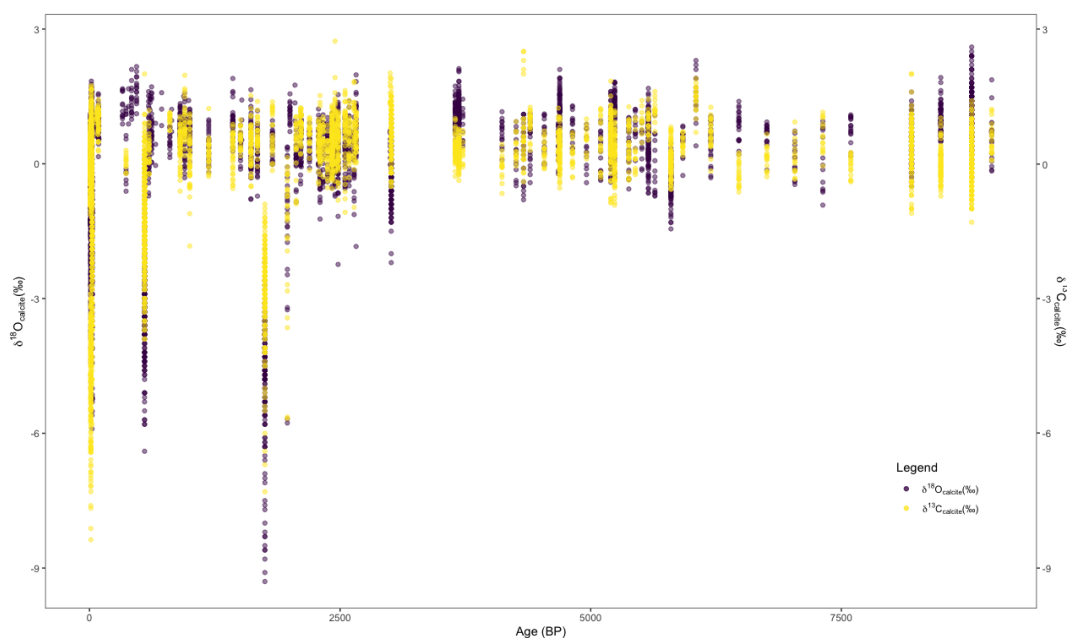



Figure 2: Oxygen (purple) and carbon (yellow) isotope values (‰VPDB) through time in years before present.

195 **3.4 Taxonomic distribution of data**

Available data represent 13 taxa: *Crassostrea gigas, Chione cortezi, Chione fluctifrage, Haliotis cracherodii, Haliotis rufescens, Macoma* sp., *Mytilus californianus, Mytilus edulis, Mytilus* sp., *Mytilus trossulus, Olivella biplicata, Panopea abrupta,* and *Protothaca staminea* (Fig 3). The available data and thus the database is largely biased to *Mytilus* taxa (3739 entries for *M. californianus,* 138 for *M. edulis,* 53 for *M. trossulus,* 464 for *Mytilus*
200 sp.,). This finding is in agreement with previous work showing that *Mytilus* spp. are highly abundant in coastal Western North American middens throughout the Holocene as *Mytilus* spp. are a common food choice of Indigenous peoples in this region (Jones and Richman, 1995; Braje et al., 2012; Thakar et al., 2017).

Oxygen and carbon isotope values vary significantly between taxa groups when analyzing all data across the entire

205 age range of the data. Results of ANOVA indicate that there are significant differences between taxa in regards to

oxygen isotope values (ANOVA, p<0.05). The Tukey post hoc test revealed five groupings of taxa that are

statistically similar to one another (p<0.05): Group a: *Haliotis rufescens*, *Haliotis cracherodii*, and *Panopea*

abrupta, Group b: *Haliotis cracherodii*, *Panopea abrupta*, *Mytilus californianus*, *Olivella biplicata*, *Protothaca*

staminea, and *Chione fluctifraga*, Group c: *Chione fluctifraga*, *Chione cortezi*, and *Mytilus edulis*, Group d:

210 *Crassostrea gigas*, *Mytilus trossulus, Macoma sp.*, and Group e: *Mytilus* sp. (Fig. 3). Results of ANOVA indicate

that there are significant differences between taxa in regards to carbon isotope values (ANOVA, p<0.05). The Tukey

post hoc test revealed six groupings of taxa that are statistically similar to one another (P<0.05): Group a: *Haliotis*

cracherodii, *Haliotis rufescens*, *Olivella biplicata*, and *Panopea abrupta*, Group b: *Mytilus californianus*, *Chione*

fluctifraga, and *Chione cortezi*, Group c: *Chione fluctifraga*, *Chione cortezi*, *Protothaca staminea*, and *Macoma sp.*,

215 Group d: *Mytilus* sp., Group e: *Mytilus edulis*, Group f: *Crassostrea gigas* (Fig. 3).

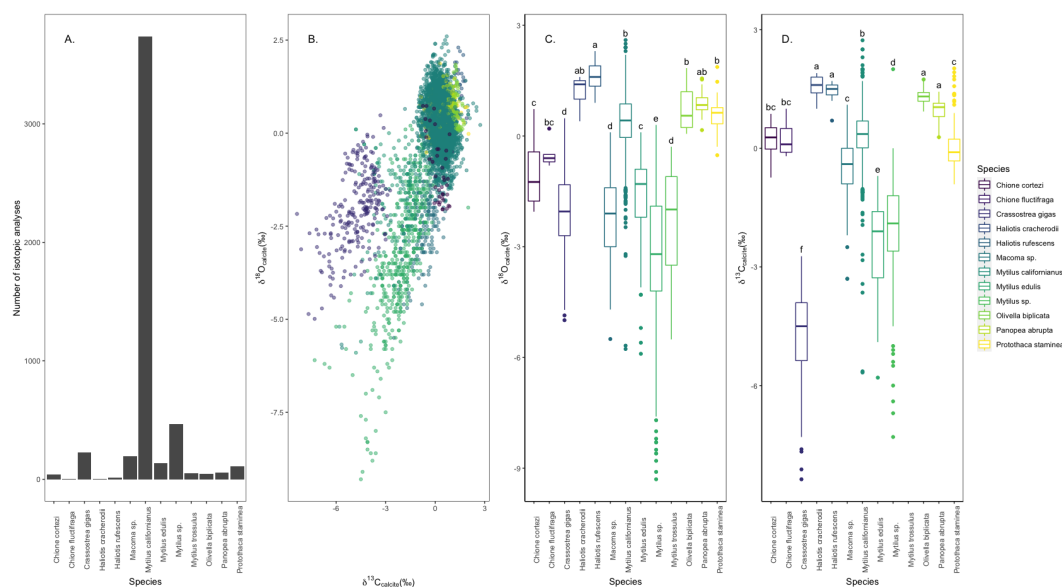



Figure 3: Taxonomic distribution of data. Histogram of number of entries in the database by taxonomic group (A.)
Carbon vs. oxygen isotope values (VPDB) colored by taxonomic group (B.). Box plot showing oxygen (C.) and
carbon (D.) isotope values by taxonomic group. Letters in panels C and D indicate which taxa are statistically

220 similar in terms of oxygen and carbon isotope values, respectively (Tukey, p>0.05).

3.6 Ecological distribution of data

The addition of several ecological traits expands the breadth of research topics that can be explored using the

database. Nearly all the species are intertidal (549) and a few (4 individuals - 1 *Olivella biplicata*, 3 *Haliotis*

225 *rufescens*) are known to be intertidal and subtidal (Fig. 4). Most specimens are from taxonomic groups with

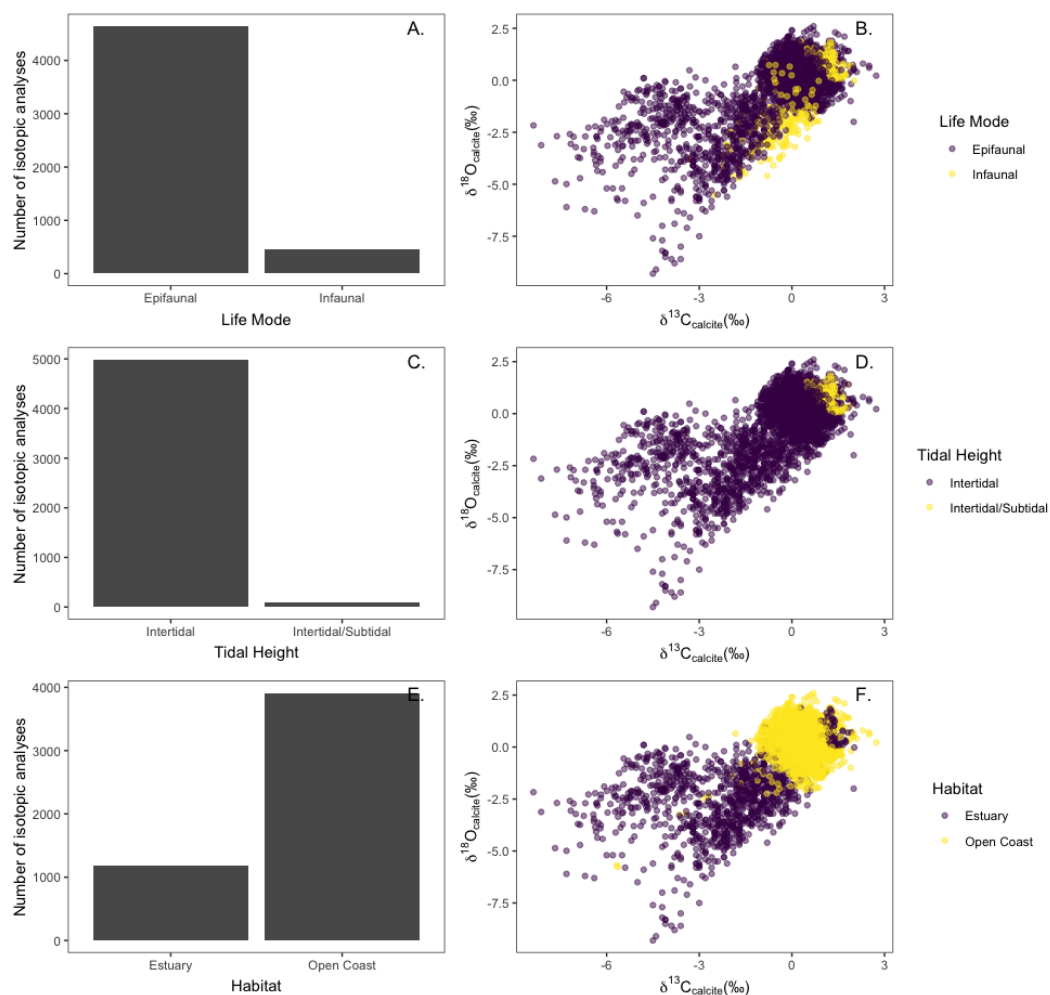
epifaunal life modes (495), and few have infaunal life modes (58) (Fig. 4). Both tidal height and life mode impact organismal exposure to air, seawater, and porewater and thus can influence oxygen and carbon isotope values. As such, future researchers may consider isolating specimens with certain life modes or tidal heights to address specific questions in paleoclimate reconstruction.

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Figure 4: Ecological distribution of data. Histogram and oxygen vs. carbon isotopes are respectively colored by category for life mode (A., B.), tidal height (C., D.), and habitat (E., F.).

3.5 Variation in sampling strategy

235   The sampling strategy for obtaining carbonate for isotopic analysis differed widely among studies and within studies with important implications for data analysis. In some studies, a single sample was obtained from the outermost growth edge of the shell (Fig. 5). We document a wide range of subsampling resolution, from 1 to 118 subsamples

from a single shell (Fig. 5). The number of subsamples reported per shell varies significantly among journal types (ANOVA, $p < 0.05$); geochemical studies utilized the most subsamples (mean = 40.8 subsamples per shell), followed

240 by paleoclimate and paleoceanography papers (mean = 19.3 subsamples per shell), and archaeology papers utilized the fewest subsamples (mean = 12.5 subsamples per shell) (Fig 5). The variation in approach and methodology in these studies impacts the resolution of data available in the database. Future research can explore how multiple approaches to subsampling impacts how informative the oxygen and carbon isotope values from each shell are for use in environmental reconstruction. Additionally, the diversity in sampling type motivates future interdisciplinary

245 collaborations that can answer multiple research questions using the same archive. For example, single shells could be utilized to answer questions about both archaeological histories and past oceanographic conditions.
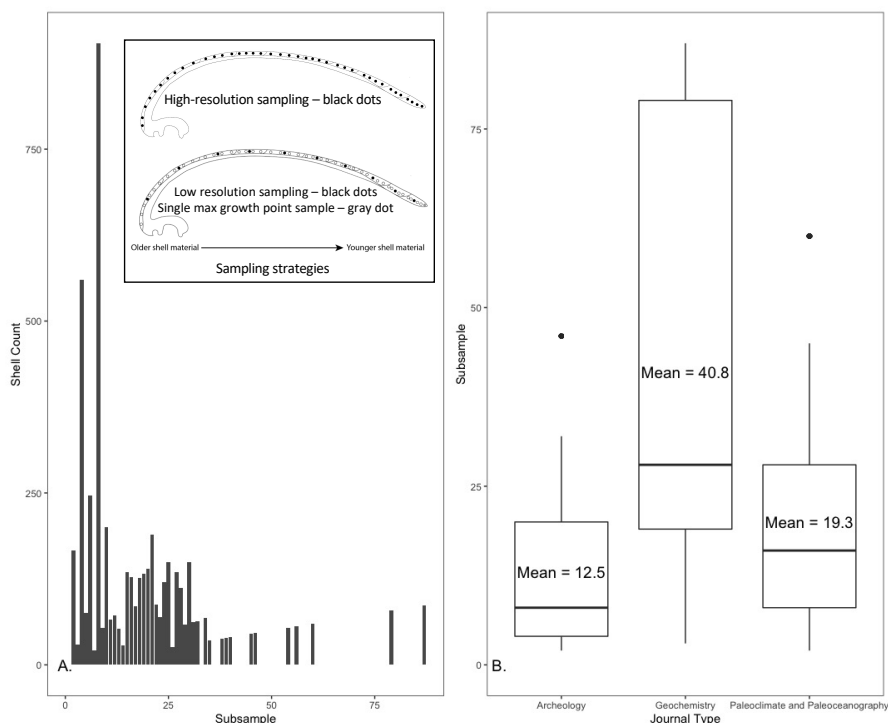
Figure 5: Distribution of occurrence of number of subsamples from an individual shell (A.) Panel A inset is a schematic of sampling strategies showing multiple degrees of sampling resolution. Box and whisker plot of

250 subsamples per shell by journal type (B.), difference between each group is significant (ANOVA, Tukey, $p < 0.05$).

4 Data Availability

The database described here is available at https://doi.org/10.1594/PANGAEA.932671 (Palmer et al., 2021). The

255 dataset is subject to a Creative Commons Attribution 4.0 International license agreement (CC-BY-4.0). In the published database, each row represents an individual geochemical analysis, and multiple rows of data are often

from the same shell. Detailed metadata are recorded for each individual data point including, when available: shell identification number (generated here), subsample identification number (generated here), number of subsamples per shell, name of publication (author, year), name of sample from original publication, name of subsample from original publication, latitude, longitude, δ^{13}C, δ^{18}O, age in years BP, age range (if reported in paper), species, source (modern, archive, burial, midden), suggested δ^{18}O correction published in the original publication, reconstructed sea surface temperature if reported in original paper, archaeological trinomial (if reported), tidal height of organism, life mode of organism, habitat type of organism, year of publication, and journal type (archaeology, geochemistry, paleoclimate and paleoceanography).

5 Conclusions

Marine mollusc geochemical data provides a record that is needed to understand changes in nearshore environments through time. In the Northeast Pacific, the abundance of previously published data on archaeological, archival, and modern specimens allows for exploration of oceanographic and climate change through the Holocene. Given the utility of archaeological records to provide long-term environmental archives, we encourage the use of these datasets in future paleoceanographic studies. Further, by synthesizing previously published data we provide an archive in which future work can be conducted without accessing culturally valued Indigenous artifacts or conducting destructive analysis on museum specimens. Future work on the data published here can explore changes in nearshore marine mollusc geochemistry across geographic, environmental, or biological gradients.

6 Land and Data Acknowledgement

Midden shells analyzed and synthesized for this paper were originally collected and gathered by Indigenous people from across the coastal Northeast Pacific. We do not attempt to name all tribes whose ancestral and present homelands make up this study area, but we acknowledge that the majority of the geographic area covered here represents unceded land of Indigenous tribes, and that data used here from previously published studies may have been acquired without consent from Indigenous peoples. We direct readers to the open-source resource: nativelands.ca to identify the homelands of the diverse Indigenous people of this region and encourage readers to use this resource as a starting place to learn about the land and marine stewardship of Indigenous peoples past and present.

7 References

Andrus, C. F. T.: Shell midden sclerochronology, Quaternary Science Reviews, 30, 2892–2905, https://doi.org/10.1016/j.quascirev.2011.07.016, 2011.

290   Becerra-Valdivia, L. and Higham, T.: The timing and effect of the earliest human arrivals in North America, 584, 93–97, https://doi.org/10.1038/s41586-020-2491-6, 2020.

Braje, T. J., Rick, T. C., and Erlandson, J. M.: A trans-Holocene historical ecological record of shellfish harvesting on California's Northern Channel Islands, 264, 109–120, 2012.

Butler, P. G., Freitas, P. S., Burchell, M., and Chauvaud, L.: Archaeology and Sclerochronology of Marine Bivalves,
295   in: Goods and Services of Marine Bivalves, edited by: Smaal, A. C., Ferreira, J. G., Grant, J., Petersen, J. K., and Strand, Ø., Springer International Publishing, Cham, 413–444, https://doi.org/10.1007/978-3-319-96776-9_21, 2019.

Díaz, F., del Río-Portílla, M. A., Sierra, E., Aguilar, M., and Re-Araujo, A. D.: Preferred temperature and critical thermal maxima of red abalone Haliotis rufescens, Journal of Thermal Biology, 25, 257–261,
300   https://doi.org/10.1016/S0306-4565(99)00032-7, 2000.

Eerkens, J. W., Byrd, B. F., Spero, H. J., and Fritschi, A. K.: Stable isotope reconstructions of shellfish harvesting seasonality in an estuarine environment: implications for Late Holocene San Francisco Bay settlement patterns, Journal of Archaeological Science, 40, 2014–2024, https://doi.org/10.1016/j.jas.2012.12.018, 2013.

Ferguson, J. E., Johnson, K. R., Santos, G., Meyer, L., and Tripati, A.: Investigating $\delta13C$ and $\Delta14C$ within Mytilus
305   californianus shells as proxies of upwelling intensity, 14, 1856–1865, https://doi.org/10.1002/ggge.20090, 2013.

Fraser and Smith, G. M.: Notes on the ecology of the littleneck clam. Paphia staminea Conrad, 3, 249–269, 1928.

Gröcke, D. R. and Gillikin, D. P.: Advances in mollusc sclerochronology and sclerochemistry: tools for understanding climate and environment, Springer, 2008.

Hendy, I. L., Kennett, J. P., Roark, E. B., and Ingram, B. L.: Apparent synchroneity of submillennial scale climate
310   events between Greenland and Santa Barbara Basin, California from 30-10 ka, Quaternary Sci Rev, 21, 1167–1184, https://doi.org/Pii S0277-3791(01)00138-X Doi 10.1016/S0277-3791(01)00138-X, 2002.

Jazwa, C. S. and Kennett, D. J.: Sea Mammal Hunting and Site Seasonality on Western San Miguel Island, California, 21, 2016.

Jones, T. L. and Richman, J. R.: On mussels: Mytilus californianus as a prehistoric resource, 16, 33–58, 1995.

315   Keen, A. M.: Sea Shells of Tropical West America: Marine Mollusks from Baja California to Peru, Stanford University Press, 1110 pp., 1971.

Kennett, D. J. and Kennett, J. P.: Competitive and cooperative responses to climatic instability in coastal southern California, Am Antiquity, 65, 379–395, https://doi.org/Doi 10.2307/2694065, 2000.

Light, S. F., Smith, and Carleton, J.: The Light and Smith Manual: Intertidal Invertebrates from Central California to
320   Oregon, 2007.

Lisiecki, L. E. and Raymo, M. E.: A Pliocene-Pleistocene stack of 57 globally distributed benthic δ^{18}O records: PLIOCENE-PLEISTOCENE BENTHIC STACK, Paleoceanography, 20, n/a-n/a, https://doi.org/10.1029/2004PA001071, 2005.

Palmer, H. M., Vriesman, V. P., Bean, Jessica R., and Banker, Roxane M. W.: A database of Holocene nearshore
325   marine mollusc shell geochemistry from the Northeast Pacific., https://doi.org/10.1594/PANGAEA.932671, 2021.

R Core Team: R: A language and environment for statistical computing. R Foundation for Statistical Computing, 2021.

Rick, T. C., Robbins, J. A., and Ferguson, K. M.: Stable Isotopes from Marine Shells, Ancient Environments, and Human Subsistence on Middle Holocene Santa Rosa Island, California, USA, 1, 233–254,
330 https://doi.org/10.1080/15564890600935480, 2006a.

Rick, T. C., Erlandson, J. M., and Vellanoweth, R. L.: Taphonomy and site formation on California's Channel Islands, 21, 567–589, https://doi.org/10.1002/gea.20124, 2006b.

Robbins, J. A. and Rick, T. C.: The analysis of stable isotoes from California coastal archaeological sites: implications for understanding human cultural developments and environmental change, 19, 5, 2006.

335 Robbins, J. A., Ferguson, K. M., and Gregory, R. T.: A 7000-year sea-surface temperature record from CA-SRI-147, Santa Rosa Island, California, USA, The Holocene, 23, 1008–1016, https://doi.org/10.1177/0959683613479619, 2013.

Seed, R. and Suchanek, T. H.: Population and communtiy ecology of Mytilus, in: The Musel Mytilus: Ecology, Physiology, Genetics, and Culture, vol. 25, 1992.

340 Suchanek, T. H.: The ecology of Mytilus edulis L. in exposed rocky intertidal communities, Journal of Experimental Marine Biology and Ecology, 31, 105–120, https://doi.org/10.1016/0022-0981(78)90139-9, 1978.

Suchanek, T. H.: The role of disturbance in the evolution of life history strategies in the intertidal mussels Mytilus edulis and Mytilus californianus, Oecologia, 50, 143–152, https://doi.org/10.1007/BF00348028, 1981.

Takesue, R. K. and van Geen, A.: Mg/Ca, Sr/Ca, and stable isotopes in modern and Holocene Protothaca staminea
345 shells from a northern California coastal upwelling region, Geochimica et Cosmochimica Acta, 68, 3845–3861, https://doi.org/10.1016/j.gca.2004.03.021, 2004.

Thakar, H. B., Glassow, M. A., and Blanchette, C.: Reconsidering evidence of human impacts: Implications of within-site variation of growth rates in Mytilus californianus along tidal gradients, 427, 151–159, 2017.

Tissot, B. N.: Morphological variation along intertidal gradients in a population of black abalone Haliotis
350 cracherodii Leach 1814, Journal of Experimental Marine Biology and Ecology, 117, 71–90, https://doi.org/10.1016/0022-0981(88)90071-8, 1988.