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Use of archaeological data in retracing diet and growth of extirpated fish populations in the California Delta: An allometric and isotopic approach to Sacramento perch (*Archoplites interruptus*) historical ecology

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ABSTRACT

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1acological data in retracting diet and isotop Sacramento perch (*Archoplites interruptus*), ubiquitous in the archaeological record throughout Central California, is now extirpated from the California Delta. Descriptions of Sacramento perch ecology, biology, and behaviour are either from relocated or declining populations. Archaeological specimens have the potential to provide insight on Sacramento perch demographics and feeding behaviour in their native range prior to large scale damming and the introduction of invasive species. We develop regression formulae to predict live length for three skeletal elements (vomer, dentary, and atlas). Formulae were applied to archaeological specimens (n = 182) from CA-CCO-647 (cal CE 1230–1440), Contra Costa County, California. Archaeological samples were then compared to length data from six contemporary relocated populations. Bulk collagen samples of specimens of varying lengths ($n = 12$) were run for $\delta^{13}C$ and $\delta^{15}N$. Archaeological specimens averaged 196 mm in standard length, and attained longer average and maximum lengths than relocated perch populations. Length distributions showed a high proportion of newly sexually mature individuals, suggesting that Sacramento perch were targeted while spawning nearshore. Nitrogen values correlated positively with standard length, suggesting that within the California Delta, Sacramento perch feeding behaviour changed as individuals grew, likely marking a shift to more piscivorous diets with age. Data highlight the potential of archaeological assemblages in reconstructing past length distributions and feeding behaviour for extirpated fish populations in their endemic ranges.

1. Introduction

The Sacramento-San Joaquin River Delta, or California Delta, is an inland river delta and estuary in central California, and is formed at the western edge of the Central Valley by the confluence of the Sacramento and San Joaquin rivers. The large size of the delta, diverse habitats, and isolation from other river systems made it a centre for fish speciation. Among the 40 native fish of the region, Sacramento perch (*Archoplites interruptus*) are the only native sunfish (family Centrarchidae) found west of the Rocky Mountains and are endemic to freshwater lakes, rivers, and streams of central California, inhabiting the Sacramento-San Joaquin river drainages, Pajaro and Salinas rivers, and Clear Lake (Fig. [1](#page-2-0)) (Gobalet, 1989; Moyle, 2002). Their historic habitats were thought to be sloughs, slow-moving rivers, and large lakes. Isotopic food web reconstructions from archaeological remains suggest that Sacramento perch within the Sacramento River drainages were mid-trophic level feeders (Talcott, 2019). Identification of ichthyofaunal remains from preindustrial and historic midden deposits indicate that they were abundant in the region, and a crucial resource to Indigenous and early historic fisheries ([Broughton,](#page-7-1) 1994; Gobalet and Jones, 1995; Gobalet et al., 2004; Miszaniec et al., 2018; Schulz, 1997, 1984, 1982, 1980; Schulz and Simons, 1973).

By the early 1850 s, Sacramento perch populations began to decline. The advent of hydraulic mining and damming eliminated floodplains, thought to be vital for spawning ([Woodley,](#page-8-1) 2007). Populations were further reduced through competition and predation by introduced sport fish such as non-native centrarchids, including sunfish (*Lepomis* spp.), crappie (*Pomoxis* spp.), and common carp (*Cyprinus carpio*) (Dill [and](#page-7-2) Cordone, 1997). In addition, over-fishing in the 19th century, along with water management practices, may have contributed to regional

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Fig. 1. Map of Sacramento perch historic (green) and current (red) ranges in California, along with locations mentioned in text. Light blue labels represent locations where length data were used. Inset map is of the San Francisco Bay and western portion of the California Delta. Sacramento perch distributions were obtained from ranges generated using PISCES (Santos et al., 2013). Map was produced using the ggplot2 package in R, version 4.0.2 (R Core Team, 2017; [Wickham,](#page-8-3) 2016). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

declines. By 1908, Sacramento perch were rare in the California Delta, and by the 1960 s were extirpated from its waterways (Fig. 1) (Moyle, 2002, p. 200; Rutter, 1908). Sacramento perch are now listed as endangered by the IUCN (NatureServe, 2013), and all current populations represent relocated fish, residing in isolated lakes and reservoirs in California, Utah, Nevada, and Colorado (Fig. 1) (Moyle, 2002). The longterm trajectory for Sacramento perch is trending towards decreasing genetic diversity and gradual disappearance from current isolated populations, eventually leading to extinction (Crain and Moyle, 2011).

Knowledge on Sacramento perch growth, behaviour, and diet is derived from populations in non-native lakes or in anthropogenically altered environments. Crain and Moyle (2011) present two alternative conceptual models of Sacramento perch life history, based on existing data. The two models are a reservoir–lake model, representing most present-day habitats, and a river model, which represents Sacramento perch in their historic range. The life cycle of Sacramento perch in rivers was presumably once closely tied to adult movement from the main channels and deep sloughs into shallow floodplains for spawning. Although reintroduction strategies of Sacramento perch populations in the California Delta have been proposed, they have not been developed due to the lack of biological knowledge within their native range (Crain et al., 2007; Moyle et al., 1995). Proposed re-introduction efforts would establish Sacramento perch in locations where populations were previously extirpated, or into constructed floodplain ponds, to approximate past conditions of the California Delta (Crain and Moyle, 2011: 30-31).

Future reintroduction strategies would benefit from baselines that would serve as a point of reference to evaluate the efficacy of management outcomes (Bull et al., 2014). Ideally baselines would reflect a time where there were fewer human impacts, and serve as an ideal to work towards .

Indigenous peoples of California have been harvesting species for thousands of years, and their archaeological midden deposits represent a wealth of ecological knowledge on past environments. Archaeological faunal remains are increasingly applied to understand the biogeography, biology, and demographics of past faunal communities [\(Erlandson](#page-7-6) and Rick, [2008\)](#page-7-6), and are especially relevant for species that are either extinct or extirpated from their native ranges (e.g. [Dombrosky](#page-7-7) et al.,

Fig. 2. A sample of measured archaeological Sacramento perch elements from CA-CCO-647 (Photographs by J. Morales).

2016; Guiry et al., 2020). Due to their ubiquity in the archaeological record, archaeological Sacramento perch specimens are uniquely poised to provide insight on their ecology within riverine habitats. We pair allometric length reconstructions with stable isotope analysis to reconstruct past Sacramento perch demographics and feeding behaviour within the California Delta.

[UN](#page-7-5)IT[E](#page-7-3)D 2013 and the state of the state In contrast to mammals, which eventually reach a maximum size with age, fish continue to grow throughout their lifespan. Consequently, size correlates with most life-history traits (e.g., age, diet, and fecundity), making it an important metric for fisheries management and assessment of population health (Shin et al., [2005](#page-8-6)). Length observations of relocated Sacramento perch populations will benefit from establishing length distributions from their native range prior to human disturbances and provide insight on the magnitude of change that damming and introduction of invasive species had on growth. Using the allometric or regression approach, formulae predicting length for three skeletal elements were developed. Formulae were applied to estimate live length of Sacramento perch from archaeological specimens from the California Delta. In addition, the application of archaeological chemistry, specifically stable isotope analysis, can highlight preferred prey species of Sacramento perch in floodplains environments before the introduction of invasive species. Pairing the two together can reveal changes in feeding strategies with age, adding insight on dietary preference through different life history stages.

Observations of relocated populations show that Sacramento perch lengths vary according to environmental conditions, such as temperature, salinity, or the occurrence of invasive species ([Aceituno](#page-7-8) and Vanicek, 1976; Marchetti, 1999; Mathews, 1962; McCarraher and Gregory, 1970; Vanicek, 1980). Water temperatures exceeding 20 °C, competition with invasive species, and lake size are considered factors that limit growth [\(Woodley,](#page-8-1) 2007). Although diets vary by location, food availability, season, and age, under optimal conditions, small perch are insectivores, first feeding on aquatic invertebrates, especially abundant insect larvae, and transitioning to a piscivorous diet as they grow larger (Mathews, 1962; Moyle et al., 1974; Vigg and Kucera, 1981). A diet of fish seems to relate to larger maximum lengths in populations inhabiting larger lakes. In contrast, when small forage fish are unavailable, growth rates are slower, and fish reach a smaller maximum length (Mathews, 1962). In small lakes, adult Sacramento perch diets consist of aquatic insect larvae, and occasionally fish and crayfish (Aceituno and Vanicek, 1976; Imler et al., 1975; Moyle et al., 1974).

To investigate the relationship between growth and diet, carbon $(\delta^{13}C)$ and nitrogen $(\delta^{15}N)$ stable isotopes were measured from a subsample of Sacramento perch bone collagen. δ¹³C values provide information about the sources of primary production. In freshwater food webs δ^{13} C varies in whether consumers derive their energy from bottom (profundal), offshore (pelagic), or nearshore (littoral) food webs (France, 1995; Guiry, 2019; Vander [Zanden](#page-7-9) et al., 2011; Vander [Zanden](#page-8-7) and [Rasmussen,](#page-8-7) 1999). Typically lentic (slow moving) waters of littoral environments are enriched in δ^{13} C, in contrast to faster moving open

pelagic waters (Guiry, 2019; Vander [Zanden](#page-7-10) et al., 2011). Globally, benthic algae in lakes are enriched in δ^{13} C by m 7%∼ compared to planktonic algae [\(France](#page-7-9) 1995). Carbon and nitrogen values of producers and consumers from Franks Tract demonstrate that differences in carbon values differ between littoral and pelagic environments in the California Delta ([Croteau](#page-7-11) et al., 2005). Epiphytes from littoral macrophytes were enriched in δ^{13} C -23.8‰ compared to phytoplankton collected offshore −28.6‰ [\(Croteau](#page-7-11) et al., 2005, p. 1516). These effects were also exhibited in consumers, such as invasive sunfish who occupied these respective environments. From contemporary populations, young Sacramento perch prefer nearshore environments, and gradually move to deep cooler waters with age.

We predict that Sacramento perch lengths will be longer on average the those of contemporary relocated populations, reflecting greater food availability, and lack of competition from invasive species. We expect carbon values to become depleted with size, reflecting a transition to more pelagic food webs. $\delta^{15}N$ will be used as an indicator of trophic position, which is based on an established stepwise 3–5‰ enrichment in δ ¹⁵N observed between trophic levels (Caut et al., [2009;](#page-7-12) Post, 2002). Based on contemporary and historic observations, we predict that longer fish will have enriched nitrogen values, reflecting a shift towards higher trophic level prey species, specifically small forage fish.

2. Materials and methods

2.1. Regression analysis

Regression formulae were created using skeletal elements from comparative Sacramento perch specimens ($n = 119$) housed in the Peter D. Schulz Osteoichthyology collection at the University of California, Davis. Comparative specimens were collected between 1974 and 1979, principally by John L. Dentler $(n = 67)$ and C. David Vanicek $(n = 33)$, and had length recorded on capture. Except for 14 individuals of unknown origin, all fish were from Californian lakes, mostly from Lake Greenhaven prior to their extirpation (Vanicek, 1980). Standard length (SL; body length from the tip of the fish's snout to end of the last vertebrae; Rojo, 1991) was selected as the output variable, as it was the most consistently recorded length among samples. Length of comparative specimens averaged 140 mm, and ranged between 80 and 255 mm. Regression formulas are constrained by the initial inputs, where the accuracy of the formulas will decrease when predicting lengths of fish smaller than 80 mm or $>$ 255 mm. This issue is difficult to correct given the rarity of large osteological Sacramento perch collections with recorded lengths.

Three separate regression formulae were created using comparative specimens for the atlas (first vertebra; $n = 90$), dentary ($n = 97$), and vomer ($n = 69$). These elements were selected due to their relative high bone density, making them more likely to preserve in the archaeological record (Hash et al., 2015, p. 92). Landmarks for measurements followed Orchard (2003), and were dentary 2: height of the symphyseal margin, vomer 1: maximum width, and atlas 1: maximum width. Measurements from selected skeletal elements for each comparative species were taken by M. Ramirez (author) using a pair of electronic calipers (RCBS: Electronic calipers) to the nearest 0.01 mm. Skeletal measurements for each comparative specimen was then plotted against its known length. Regression formulae were fitted using the "lm" function in base R version 4.0.3. to derive linear equations, $y = ax + b$, representing the relationship between selected skeletal measurement (x) and estimated standard length (y). Archaeological skeletal lengths were then inputted into the equation to derive length values.

2.2. Archaeological and contemporary specimens

Archaeological samples are from CA-CCO-647 (unincorporated Oakley) in the territory of the Bay or Eastern Miwok, Contra Costa County,

Fe between thresh and costings and continue the remains were corrected with a 17-fix-th map, and therefore the state in the state of the state in the state of the state in the state of the state in the state in the state California (Basin Research [Associates](#page-7-14) Inc., 2016, 2008). Radiocarbon dates and artefact typologies place the site to cal CE 1230–1440 [\(Basin](#page-7-14) Research [Associates](#page-7-14) Inc., 2016, 2008), representing the Middle-Late Transition to Late Phase 1 Periods [\(Groza](#page-7-15) et al., 2011). Ichthyofaunal remains were screened with a 1/8-inch mesh, and identified by Kenneth Gobalet, using comparative collections housed at the Department of Biology, California State University, Bakersfield [\(Gobalet](#page-7-16) et al., [2016](#page-7-16)). Of the 10,482 fish bones identified, the family Cyprinidae (NISP = 4422, 42%) dominate, followed by Sacramento perch (NISP = 3812, 36%), and Sacramento sucker (*Catostomus occidentalis*; NISP = 1784, 17%). The remaining 5% represent twelve taxa (NISP = 464). In total, 182 Sacramento perch elements were measured, comprising of atlas ($n = 88$), dentary ($n = 68$), and vomer $(n = 26)$ (Fig.2). Archaeological lengths were compared to length data from contemporary relocated populations from six ponds, lakes, or reservoirs within California, collected using clover traps, electrofishing, and hook and line, by the California Department of Fish and Wildlife's Inland Fisheries Conservation and Management Program between 2016 and 2017 [\(Fig.](#page-2-0) 1) (Coen et al., 2021; M. Fish, pers. comm.). There are multiple ways of measuring fish length: standard length, fork length (FL), and total length (TL). To standardize the data, all presented fish lengths are in standard length. Fork and total lengths for historic and contemporary specimens were converted to standard lengths using the FishBase Length-Length table for Sacramento perch ([Binohlan](#page-7-18) et al., 2011).

2.3. Isotopic analysis

Bones for isotopic analysis ($n = 12$) were selected based on the predicted standard length, to reflect a representative range of lengths. Selected specimens ranged from 115 to 366 mm in predicted length. Although specimens with predicted lengths smaller than 115 mm were processed, they did not yield adequate collagen $(>\frac{1}{2}$ for isotopic analysis.

A modified Longin procedure was followed to isolate bone collagen (Longin, 1971). Possible contaminants on the surface of the bone were cleaned with a microscope and dental pick. Once clean, specimens were sonicated in deionized H_2O (d H_2O) for five five-minute interval baths, where the dH₂O was replaced after each bath. After drying overnight, samples were weighed, and demineralized with a 0.5 M hydrochloric acid (HCI) solution, which was replaced every 1–2 days until complete demineralization. Residual humic acid was removed by washing the bone in dH2O and soaking it in in 0.125 M NaOH (sodium hydroxide) for 24 h. Samples were then rinsed in $dH₂O$ to remove any remaining NaOH.

To solubilize the collagen, pH3 water was added, and the sample was placed in an oven and heated to 70°–90 °C, over a 24–48 h period. Once solubilized, collagen was removed from any residual material, and placed in a freeze-dryer to remove water and isolate the collagen fraction. ¹³C/¹²C (δ ¹³C) and nitrogen ¹⁵N/¹⁴N (δ ¹⁵N) was measured by continuous-flow mass spectrometry (PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20–20 isotope ratio mass spectrometer) at the Stable Isotope Facility, University of California, Davis. δ^{13} C is presented in per-mil notation (parts per thousand) relative to the PeeDee Belemnite standard (arbitrarily set at 0%), while $\delta^{15}N$, is expressed against N_2 in modern atmospheric air (also arbitrarily set to 0‰). Long term reproducibility is approximately 0.1‰ for $\delta^{13}C$ and $0.2%$ for δ¹⁵N.

3. Results

3.1. Regression analysis

[Table](#page-4-0) 1 presents three separate univariate linear regression equations generated for the three Sacramento perch elements. Measure-

Table 1

Linear regressions for three Sacramento perch elements showing the slope (a) and intercept (b) for each formula, along with average error, percent error, standard deviation (StDv) for error between predicted and actual lengths.

	Element Orchard (2003) measurement	a b		\mathbf{r} squared error	(mm)	Average Average error (%)	StDv (mm)	n
Atlas			30 31	0.96	5	4%	5	90
Dentary 2			35 35	0.95	6	4%	5	97
Vomer			22 35	0.98	5	4%	4	69

ments are highly correlated with total length, where coefficients of determination (r^2) values range from 0.95 to 0.98 ([Table](#page-4-0) 1; [Fig.](#page-4-1) 3). The regressions predict standard lengths within 4 to 5 mm, or 4–5% of the actual standard lengths of the comparative fish. Total mean predicted standard length from CA-CCO-647 specimens (NISP = 182) range from 113 to 367 mm, where the average length was $196 + (-40 \text{ mm}$ ([Table](#page-4-2) 2; [Fig.](#page-4-3) 4; Fig. 5). Mean length for modern data from six localities ranged from 55 to 170 mm, while minimum length ranged between 33 and 120 mm, and maximum lengths ranged from 150 to 306 mm [\(Table](#page-4-2) 2).

Fig. 3. Osteological element measurements plotted against standard length for comparative Sacramento perch specimens, confidence interval of 0.95, along with regression formulae, and where measurements were taken for each osteological element. Figure was produced using the ggplot2 package in R, version 4.0.2 (R Core Team, 2017; Wickham, 2016).

Table 2

Descriptive statistics for predicted standard lengths for Sacramento perch elements from CA-CCO-647 and from contemporary relocated populations collected between 2016 and 2017. Contemporary lengths were converted from TL to SL.

	Location	County	Mean (mm)	Max (mm)	Min (mm)	StDv (mm)	n
Archaeological CE 1230-	CA-CCO-647 Atlas	Contra Costa	189	333	115	35	88
1440	CA-CCO-647 Dentary		208	367	113	54	68
	$CA-CCO-647$ Vomer		187	309	129	32	26
	CA-CCO-647 Total		196	367	113	40	182
Modern	Lake Almanor	Plumas	170	306	120	45	61
2016-2017	Biscar Reservoir	Lassen	163	226	111	41	37
	BP4	Mono	107	178	34	24	60
	Bridgeport Reservoir	Mono	119	175	86	37	46
	Gray Lodge Wildlife Area	Butte	55	150	33	30	37
	West Valley Reservoir	Modoc	138	171	77	18	50

Fig. 4. Histogram with superimposed density plot for estimated Sacramento perch lengths for all elements from CA-CCO-647 (number of bins = 30). Figure was produced using the ggplot2 package in R, version 4.0.2 (R Core [Team,](#page-8-3) 2017; Wickham, 2016).

Fig. 5. Box plot comparing archaeological Sacramento perch length from the California Delta to those of modern relocated samples. Horizontal line represents median value for each location. Rectangle encompasses the interquartile range from the 25th to the 75th percentiles. Dots represent individual specimens. Figure was produced using the ggplot2 package in R, version 4.0.2 ([R](#page-8-3) Core Team, 2017; Wickham, 2016).

3.2. Stable isotopes

Bone collagen showed C/N values within the range expected for archaeological fish bone [\(Szpak,](#page-8-9) 2011). Average isotopic values were as follows, $\delta^{15}N$: 8.6 + /-1.1, $\delta^{13}C$: -24.3 + /- 2.1 ([Table](#page-5-0) 3; [Fig.](#page-5-1) 6). A general linear model was run to test the effect of length on $\delta^{15}N$ and $\delta^{13}C$. Data were analysed in R, version 4.0.3 (R Core [Team,](#page-8-3) 2017). General linear models were fitted using the "lm" function in base R. Homogeneity of variance and normality was confirmed using residuals vs fits plots and Q-Q plots, respectively. Length and δ15N were significantly correlated (F = 11.6, p = 0.007), while length and δ 13C showed a slight correlation (F = 3.2, p = 0.102) [\(Fig.](#page-5-2) 7).

4. Discussion

Generally, Sacramento perch length correlates with age, where at the end of years 1, 2, 3, 4, 5, and 6, fish are typically 51 to 110 mm, 102 to 161 mm, 144 to 212 mm, 170 to 238 mm, 178 to 272 mm, and 238 to 306 mm, respectively ([Moyle,](#page-8-4) 2002). Although historically the longest Sacramento perch specimen caught measured 518 mm from Pyramid Lake, Nevada (area of 48690 ha) (Jordan and [Evernmann,](#page-7-20) [1896](#page-7-20)), most fish from relocated populations do not attain that size, and

Table 3

Stable isotope results from CA-CCO-647 Sacramento perch bone collagen.

Lab ID	Element	Element measurement (mm)	Predicted standard length (mm)	$\delta^{13}C$	C amount (ug)	$\delta^{15}N$	N amount (ug)	C/N	Collagen amount (mg)
1503415	Atlas	2.9	115.1	-29.4	215.9	8.3	77.4	3.3	0.82
1632586	Atlas	3.1	121.6	-23.1	247.3	7.6	81.8	3.5	0.78
1632587	Vomer	4.2	128.5	-26.4	171.3	8.5	57.2	3.5	0.62
1632585	Atlas	4.0	147.9	-25.2	202.4	6.4	70.5	3.4	0.70
1503414	Dentary	4.1	179.1	-24.1	323.9	8.9	113.9	3.3	1.03
1503419	Dentary	4.7	200.4	-24.0	381.8	7.9	132.3	3.4	1.09
1503031	Atlas	6.7	227.5	-22.1	440.1	8.5	155.9	3.3	1.17
1503412	Dentary	6.5	263.0	-23.2	417.2	7.7	142.2	3.4	1.18
1503416	Dentary	7.0	281.2	-21.7	456.8	9.3	159.0	3.4	1.18
1503413	Vomer	12.4	308.7	-25.4	321.9	9.9	107.7	3.5	1.21
1503417	Dentary	8.1	320.1	-22.8	486.6	10.1	171.8	3.3	1.49
1503418	Dentary	9.5	366.5	-23.9	512.5	10.0	174.1	3.4	1.43

Fig. 6. $\delta^{13}C$ and $\delta^{15}N$ stable isotope signatures for twelve Sacramento perch specimens from CA-CCO-647 samples, grouped by arbitrary 100 mm length categories. Figure was produced using the ggplot2 package in R, version 4.0.2 (R Core Team, 2017; Wickham, 2016).

Fig. 7. $\delta^{13}C$ (left) and $\delta^{15}N$ (right) values plotted against Standard length estimates, with confidenceinterval of 0.95. Figure was produced using the ggplot2 package in R, version 4.0.2 (R Core Team, 2017; Wickham, 2016).

show reduced growth rates. For instance, individuals of 4 years of age from Curved Pond (0.4 ha), Davis, were on average 159 mm (Crain et al., [2007\)](#page-7-4). At Clear Lake (18000 ha), a relatively large lake, small sizes (165–196 mm) in older fish (6–9 years) were attributed to competition with invasive sunfish (Moyle, 2002). Similarly from Lake Greenhaven (1760 ha), Sacramento perch growth rates declined after the introduction of bluegills (Vanicek, 1980).

Average predicted Sacramento perch length from CA-CCO-647 is 196 mm. Using Moyles's (2002) age classes, this would represent fish from 3 to 5 years of age. The mortality curve is unimodal with a right skew [\(Fig.](#page-4-0) 4) (skewness = 1.5). The exclusion of small individuals may reflect targeting of spawning adults. Observations from Pyramid Lake, Nevada, indicate that by the time Sacramento perch were 189 mm they spawned for the first time. This is during their second or third year of life. Thus, the high frequency of fish around 200 mm in length may represent a selection for newly sexually mature individuals. Sacramento perch move into shallow waters (15–60 cm) to spawn beginning at the end of March and continuing through the first week of August (Mathews, 1962; Moyle, 2002). From Clear Lake, Sacramento Perch shoal during spawning, where 50 spawning fish were in a 1.2×3.7 m area, putting nest density at nine spawning pair per 0.2 m^2 ([Murphy,](#page-8-7) [1948](#page-8-7)). Assuming that similar behaviour was exhibited in the California Delta, these dense aggregations would have made them a lucrative nearshore fishery for preindustrial Indigenous populations.

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234 234 Harvesting technology (i.e., spears, hook and line, nets of varying mesh sizes) would have further biased fish length distribution (see Colley, 1990, 1987; Greenspan, 1998). Unfortunately, ethnographic and historical mentions of Sacramento perch and how they were caught in the California Delta are scant. From historical accounts, Bay Miwok people fished primarily with nets from tule rafts [\(Cook,](#page-7-22) 1957, pp. 133–137). Cook (1960, p. 242) noted that the Northern Valley Yokuts people of the San Joaquin Valley fished for river perch (referring to Sacramento perch or tule perch [*Hysterocarpus traskii*]) using small dragnets equipped with stone sinkers. [Talcott](#page-8-0) (2019) argues that Sacramento perch, along with endemic cyprinids species, were harvested when flood waters receded in the summer, leaving spawning fish stranded in residual pools where they could easily be caught by hand, net, or basket. Excavations from CA-CCO-647 did not yield any fishing related artifacts directly or indirectly related to mass-capture technologies (traps or nets) and consist entirely of piercing (n = 5; e.g., harpoon heads) or hook and line technologies ($n = 6$; e.g., gorges and fishhooks) (Basin Research Associates Inc., 2016, p. 60). The emphasis in piercing fishing technologies in the archaeological record is also reflected in ethnographic accounts, where bone- or antler-tipped harpoons were used [\(Bennyhoff,](#page-7-24) 1950, pp. 312–316). If fish were targeted during spawning, then only mature, larger fish would be available, thus producing a wide unimodal mortality profile regardless of the technology used. In the future, expanding the sample size to include specimens from different sites and time periods can further aid in deciphering the effects of technologies on length.

Archaeological Sacramento perch from the California Delta show greater average and maximum lengths when compared to contemporary relocated populations ([Fig.](#page-4-3) 5). Relocated populations were between 26 mm and 131 mm smaller, on average, than the archaeological fish. Although mean length was likely biased by differences in harvesting methods, longer individuals are noticeably absent from modern fish. Of the contemporary populations only fish from Lake Almanor attained maximum lengths (306 mm) close to those from the archaeological specimens, which is likely due to the lake's relatively large size (11331 ha). Longer maximum lengths of Sacramento perch within the California Delta is consistent with observations from contemporary populations, which cite size of body of water, availability of prey, and competition with invasive species as limiting factors to growth. Although prey availability cannot be assessed at this time, at the very least these data provide insight into Sacramento perch length within their native range, and in the absence of invasive species. This preliminary data suggests that growth is significantly reduced in relocated populations.

Contrary to our hypothesis, δ^{13} C values showed a slight increase with length. This is likely due to the fact that $\delta^{13}C$ has a slight trophic level effect which may offset any habitat differences. In addition, carbon values (-24.3 +/- 2.1) for all size ranges fell within the ranges for nearshore (littoral) producers and consumers [\(Croteau](#page-7-11) et al., 2005, p. 1516). It is likely that both larger and smaller Sacramento perch fed in littoral environments; although large fish may have moved into deeper waters, they may still have fed in nearshore environments.

Is likely due to be for that are [C](#page-8-15)han sight repoiled to the materpaos (c_6 is an $\frac{1}{2}$ is an $\frac{1}{2}$ is an $\frac{1}{2}$ is a sight response to be for the different interest in the material of the material of the mate Estimated standard length was strongly correlated with nitrogen values ([Fig.](#page-5-2) 7). The relationship between length and nitrogen demonstrates that as Sacramento perch grew in the California Delta, they adjusted feeding strategies, with older/larger individuals feeding on higher trophic level prey species. These results are concurrent with observations from relocated populations [\(McCarraher](#page-8-10) and Gregory, [1970\)](#page-8-10). Although baseline isotopic data is required, enriched nitrogen in longer specimens likely represents a shift to a primarily piscivorous diet. Larger Sacramento perch exhibit cannibalistic behaviour ([Moyle,](#page-8-4) [2002\)](#page-8-4), which could further increase their nitrogen values. Interestingly, nitrogen values only surpass 9.0‰once fish either reached or exceed a length of 300 mm (Fig. 4). Of individuals measuring > 300 mm, nitrogen values on average were $9.8 +/- 0.4\%$, while those \lt 300 mm were $8.0 + (-0.8\%,$ which suggests that the transition to higher trophic foods represents an abrupt dietary change rather than a gradual shift. Such a strict division between length and diet was also exhibited in stomach contents from Sacramento perch in Pyramid Lake, where the proportion of fish in stomach content of large (>255 mm) Sacramento perch was 98% by volume, in contrast to smaller individuals measuring 172–248 mm($n = 11$) where fish made up just 6% of stomach content (Vigg and Kucera, 1981, p. 284). As Sacramento perch eat prey items corresponding to their gape, it is likely that a shift to a piscivorous diet may have either an environmental or physiological constraint that limits this dietary transition until individuals attain a specific size.

4.1. Archaeological implications

Despite dominating ichthyofaunal collections, and contributing significantly to past human diets in the California Delta, Sacramento perch have received disproportionately less archaeological attention, when compared to large anadromous fish such as Pacific salmon (*Oncorhynchus* spp.) and sturgeon (*Acipenser* sp.) (Broughton et al., 2015; Eerkens et al., 2021; Gobalet et al., 2004). Increasingly, zooarchaeological studies have revealed the importance of small fish to preindustrial fisheries along the North American west coast: e.g., northern anchovy (*Engraulis mordax*) (McKechnie, 2005), Pacific herring (*Clupea pallasii*) (McKechnie et al., 2014; Moss et al., 2015; Sanchez, 2020), surf smelt (*Hypomesus pretiosus*), night smelt (*Spirinchus starski*) (Tushingham et al., [2013](#page-8-14)), saffron cod (*Eleginus gracilis*) (Miszaniec et al., 2019; Partlow and [Munk,](#page-8-15) 2015). Future research exploring the resilience of native freshwater fish communities to persistent fishing pressures and climate change in the late-Holocene can characterize why Sacramento perch were such a persistent protein source to Indigenous peoples. For instance, the abundance of Sacramento perch may have been a product of them evolving in the highly variable environments of the California Delta, making them well adapted to drought, increased salinity, and wide temperature ranges (Crain and Moyle, 2011). Their opportunistic omnivorous diets, in conjunction with adaptive life history strategies, would have also contributed to their environmental resilience. They may have been targeted due to their adaptability and wide physiological tolerance, making them a reliable and sustainable food source.

This study has shown that length estimates can provide insight on population structure of captured fish as well as possible time of harvest. The application of these regression formulae to other collections can potentially further contribute to studies of resource depression, resilience, and intensification by examining if size may have been affected by anthropogenic pressures through time. Size reconstruction can also be used as a tool to infer indigenous management or conservation strategies (e.g. Braje et al., 2017; Sanchez, 2020; Whitaker, 2008).

Incorporating length with carbon and nitrogen isotopes has the potential of refining studies of past human diets. Carbon and nitrogen values of potential prey species are often used as baselines or incorporated into models to infer proportion of dietary contribution to consumer diets. This data shows that there is variability in nitrogen and carbon content within fish of differing lengths. Thus, baseline values will be influenced by length of the fish incorporated into the comparison. Time of capture and fishing technologies could bias length distribution of fish captured, influencing carbon and nitrogen values. Future studies incorporating Sacramento perch, and other fish, in stable isotope dietary reconstructions would merit from taking length into account, to provide more accurate baseline data.

5. Conclusions: Archaeological records and the future of Sacramento perch

The application of osteologically derived regression formulae demonstrates that Sacramento perch were on average longer in the floodplain environments of the California Delta when compared to current relocated populations. Our data suggests that restricted habitat size, and introduction of invasive species greatly reduces growth potential in Sacramento perch populations residing in reservoirs and lakes. Pairing length reconstruction with carbon and nitrogen isotopes shows that as they grow, Sacramento perch consume higher trophic level foods in floodplain environments. These data suggest that availability of higher trophic food items may be a limiting factor for growth in Sacramento perch in their native range.

Although the prospect of reintroduction into the California Delta is unlikely, archaeological collections hold valuable untapped data in evaluating growth and behaviour that would be expected in populations in river-model ecosystems versus observed patterns from current populations in reservoir–lake model ecosystems (Crain and [Moyle,](#page-7-3) 2011). Crain and Moyle (2011, p. 26) list 7 categories where information is needed to improve management strategies for Sacramento perch: floodplain use, reproductive behaviour, life history strategies, effects of alien species, effects of water quality, genetics, and other potentially limiting factors. Archaeological data hold enormous potential in addressing several of these areas by providing baseline data for Sacramento perch growth and feeding behaviour in their natural ranges.

Sacramento perch remains have been identified in the San Francisco Bay, San Joaquin Valley, and Sacramento Bay river drainages. By pairing length and isotope data to collections from sites across the Central Valley we can begin to understand the effects of local environments on feeding and growth rates in different watersheds. In addition, diachronic analysis paired with paleoclimatic records can further highlight their resilience and adaptability to climatic cooling and warming events. Ancient DNA holds baseline information of how much genetic variability has been lost in relocated populations, and potential genetic variability within past watersheds. Such data would complement genetic studies of modern relocated populations (e.g. Coen et al., [2021\)](#page-7-17). In addition, isotopic food web reconstructions, as shown by [Talcott](#page-8-0) (2019), can reconstruct freshwater food-web dynamics preintroduction of invasive species, and when paired with modern samples, can indicate how these food-webs were disrupted. The analysis of archaeological otoliths can also discern past growth rates and life history strategies ([Campana,](#page-7-27) 1999; Disspain et al., 2016).

This research highlights the potential of archaeological data in understanding the biology of Sacramento perch, as well as of other endemic fish native to the California Delta prior to the damaging environmental effects of hydraulic mining, damming, and the introduction of invasive sport fish.

Uncited references

Jones and [Schwitalla](#page-7-28) (2008), Stine (1994).

CRediT authorship contribution statement

Jason I. Miszaniec: Conceptualization, Methodology, Investigation, Writing – review & editing, Writing – original draft, Visualization. **Matthew Ramirez:** Validation, Investigation. **Jessica Morales:** Investigation, Writing – review & editing. **Jelmer W. Eerkens:** Resources, Writing – review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

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

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