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Short Communication

Investigating fishing strategies and habitat differences in late Holocene Oregon Coast sturgeon (*Acipenser* spp.) through coupled genetic and isotope analyses

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ABSTRACT

Understanding the habitats people were fishing in the past is central to evaluating the relationship between coastal environmental change and human behavior. Researchers often use zooarchaeological identification of fishes and modern ecological data to infer the habitats people fished in the past. However, these inferences assume stable environmental conditions through time and can be hindered by precision issues in identification of archaeological specimens (species vs. genus or family). Here, we integrate genetic and bulk tissue stable isotope data to investigate a late Holocene sturgeon fishery in northern Oregon. Ancient DNA analysis indicated that people were fishing for both green and white sturgeon (*Acipenser medirostris* and *Acipenser transmontanus*) in comparable numbers. Stable isotope analyses of these same bones documented distinct isotope values for each species, correlating with species-specific habitat preferences. These findings highlight the value of paired isotope and genetic data to elucidate human fishing strategies and environmental change and provide baseline ecological data for modern fisheries.

1. Introduction

Coastal regions around the world contain a variety of aquatic ecosystems, ranging from rivers, lakes, and streams to marshes, estuaries, and fully marine environments, providing a range of animal and plant species for human subsistence. Evaluating the habitats that people fished in the past is central for documenting a range of past and present cultural and environmental issues [see (Casteel, 1976; Wheeler et al., 1989; Colley, 1990; Morales-Muñiz and Llorente-Rodriguez, 2020)]. These include questions about the types of technologies people were using through time, evidence for intensification or diversification of subsistence strategies, and possible anthropogenic or climatic induced changes to coastal ecosystems. The most common approach for paleoenvironmental reconstruction and inferring past habitats from zooarchaeological and paleontological assemblages is by extrapolation from the known ecological preferences of modern fish species (Casteel, 1976; Wheeler et al., 1989). While this comparative approach is essential for historical ecology investigations, it hinders fine-grained analyses of generalist fishes which may occupy different habitats, or when taxonomic identifications are to genus or family level for functionally diverse groups (e.g., *Sebastes* spp. *Acipenser* spp.).

In this paper, we present stable isotope data from late Holocene green (*Acipenser medirostris*) and white (*Acipenser transmontanus*) sturgeon from the northern Oregon Coast. Zooarchaeological identification of eastern Pacific sturgeon is typically done to genus level due to interspecific similarities between the two species, especially in fragmentary specimens [see (Gobalet, 1994; Broughton et al., 2015; Grindle et al., 2021)]. Prior ancient DNA analysis of the same sturgeon bones we analyzed here for stable isotopes provided elements identified to species, with roughly 60% from white sturgeon and 40% from green sturgeon (Grindle et al., 2021). We explore if bulk tissue stable isotope values vary between these species, which are known to have overlapping but distinct habitat preferences (Hildebrand et al., 2016; Moser et al., 2016). Our work builds on past stable isotope studies of fish specimens from zooarchaeological collections [e.g. (Szpak et al., 2009; Fuller et al., 2012; Reitsema et al., 2013; Guiry et al. 2016, 2021; Zangrando et al., 2016; Braje et al., 2017; Jovanović et al., 2019; Dombrosky et al., 2020)] in providing important pre-industrial ecological data of endemic fish, as

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well as inferences into the types of habitats that were used by people during the late Holocene.

2. Materials and methods

Archaeological context and methods. All archaeological samples used in this study come from the Par Tee site (35CLT20), located at Seaside, Oregon about 24 km south of the Columbia River mouth (Fig. 1). The site was extensively excavated in the late 1960s–70s, including 256 1.5 × 1.5 m units with roughly 550 m^3 of excavated deposits [see (Sanchez et al., 2018)]. The deposits appear to have primarily been screened over ¼-inch mesh, with the extensive nature of the excavation producing a massive assemblage of archaeological faunal remains. These materials have been the focus of several recent studies, including work on human subsistence and historical ecology of sea otters, cetaceans, pinnipeds, shellfish, and finfish (Losey and Power, 2005; Losey and Yang, 2007; Colten, 2015; Wellman et al. 2017, 2020; Wellman, 2018; Loiselle, 2020; Grindle et al., 2021; Sanchez et al., 2022). These analyses have been enhanced by high resolution radiocarbon dating of the Par Tee deposits, which places most of the material at the site between cal AD 100–800 (Sanchez et al., 2018).

Subsequent analysis of fish bones from 1/8-inch residuals in bulk soil samples demonstrated that a range of fishes were captured by people living at the Par Tee site, including sharks, skates and rays (Elasmobranchii), rockfish (*Sebastes* sp.), lingcod (*Ophiodon elongatus*), cabezon (*Scorpaenichthys marmoratus*), flatfishes (Pleuronectiformes), Pacific hake (*Merluccius productus*), salmonids (*Oncorhynchus* sp.), and sturgeon (*Acipenser* spp.) (Sanchez et al., 2022). Grindle et al. (2021) complemented this analysis by studying 1770 sturgeon bones from 98 excavation units distributed across the site. To determine if both green and white sturgeon were present, ancient DNA analysis was performed on 30 specimens to determine which species the bones represented. Specimens were chosen from across the site to minimize the likelihood of sampling the same individual. Twenty-seven of these samples yielded DNA, with 16 from white sturgeon (59%) and 11 from green sturgeon (41%). These 27 samples then formed the basis for the bulk stable isotope analyses presented here.

Isotopic analysis. We measured $\delta^{13}C$ and $\delta^{15}N$ values of bulk bone protein for the 27 *Acipenser* specimens previously analyzed for ancient DNA and identified to species by Grindle et al. (2021). Sturgeon bone samples were demineralized with 0.25 M hydrochloric acid at 5 °C for 48–120 h depending on sample size and density; acid was replaced as needed every 24 h. Samples were then rinsed in deionized H_2O, lyophilized, and lipid-extracted via three sequential 24 h soaks in 2:1 chloroform:methanol at room temperature. Lipid extracted samples were rinsed in deionized H_2O, lyophilized, and weighed to evaluate percent protein yield. Following this, 0.5–0.6 mg of each sample was sealed in a tin capsule for bulk tissue isotopic analysis.

Bulk bone protein $\delta^{13}C$ and $\delta^{15}N$ values, along with weight percent [C] and [N], were measured via EA-IRMS using a Costech 4010 elemental analyzer (Valencia, CA) coupled to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer (Bremen, Germany) at the University of New Mexico Center for Stable Isotopes (UNM-CSI; Albuquerque, NM). All samples and reference materials were calibrated against the internationally accepted standards for stable carbon and nitrogen isotope ratios, respectively Vienna-Pee Dee Belemnite (V-PDB) and atmospheric N_2 (Sharp, 2017). We report all isotopic data as δ values in parts per thousand, or per mil (‰), where $\delta^{13}C$ or $\delta^{15}N = 1000^*[(R_{samp}/R_{std}) - 1]$. Here, R_{samp} and R_{std} are the ^{13}C:^{12}C or ^{15}N:^{14}N ratios of the sample and standard, respectively. The standard deviations of organic in-house reference materials (milk casein and tuna muscle) were ≤ 0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. As a control for the quality of our collagen samples (Ambrose, 1990; Szpak, 2011), we converted measured weight % [C]:[N] to atomic ratios via the following equation: $[C]:[N]_{atomic} = [C]:[N]_{weight} \times (14/12)$.

Statistical analysis. We conducted analyses in Program R [v. 4.1.2; (R Development Core Team, 2021)] with R Studio interface (v. 2022.02.3 + 492). We tested assumptions of normality (Shapiro-Wilk) and homogeneity of variance (F-test) and used unpaired Student's t-test to evaluate differences among *A. medirostris* and *A. transmontanus* in $\delta^{13}C$ and $\delta^{15}N$ values. We characterized the isotopic niche space occupied by each species, as well as the isotopic overlap using Bayesian standard ellipse areas (Jackson et al., 2011). We calculated the median Bayesian 95% ellipse areas for each group with 95% credibility intervals from 10,

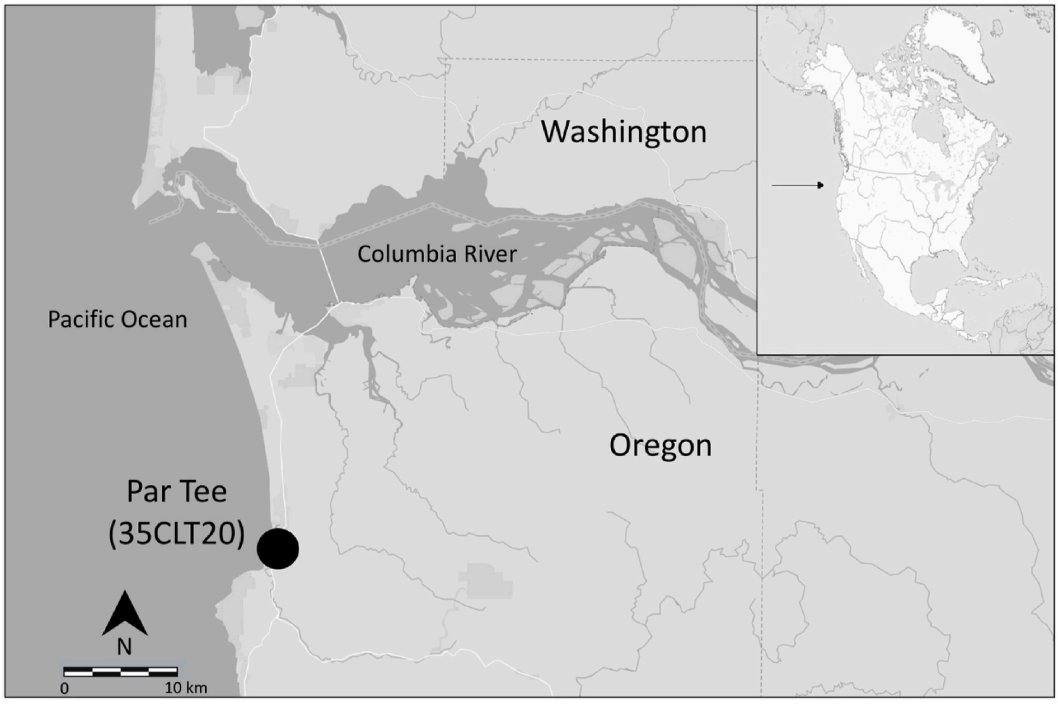

Fig. 1. Location of study area. Adapted from Grindle et al. (2021).

000 iterations, discarding the first 1,000. We express the overlap in isotopic ellipse area among *A. medirostris* and *A. transmontanus* relative to the sum of non-overlapping ellipse areas as: $\frac{Overlap\ in\ SEA}{(SEA_1 + SEA_2) - Overlap}$. This metric ranges from a value of 0 (no isotopic overlap) to 1 (complete isotopic overlap). We computed this metric across 1,000 Bayesian ellipse area calculations and report the median.

3. Results

We obtained reliable isotopic data for 18 *Acipenser* specimens (Table 1). Of the 27 samples we measured, 18 exhibited $[C]:[N]_{atomic} \leq 3.6$, 2 exhibited $[C]:[N]_{atomic} = 3.7$, and the remaining seven specimens had $[C]:[N]_{atomic}$ from 3.8 to 4.4. The generally accepted range of $[C]:[N]_{atomic}$ values for unaltered bone collagen is between 2.8 and 3.6 (Ambrose, 1990; Szpak, 2011; Guiry and Szpak, 2021). We excluded specimens with $[C]:[N]_{atomic} \geq 3.7$ from subsequent analyses, though we present all data in Table 1.

Par Tee green sturgeon (*A. medirostris*) exhibited higher mean $\delta^{13}C$ ($t_{16} = 3.5$, $p < 0.01$), and $\delta^{15}N$ values ($t_{16} = 3.0$, $p < 0.01$) than white sturgeon (*A. transmontanus*) (Fig. 2). The Bayesian standard ellipse areas of each species, a metric for the 'isotopic niche' also varied, with white sturgeon occupying a larger isotopic niche (median SEA_B [95% CI] = 3.9‰^{2} [2.2‰^{2}, 7.9‰^{2}]) than green sturgeon (SEA_B = 1.6‰^{2} [0.9‰^{2}, 3.5‰^{2}]). The median proportion of ellipse overlap relative to non-overlapping areas (0 = no overlap, 1 = complete overlap) was 0.24.

4. Discussion and conclusions

Bulk tissue isotopic measurements and previous genetic research of archaeological sturgeon bones provide important baseline ecological data for these endemic fish, as well as the types of species and habitats that people were targeting in the late Holocene. Green sturgeon are broadly considered the most marine of all *Acipenser*, spending most of their adult lives in estuaries and coastal habitats, and only returning to freshwater every few years to spawn (Moser et al., 2016). In contrast, the extent of marine habitat use by white sturgeon is not known (Hildebrand et al., 2016). Aggregations of white sturgeon do occur in estuarine environments (Patton et al., 2020), but the species can complete its entire life cycle within a single river basin (Hildebrand et al., 2016). Adult green sturgeon are opportunistic consumers of benthic intertidal fauna (e.g., *Neotrypaea californiensis*), as well as subtidal crustaceans, bivalves, and fish (Dumbauld et al., 2008). White sturgeon diets are similarly broad and vary with size (Muir et al., 1988), including fish such as lamprey (*Lampetra tridentata*), eulachon (*Thaleichthys pacificus*), and benthic invertebrates (Muir et al., 1988; Dumbauld et al., 2008).

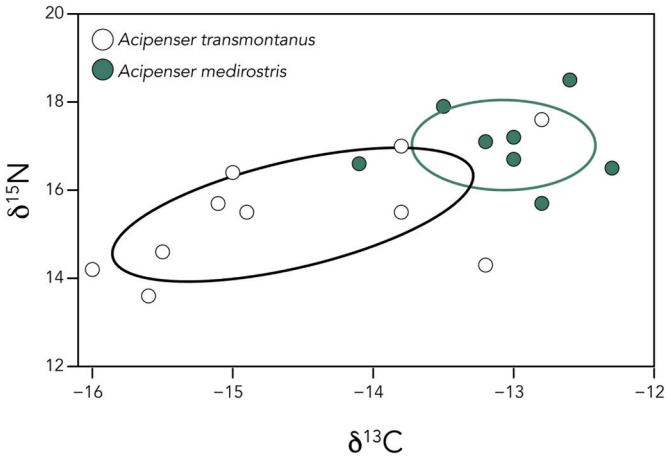

Fig. 2. Isotopic niche space of archaeological sturgeon specimens. Shown are bulk tissue carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values of green (*A. medirostris*; green circles) and white (*A. transmontanus*; white circles) sturgeon. Ellipses represent 50% of the total amount of bivariate isotope space occupied by each species. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Specimen ID	Provenience♣	Taxa*	Element	% Yield°	$\delta^{13}C$	$\delta^{15}N$	$\%N_{weight}$	$\%C_{weight}$	$[C]:[N]^{\nabla}_{atomic}$
ACME-91	SW20B7	*Acipenser medirostris*	Cranial	13	−12.6	18.5	16	44	3.2
ACME-101	SW20G6	*Acipenser medirostris*	Cranial bone	14	−12.3	16.5	16	45	3.3
ACME-110	NE8B6	*Acipenser medirostris*	Cranial	11	−13.0	17.2	16	45	3.4
ACME-95	SE6D7	*Acipenser medirostris*	Scute fragment	8	−13.0	16.7	16	46	3.4
ACME-107	NE10D4	*Acipenser medirostris*	Cranial	12	−12.8	15.7	15	46	3.5
ACME-93	SE8I10	*Acipenser medirostris*	Pectoral girdle	9	−13.2	17.1	12	37	3.5
ACME-89	SW20A8	*Acipenser medirostris*	Scute fragment	10	−13.5	17.9	15	46	3.5
ACME-90	SW20B6	*Acipenser medirostris*	Scute fragment	16	−14.1	16.6	9	29	3.6
ACME-100	SE6D5	*Acipenser medirostris*	Fragment	7	−14.1	16.2	13	43	3.7
ACME-88	NE17G7	*Acipenser medirostris*	Cranial	8	−15.2	17.6	13	44	4.0
ACME-92	NE8B5	*Acipenser medirostris*	Cranial	7	−15.9	16.8	14	46	4.0
ACME-99	SW20G2	*Acipenser medirostris*	Fragment; not scute	15	−17.9	14.6	11	42	4.4
ACTR-85	NE7I8	*Acipenser transmontanus*	Scute fragment	11	−16.0	14.2	16	45	3.3
ACTR-102	SE13L6	*Acipenser transmontanus*	Scute	14	−13.8	17.0	16	45	3.3
ACTR-103	SE13L7	*Acipenser transmontanus*	Pectoral girdle	12	−14.9	15.5	16	45	3.3
ACTR-113	SW20A6	*Acipenser transmontanus*	Scute	13	−15.6	13.6	16	46	3.3
ACTR-105	NE17F5	*Acipenser transmontanus*	Scute	15	−13.8	15.5	17	50	3.4
ACTR-86	NE7I6	*Acipenser transmontanus*	fragment	10	−13.2	14.3	15	45	3.4
ACTR-87	NE8H6	*Acipenser transmontanus*	Scute	13	−15.1	15.7	16	45	3.4
ACTR-97	SE5K10	*Acipenser transmontanus*	Scute fragment	8	−15.5	14.6	15	44	3.4
ACTR-98	NE7C7	*Acipenser transmontanus*	Fragment	9	−12.8	17.6	14	44	3.5
ACTR-109	SE8I5	*Acipenser transmontanus*	Cranial	9	−15.0	16.4	14	45	3.6
ACTR-108	SE8I7	*Acipenser transmontanus*	Fragment	9	−15.4	15.8	14	43	3.7
ACTR-106	NE10D3	*Acipenser transmontanus*	Scute	13	−16.4	14.8	13	43	3.8
ACTR-111	NE10D6	*Acipenser transmontanus*	Scute fragment	7	−14.1	16.5	13	44	3.8
ACTR-104	SE13L9	*Acipenser transmontanus*	Scute	7	−16.0	14.8	14	46	3.8
ACTR-96	SE5K8	*Acipenser transmontanus*	Scute	9	−15.3	16.2	13	43	3.8

♣ Unit and level specimen was recovered from, as in Grindle et al. (2021).
* Taxonomic identifications from Grindle et al. (2021).
°Calculated as: [(mass of specimen post demineralization, lipid extraction, and lyophilization) ÷ initial mass of specimen] × 100.
$^{\nabla}$Specimens with $[C]:[N]_{atomic}$ values ≥ 3.7 have likely undergone significant diagenetic alteration (Ambrose, 1990; Szpak, 2011) and were not included in statistical analyses or data interpretation.

Our analyses of sturgeon from Par Tee support this existing body of knowledge while providing new insights through stable isotope analysis from a pre-industrial context. Green sturgeon recovered from the site had high $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 2) and occupied a small isotopic niche space (1.6‰^{2}), indicating minimal ecological variation among individuals. Generally, species living or foraging in marine/estuarine ecosystems tend to have higher $\delta^{13}C$ and $\delta^{15}N$ values than those in freshwater habitats (Hobson, 1999), a pattern observed in populations of both modern *Acipenser* (Gu et al., 2001; Sulak et al., 2012) and their prey (Stewart et al., 2004; Zeug et al., 2014). Our results thus suggest that green sturgeon in the past were heavily reliant on marine environments and had similar ecological preferences to what is observed today.

In contrast, white sturgeon from Par Tee exhibited a much larger isotopic niche (3.9‰^{2}) and lower mean $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 2), suggesting a freshwater preference for the species (Hobson, 1999). A closer examination reveals two distinct clusters of white sturgeon in bivariate $\delta^{13}C$ and $\delta^{15}N$ space – one group with lower $\delta^{13}C$ and $\delta^{15}N$ values, and one group with higher values. The former matches $\delta^{15}N$ values of modern white sturgeon collected in San Francisco Bay (Stewart et al., 2004; Zeug et al., 2014). The $\delta^{13}C$ values of Par Tee sturgeon are higher than observed in modern individuals, though this may result from a combination of temporal [~1.5‰–2.0‰ (Dombrosky, 2020)], and tissue-specific [~1.0‰–5.5‰ (Sholto-Douglas et al., 1991; Guiry and Hunt, 2020);] isotopic differences.

The second grouping of Par Tee white sturgeon maps onto our measured isotopic niche for green sturgeon (Fig. 2). One possible explanation for this is consumption of migrating salmonids or eulachon, which is supported by movement patterns of modern white sturgeon (Hildebrand et al., 2016), and could serve to increase $\delta^{13}C$ and $\delta^{15}N$ values. However, seasonal consumption of anadromous fish is unlikely to be the sole explanation as the turnover rate of bone is slow, and collagen isotope values reflect decades of dietary information in a long lived species (Hobson and Clark, 1992; Hedges et al., 2007). Instead, our data suggest potential habitat segregation among white sturgeon in the past, with some individuals foraging predominantly in freshwater, and others in coastal or marine environments. However, substantial isotopic variability exists within both freshwater and marine ecosystems (Fuller et al., 2012; Sulak et al., 2012; Guiry, 2019), and studies employing essential amino acid $\delta^{13}C$ analyses [e.g. (Larsen et al., 2009, Elliott Smith et al., 2022)] are needed to confirm marine resource use by archaeological *A. transmontanus*. These studies could be paired with population genetic studies of both ancient and modern sturgeon to explore potential correlations among population structures and isotopic (e.g., dietary) niches (Cook et al., 2007; Brophy et al., 2020).

Previous studies of Par Tee (Colten, 2015; Grindle et al., 2021; Wellman, 2021; Sanchez et al., 2022) have highlighted the diversity of species and environments used by local people. Our isotopic measurements of Par Tee sturgeon demonstrate that these fish were ultimately sourced from a combination of marine and freshwater/estuarine environments and by extension people were utilizing resources from these habitats. However, it is unclear precisely where people obtained sturgeon. A large range of aquatic habitats existed historically in the Seaside region (Fig. 1) including coastal reefs, freshwater streams such as the Neawanna Creek and Necanicum River, a small embayment to the open ocean, and the massive Columbia River estuary about 24 km north (see Colten, 2015; Sanchez et al., 2022). Sturgeon could potentially have been taken from all these habitats using a variety of fishing methods (e.g., seines and nets, harpoons, and hook and line; Grindle et al., 2021; Sanchez et al., 2022). Indeed, the lower Columbia River (south of Bonneville Dam) is a known spawning and foraging area for modern populations of white sturgeon (McCabe Jr and Tracy, 1994; Parsley et al., 2008). Given the wide range of marine, freshwater, and terrestrial fauna available in the Par Tee assemblage (Colten, 2015; Sanchez et al., 2022), we suspect people were strategically and opportunistically obtaining sturgeon during fish migrations or summer foraging aggregations (see Parsley et al., 2008).

More broadly, our study highlights the importance of pairing genetic and isotopic analyses when studying faunal remains from archaeological or subfossil contexts; isotopic data alone would have incorrectly inferred several white sturgeon samples to be green sturgeon (Fig. 2), and genetic analyses cannot provide evidence of long-term consumer habitat use and diet. Pre-industrial data on sturgeon ecology (Fuller et al., 2012; Reitsema et al., 2013; Jovanović et al., 2019) are valuable for the management of modern fisheries, as ecological studies of *Acipenser* have been predominantly conducted in highly altered habitats (Gu et al., 2001; Secor et al., 2002; Sulak et al., 2012; Zeug et al., 2014; Hildebrand et al., 2016; Bruestle et al., 2019). Interdisciplinary analyses have great potential for future studies of the past hunting and fishing strategies of people and the historical ecology of native fauna.

Declaration of competing interest

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

Data availability

All data are available in the text (Table 1).

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References

Ambrose, S.H., 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. J. Archaeol. Sci. 17, 431–451.
Braje, T.J., Rick, T.C., Szpak, P., Newsome, S.D., McCain, J.M., Elliott Smith, E.A., Glassow, M., Hamilton, S.L., 2017. Historical ecology and the conservation of large, hermaphroditic fishes in Pacific Coast kelp forest ecosystems. Sci. Adv. 3, e1601759.
Brophy, D., Rodríguez-Ezpeleta, N., Fraile, I., Arrizabalaga, H., 2020. Combining genetic markers with stable isotopes in otoliths reveals complexity in the stock structure of Atlantic bluefin tuna (*Thunnus thynnus*). Sci. Rep. 10, 14675.
Broughton, J.M., Martin, E.P., McEneaney, B., Wake, T., Simons, D.D., 2015. Late holocene anthropogenic depression of sturgeon in san Francisco Bay, California. J. Calif. Great Basin Anthropol. 3–27.
Bruestle, E.L., Karboski, C., Hussey, A., Fisk, A.T., Mehler, K., Pennuto, C., Gorsky, D., 2019. Novel trophic interaction between lake sturgeon (*Acipenser fulvescens*) and non-native species in an altered food web. Can. J. Fish. Aquat. Sci. 76, 6–14.
Casteel, R., 1976. Fish Remains in Archaeology and Paleoenvironmental Studies. Academic Press, London.
Colley, S., 1990. The analysis and interpretation of archaeological fish remains. Archaeol. Method Theor. 2, 207–253.
Colten, R.H., 2015. Prehistoric coastal adaptations at Seaside, Oregon: vertebrate fauna from the Palmrose and Par-tee sites. J. I. Coast Archaeol. 10, 253–276.
Cook, B.D., Bunn, S.E., Hughes, J.M., 2007. Molecular genetic and stable isotope signatures reveal complementary patterns of population connectivity in the regionally vulnerable southern pygmy perch (*Nannoperca australis*). Biol. Conserv. 138, 60–72.
Dombrosky, J., 2020. A 1000-year 13C Suess correction model for the study of past ecosystems. Holocene 30, 474–478.
Dombrosky, J., Besser, A.C., Elliott Smith, E.A., Conrad, C., Barceló, L.P., Newsome, S.D., 2020. Resource risk and stability in the zooarchaeological record: the case of Pueblo fishing in the Middle Rio Grande, New Mexico. Archaeol. Anthropol. Sci. 12, 1–11.
Dumbauld, B.R., Holden, D.L., Langness, O.P., 2008. Do sturgeon limit burrowing shrimp populations in Pacific Northwest Estuaries? Environ. Biol. Fish. 83, 283–296.
Elliott Smith, E.A, Fox, M.D, Fogel, M.L, Newsome, S.D, 2022. Amino acid δ13C fingerprints of nearshore marine autotrophs are consistent across broad

spatiotemporal scales: an intercontinental isotopic dataset and likely biochemical drivers. Funct. Ecol. 36, 1191–1203. https://doi.org/10.1111/1365-2435.14017.
Fuller, B.T., Müldner, G., Van Neer, W., Ervynck, A., Richards, M.P., 2012. Carbon and nitrogen stable isotope ratio analysis of freshwater, brackish and marine fish from Belgian archaeological sites (1 st and 2 nd millennium AD). J. Anal. At. Spectrom. 27, 807–820.
Gobalet, K., 1994. A prehistoric sturgeon fishery in San Pablo, Contra Costa County, California: an addendum. Calif. Fish Game 80, 125–127.
Grindle, E.D., Rick, T.C., Dagtas, N.D., Austin, R.M., Wellman, H.P., Gobalet, K., Hofman, C.A., 2021. Green or white? Morphology, ancient DNA, and the identification of archaeological North American Pacific Coast sturgeon. J. Archaeol. Sci.: Report 36, 102887.
Gu, B., Schell, D., Frazer, T., Hoyer, M., Chapman, F., 2001. Stable carbon isotope evidence for reduced feeding of Gulf of Mexico sturgeon during their prolonged river residence period. Estuar. Coast Shelf Sci. 53, 275–280.
Guiry, E., 2019. Complexities of stable carbon and nitrogen isotope biogeochemistry in ancient freshwater ecosystems: implications for the study of past subsistence and environmental change. Front. Ecol. Evol. 7, 313.
Guiry, E.J., Hunt, B.P.V., 2020. Integrating fish scale and bone isotopic compositions for 'deep time' retrospective studies. Mar. Environ. Res. 160, 104982.
Guiry, E.J., Kennedy, J.R., O'Connell, M.T., Gray, D.R., Grant, C., Szpak, P., 2021. Early evidence for historical overfishing in the Gulf of Mexico. Sci. Adv. 7 eabh2525.
Guiry, E.J., Needs-Howarth, S., Friedland, K.D., Hawkins, A.L., Szpak, P., Macdonald, R., Courtemanche, M., Holm, E., Richards, M.P., 2016. Lake Ontario salmon (*Salmo salar*) were not migratory: a long-standing historical debate solved through stable isotope analysis. Sci. Rep. 6, 1–7.
Guiry, E.J., Szpak, P., 2021. Improved quality control criteria for stable carbon and nitrogen isotope measurements of ancient bone collagen. J. Archaeol. Sci. 132, 105416.
Hedges, R.E.M., Clement, J.G., Thomas, C.D.L., O'Connell, T.C., 2007. Collagen turnover in the adult femoral mid-shaft: modeled from anthropogenic radiocarbon tracer measurements. Am. J. Phys. Anthropol. 133, 808–816.
Hildebrand, L., Drauch Schreier, A., Lepla, K., McAdam, S., McLellan, J., Parsley, M.J., Paragamian, V., Young, S., 2016. Status of White Sturgeon (*Acipenser transmontanus* Richardson, 1863) throughout the species range, threats to survival, and prognosis for the future. J. Appl. Ichthyol. 32, 261–312.
Hobson, K.A., 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120, 314–326.
Hobson, K.A., Clark, R.G., 1992. Assessing avian diets using stable isotopes I: turnover of 13C in tissues. Condor 94, 181–188.
Jackson, A.L., Inger, R., Parnell, A.C., Bearhop, S., 2011. Comparing isotopic niche widths among and within communities: SIBER–Stable Isotope Bayesian Ellipses in R. J. Anim. Ecol. 80, 595–602.
Jovanović, J., de Becdelièvre, C., Stefanović, S., Živaljević, I., Dimitrijević, V., Goude, G., 2019. Last hunters–first farmers: new insight into subsistence strategies in the Central Balkans through multi-isotopic analysis. Archaeol. Anthropol. Sci. 11, 3279–3298.
Larsen, T., Taylor, D.L., Leigh, M.B., O'Brien, D.M., 2009. Stable isotope fingerprinting: a novel method for identifying plant, fungal, or bacterial origins of amino acids. Ecology 90, 3526–3535.
Loiselle, H., 2020. Humans, Dolphins, and porpoises. Ethnobiology Letters 11, 58–66.
Losey, R.J., Power, E., 2005. Shellfish remains from the Par-Tee Site (35-CLT-20), Seaside, Oregon: making sense of a biased sample. J. Northwest Anthropology 39, 1–20.
Losey, R.J., Yang, D.Y., 2007. Opportunistic whale hunting on the southern Northwest Coast: ancient DNA, Artifact, and Ethnographic evidence. Am. Antiq. 72, 657–676.
McCabe Jr., G., Tracy, C.A., 1994. Spawning and early life history of white sturgeon, *Acipenser transmontanus*, in the lower Columbia River. Fish. Bull. 92, 760–772.
Morales-Muñiz, A., Llorente-Rodriguez, L., 2020. Ichthyoarchaeology. In: Encyclopedia of Global Archaeology. Springer, pp. 5484–5502.
Moser, M., Israel, J., Neuman, M., Lindley, S., Erickson, D., McCovey Jr., B., Klimley, A., 2016. Biology and life history of Green Sturgeon (*Acipenser medirostris* Ayres, 1854): state of the science. J. Appl. Ichthyol. 32, 67–86.
Muir, W.D., Emmett, R.L., McConnell, R.J., 1988. Diet of juvenile and subadult white sturgeon in the lower Columbia River and its estuary. Calif. Fish Game 74, 49–54.
Parsley, M.J., Popoff, N.D., Wright, C.D., van der Leeuw, B.K., 2008. Seasonal and diel movements of white sturgeon in the lower Columbia River. Trans. Am. Fish. Soc. 137, 1007–1017.
Patton, O., Larwood, V., Young, M., Feyrer, F., 2020. Estuarine habitat use by white sturgeon (*Acipenser transmontanus*). San Franc. Estuary Watershed Sci. 18.
R Development Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
Reitsema, L.J., Kozłowski, T., Makowiecki, D., 2013. Human–environment interactions in medieval Poland: a perspective from the analysis of faunal stable isotope ratios. J. Archaeol. Sci. 40, 3636–3646.
Sanchez, G.M., Gobalet, K., Rick, T., 2022. New insights on the Par-Tee (35CLT20) site: collections-based research of northern Oregon Coast fisheries. J. I. Coast Archaeol. 17, 274–296.
Sanchez, G.M., Rick, T.C., Culleton, B.J., Kennett, D.J., Buckley, M., Erlandson, J.M., Losey, R.L., 2018. Radiocarbon dating legacy collections: a Bayesian analysis of high-precision AMS 14C dates from the Par-Tee site, Oregon. J. Archaeol. Sci.: Report 21, 833–848.
Secor, D.H., Anders, P.J., Van Winkle, W., Dixon, D.A., 2002. Can we study sturgeons to extinction? What we do and don't know about the conservation of North American sturgeons. In: *In* American Fisheries Society Symposium, pp. 3–10.
Sharp, Z., 2017. Principles of Stable Isotope Geochemistry, second ed.
Sholto-Douglas, A., Field, J., James, A., Van der Merwe, N., 1991. 13 C/12 C and 15 N/14 N isotope ratios in the Southern Benguela Ecosystem: indicators of food web relationships among different size-classes of plankton and pelagic fish; differences between fish muscle and bone collagen tissues. Mar. Ecol. Prog. Ser. 23–31.
Stewart, A.R., Luoma, S.N., Schlekat, C.E., Doblin, M.A., Hieb, K.A., 2004. Food web pathway determines how selenium affects aquatic ecosystems: a San Francisco Bay case study. Environ. Sci. Technol. 38, 4519–4526.
Sulak, K.J., Berg, J.J., Randall, M., 2012. Feeding habitats of the Gulf sturgeon, *Acipenser oxyrinchus desotoi*, in the Suwannee and Yellow rivers, Florida, as identified by multiple stable isotope analyses. Environ. Biol. Fish. 95, 237–258.
Szpak, P., 2011. Fish bone chemistry and ultrastructure: implications for taphonomy and stable isotope analysis. J. Archaeol. Sci. 38, 3358–3372.
Szpak, P., Orchard, T.J., Gröcke, D.R., 2009. A late holocene vertebrate food web from southern Haida Gwaii (Queen Charlotte Islands, British Columbia). J. Archaeol. Sci. 36, 2734–2741.
Wellman, H., 2021. Marine Mammals before Extirpation: Using Archaeology to Understand Native American Use of Sea Otters and Whales in Oregon Prior to European Contact. University of Oregon, Eugene.
Wellman, H.P., 2018. Applied zooarchaeology and Oregon Coast sea otters (*Enhydra lutris*). Mar. Mamm. Sci. 34, 806–822.
Wellman, H.P., Austin, R.M., Dagtas, N.D., Moss, M.L., Rick, T.C., Hofman, C.A., 2020. Archaeological mitogenomes illuminate the historical ecology of sea otters (*Enhydra lutris*) and the viability of reintroduction. Proc. Roy. Soc. B 287, 20202343.
Wellman, H.P., Rick, T.C., Rodrigues, A.T., Yang, D.Y., 2017. Evaluating ancient whale exploitation on the northern Oregon coast through ancient DNA and zooarchaeological analysis. J. I. Coast Archaeol. 12, 255–275.
Wheeler, A., Alwyne, W., Jones, A.K., Wheeler, W.A., Jones, J.A.K., 1989. Fishes. Cambridge University Press.
Zangrando, A.F., Riccialdelli, L., Kochi, S., Nye, J.W., Tessone, A., 2016. Stable isotope evidence supports pelagic fishing by hunter-gatherers in southern South America during the Late Holocene. J. Archaeol. Sci.: Report 8, 486–491.
Zeug, S.C., Brodsky, A., Kogut, N., Stewart, A.R., Merz, J.E., 2014. Ancient fish and recent invaders: white sturgeon *Acipenser transmontanus* diet response to invasive-species-mediated changes in a benthic prey assemblage. Mar. Ecol. Prog. Ser. 514, 163–174.