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A 200-year archaeozoological record of Pacific cod (*Gadus macrocephalus*) life history as revealed through ion microprobe oxygen isotope ratios in otoliths

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ABSTRACT

We measured $\delta^{18}O$ values in modern and archaeological Pacific cod (*Gadus macrocephalus*) otoliths recovered from Aialik Bay on the Pacific coast of the Kenai Peninsula, Alaska, using a high precision ion microprobe. Values of $\delta^{18}O$ were measured in as many as sixty 10-μm spots along 2–3 mm transects from the otolith core to its margin with high spot-to-spot analytical precision ($\delta^{18}O \pm 0.3‰$). We obtained sample densities along a linear transect that were at least 2 to 3 times greater than micromilling/conventional mass spectrometry techniques. From modern Pacific cod otoliths (using *in situ* temperatures from electronic archive tags) we calibrated an empirical fractionation equation of aragonite $\delta^{18}O$ to sea water temperature ($r^2 = 0.75$, $p < 0.001$, $\delta^{18}O_A = 2.13–0.25\,T\,^{\circ}C$) and from which we predicted the thermography of fish life history and historic nearshore water temperature in the Gulf of Alaska (GOA). Sinuous variability of $\delta^{18}O$ values along core-to-margin transects likely reflect seasonal temperature changes and suggest similar longevity between modern and archaeological cod. Generally increasing $\delta^{18}O$ values from the otolith core region to the margin revealed an ontogenetic migration from warmer nearshore habitat during the first year of life to cooler deeper waters at later ages, a behavior that has not changed over the past 200 years. A decline in the average $\delta^{18}O$ of otolith cores from archaeological (~200 +, ~100 + years before present, YBP) to modern otoliths suggest increasing sea surface temperatures from the late Little Ice Age to present. Temperatures calculated from the $\delta^{18}O$ in aragonite suggest a 2–3 °C rise in coastal marine sea surface temperatures in the GOA over the last 200 years. Implications of indigenous subsistence resource use and settlement patterns are discussed in light of major shifts in GOA water temperatures and biological regimes.

1. Introduction

Pacific cod (*Gadus macrocephalus*) is a demersal marine fish species that has a pan-Pacific distribution with abundances concentrated over continental shelves and slopes to 500 m and marginal seas in the northern hemisphere (Allen and Smith, 1988). Recent genetic studies point to contemporary population structure of Pacific cod that has been shaped by genetic divergences from ice-age isolations and postglacial colonization (Canino et al., 2010). In the Gulf of Alaska and Bering Sea, where present day Pacific cod are most abundant in the Northeast Pacific, populations originated from a southern refuge population from colonizations as late as 14,000–15,000 YBP (Canino et al., 2010). Subsequent to the ice-age maxima, interglacial periods would have been favorable for reconnection of divergent populations and increased gene flow resulting in gradients of genetic subdivision which is observed today in the Gulf of Alaska (GOA) and Aleutian Islands (Cunningham et al., 2009; Canino et al., 2010; Spies, 2012). Since the "Medieval Warm period" (MWP) ca. 900–1350 CE and subsequent Little Ice Age ca. 1350–1900 CE (Mann et al., 1998), climate system changes, particularly in the North Pacific Ocean circulation patterns

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and coast thermal structure, probably had a substantial impact on how these genetic subdivisions interacted and adapted to local environmental processes.

All life stages of Pacific cod have unique geographic area, depth, and temperature regimes, which may have been affected by ice-age reorganizations. For instance, adults generally spawn widely over the continental shelf in water up to about 200 m with eggs loosely adhering to benthic habitat. After hatching larvae are carried into the upper layers of the water column where they are transported shoreward and then westward by the Alaska Coastal Current (Matarese et al., 2003; Hurst et al., 2009; Rugen and Matarese, 1988). Juvenile Pacific cod in their first year of life (age-0) are thought to settle into shallow coastal areas and embayments where they are associated with seagrass, kelp and other structure for nursery habitat (Abookire et al., 2007; Laurel et al., 2007; Stoner et al., 2008). Following the early juvenile stage, age-1 Pacific cod are still found near coastal margins (Laurel et al., 2009). As they mature to sub-adult and adult life stages they go through an ontogenetic offshore migration to cooler continental shelf waters (Nichol et al., 2007). Thus, habitat requirements for reproduction, rearing, growth, and survival are on a continuum of habitat type from nearshore to deeper offshore continental shelf waters.

In ecological time scales, distribution and life history characteristics of contemporary populations responded to historic changes in temperatures. Pacific cod have been found to actively avoid the summer 'cold' pool (0–2 °C), a reoccurring cool dense water mass in the Bering Sea (Ciannelli and Bailey, 2005). During recent climatic warming events in the Bering Sea, Pacific cod have followed northward ice retreat (Mueter and Litzow, 2008) and in some years have been found as far north as the Bering Strait (Lauth, 2011). Pacific cod have high fecundity, fast growth rates, and planktonic larval stages (Paul et al., 1990; Ormseth and Norcross, 2009) which can facilitate high levels of gene flow between populations, swift colonization, and rapid population growth. Despite the large potential for gene flow, several discrete populations have been identified on relatively small geographical scales (Canino et al., 2010) from the Gulf of Alaska to the Aleutian Islands and Bering Sea (Spies, 2012).

Pacific cod have been an important food source in the GOA for centuries, utilized by modern industrial fisheries and indigenous Alutiiq (Sugpiaq) residents (Birket-Smith, 1953; Davydov, 1977; Steffian et al., 2015). As reported by 18th and 19th century observers and written historical accounts (Holmberg in 1851), Alutiiq fishers in kayaks took adult cod in water depths of 85–128 m using a bottom-fishing rig made up of a dried kelp line, bone hooks suspended from a wooden spreader, and a grooved anchor stone (Birket-Smith, 1941; Heizer, 1952; Holmberg, 1985; Korsun, 2012; Shelikhov, 1981; Steffian et al., 2015). Russian naval officer Gavriil Davydov, who was stationed on Kodiak Island in 1802–03, wrote that in spring, cod arrived "off the shore in great shoals" and that Alutiiq residents harvested them until the first salmon became available (Davydov, 1977).

Pacific cod otoliths for the present study were collected at two historic village sites in Aialik Bay on the GOA coast of the Kenai Peninsula (Fig. 1). The Early Contact Village site (XBS-029) includes pit houses and a stratified shell/bone midden (Fig. 2). It was occupied in ~1790–1820 CE based on the predominance of bone and stone artifacts combined with trade artifacts (glass beads, pieces of iron and copper, a 1748 ½ kopek coin) indicative of early Russian contact (Crowell et al., 2008; Crowell and Mann, 1998). A single radiocarbon date on a wood charcoal (species unidentified) from the base of the stratified midden 25 cm below surface was 180 +/− 60 RCYBP (Beta 74,860), which most likely falls within the calibrated interval 1720–1820 CE ($p = 36.4\%$ at 2 SD). During the archaeological excavations at this site 12,709 fish bones were recovered, of which 2620 were taxonomically identifiable to at least the family level (Hanson, 2007). Of the identifiable bones, 1815 (69.3%) of these were cod (Gadidae) followed by rockfish (Scorpaenidae), flatfish (Paralichthyidae, Pleuronectidae), greenlings (Hexagrammidae), sculpins (Cottidae), salmon (Salmonidae), and herring (Clupeidae). Most gadid bones were presumed to be Pacific cod although walleye pollock (*Gadus chalcogrammus*), saffron cod (*Eleginus gracilis*), and Pacific tom cod (*Microgadus proximus*) could also have been represented. The faunal assemblage included 31 otoliths identified as Pacific cod. The adjacent Denton Site (XBS-014) includes seven debris mounds left nearby former log cabins (Fig. 2) and was occupied during ~1850–1920 CE based on the range of manufacturing dates for > 700 glass, ceramic, and metal trade artifacts, with a mean date of 1880 CE (Crowell, 2006; Crowell and Mann, 1998). Of 12,800 fish bones recovered during Denton Site excavations, 2243 were identifiable to family and of these 1349 (60%) were cod (Gadidae), followed by rockfish and other minor taxa (Hanson, 2009). Six otoliths from the Denton site were identified as *Gadus macrocephalus*, of which three were selected for the present study. Four additional otoliths were of the family Gadidae.

Otoliths are calcium carbonate structures found in the inner ear of teleost fish. In most fish, including Pacific cod, a new layer of calcium carbonate (in the form of aragonite) is deposited over the course of each year forming annual growth zones (Matta and Kimura, 2012; Kastelle et al., 2017). Calcium carbonate is usually precipitated in isotopic equilibrium with the surrounding seawater (Campana, 1999; Thorrold et al., 1997). In otoliths, and other marine carbonates, the oxygen isotope fractionation, $^{18}O/^{16}O$, (measured as $\delta^{18}O$) is dependent on temperature and has been shown to decline as water temperature increases (Hoie et al., 2004a; Kastelle et al., 2017). The otolith's $\delta^{18}O$ is also a function of $\delta^{18}O$ in the surrounding seawater, which varies due to such things as continental freshwater runoff and atmospheric inputs. Salinity is often used as a predictor of the water $\delta^{18}O$ and the relationship between salinity and $\delta^{18}O$ has been reported in numerous studies (Grossman and Ku, 1986; Jones and Campana, 2009; Lécuyer et al., 2004; Campana, 1999), implications regarding this are discussed later in this paper. Otoliths are metabolically stable throughout the life of the fish. Therefore, they provide a recording mechanism and a way to reconstruct temperature over the fish's life history (Hoie and Folkvord, 2006; Darnaude et al., 2014; Thorrold et al., 1997). Indeed, this relationship between temperature and $\delta^{18}O$ has been used in a range of marine carbonates including corals and shells (Grossman and Ku, 1986; Culleton et al., 2009; Nielsen and Nielsen, 2009; Lopez Correa et al., 2010) and also in fish otoliths (Weidman and Millner, 2000; Hoie et al., 2004a; Hoie et al., 2004b; Kastelle et al., 2017). Further, some studies have investigated oxygen isotopes in Pacific cod otoliths as paleothermometers (West et al., 2012) and Atlantic cod (*Gadus morhua*) otoliths found at archaeological sites as a record of historical interactions between climate, fish populations, and early coastal inhabitants (Geffen et al., 2011).

Our goal was to reconstruct the nearshore temperature regime and ontogenetic Pacific cod habitat use in the GOA since the late Little Ice Age. Intact Pacific cod otoliths found at the ~200 + YBP (Years Before Present = Years Before 2K). Early Contact Village and the ~100 + YBP Denton site provided a unique opportunity to explore interactions between climate and fish populations on temporal scales not typically available to modern ecologists. By using a high-resolution sampling method and applying an empirical oxygen-temperature fractionation curve, we analyzed oxygen isotope ratios ($\delta^{18}O$) for otoliths from each of the two sites and from modern (2004) Aialik Bay fish. We anticipated that isotopically derived water temperatures for the ~200 + YBP samples should be significantly colder than present since they derive from the late Little Ice Age (LIA). During the final cooling phase of the LIA from 1810 CE to 1880 the mean air temperature from February to August on the GOA coast has been reconstructed from tree ring data to have been 6.7 °C, compared to a mean of 7.7 °C from 1880 CE to 2010 (Wiles et al., 2014). Therefore, the $\delta^{18}O$ values from the ~200 + and ~100 + YBP and modern otoliths should reflect this post-LIA warming trend. Cultural transitions and altered settlement patterns in relation to possible shifts in GOA water temperatures and biological regimes were also examined.

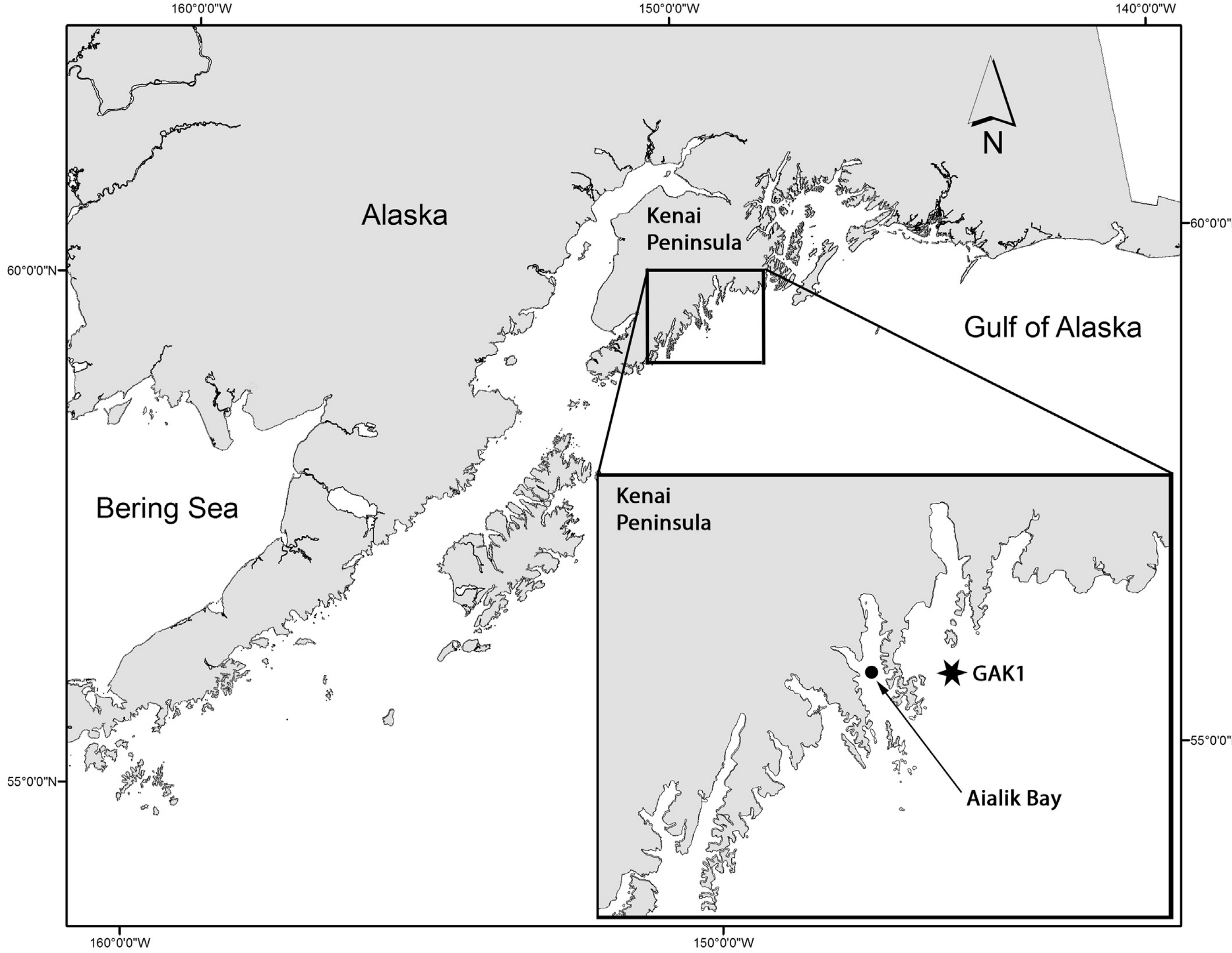

Fig. 1. Recovery location (yellow arrow) of Pacific cod (*Gadus macrocephalus*) otoliths from archaeological sites in Aialik Bay, Alaska. The location of the GAK1 oceanographic mooring is shown (red star) which is at 59° 50.7′ N, 149°28.0′W, within the Alaska Coastal Current. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2. Material and methods

Nine Pacific cod otoliths were chosen, 3 from each of the two sites described above (representing ~200 + YBP from XBS-029 and ~100 + YBP from XBS-014) and 3 recently collected (modern) otoliths. The modern otoliths were from adult fish captured in 2004 near the entrance of Aialik Bay. These were processed and analyzed in 2007 (Table 1). Another set of 7 otoliths which came from adult Pacific cod tagged with archival recoding tags (*in situ* bihourly measurements of depth and water temperature were recorded) and at liberty for 1–2 years (Nichol et al., 2007) were analyzed in 2011–2012. Otoliths were sonically cleaned, dried, weighed, and embedded in polyester resin. Fish lengths were estimated by using a relationship between otolith weight and fish length established by the International Pacific Halibut Commission (Kastelle et al., 2017). The embedded otoliths were thin sectioned on a high speed IsoMet 5000 saw. Three parallel cuts were made, and two transverse thin sections centered on the otolith's focus were extracted. The thin sections were mounted on glass slides and polished on an EcoMet 3 (Buehler Inc.) polishing wheel with 1200 grit which produced thin sections about 0.75 mm thick. Annual growth zones, which consist of paired opaque and translucent zones, were examined using reflected light under a Leica stereomicroscope. Ages of the Pacific cod were determined by counting the translucent zones (Matta and Kimura, 2012) from high-resolution digital images of the sectioned otoliths, and the innermost growth zone was identified. This innermost growth zone represents the first year of life, a stage when Pacific cod are using nearshore coastal areas as nursery habitat. Thin sections were remounted in epoxy disks (2.5 cm diameter and 4 mm thick), such that the polished side of the thin section was exposed on one surface of the disk, along with small crystals of a calcite standard. The disks and thin sections were finely polished using an EcoMet grinder/polisher (Buehler Inc.) with sequentially higher grits (600, 800, 1200), followed by a final 0.05 μm diamond polishing compound. Next, they were cleaned in a sonic cleaner after which they were dried in a vacuum oven at 40 °C for 2.5 h. Finally, prior to instrumental sampling, the epoxy plugs with embedded otolith thin sections were sputter coated with an even layer gold ~60 nm thick.

In situ oxygen isotope ratios were obtained using a CAMECA IMS-1280 large radius, multi-collector ion microprobe at the WiscSIMS Laboratory, University of Wisconsin-Madison (Valley and Kita, 2009). In the ion microprobe sampling, transects of 10 μm diameter spots were made from otolith core region to edge (Fig. 3); this ensured sample coverage for the entire life history. Generally, transects were approximately 3–4 mm long in either a dorsal or ventral axis; the choice of axis depended on the clarity of annual growth zones and avoidance of cracks and occlusions. The sampling strategy consisted of equally spaced spots with higher density near the otolith core. This was intended to provide good sub-annual resolution for pre-adult and adult life stages, including inside of the first translucent growth zone (*i.e.*, the first year of life).

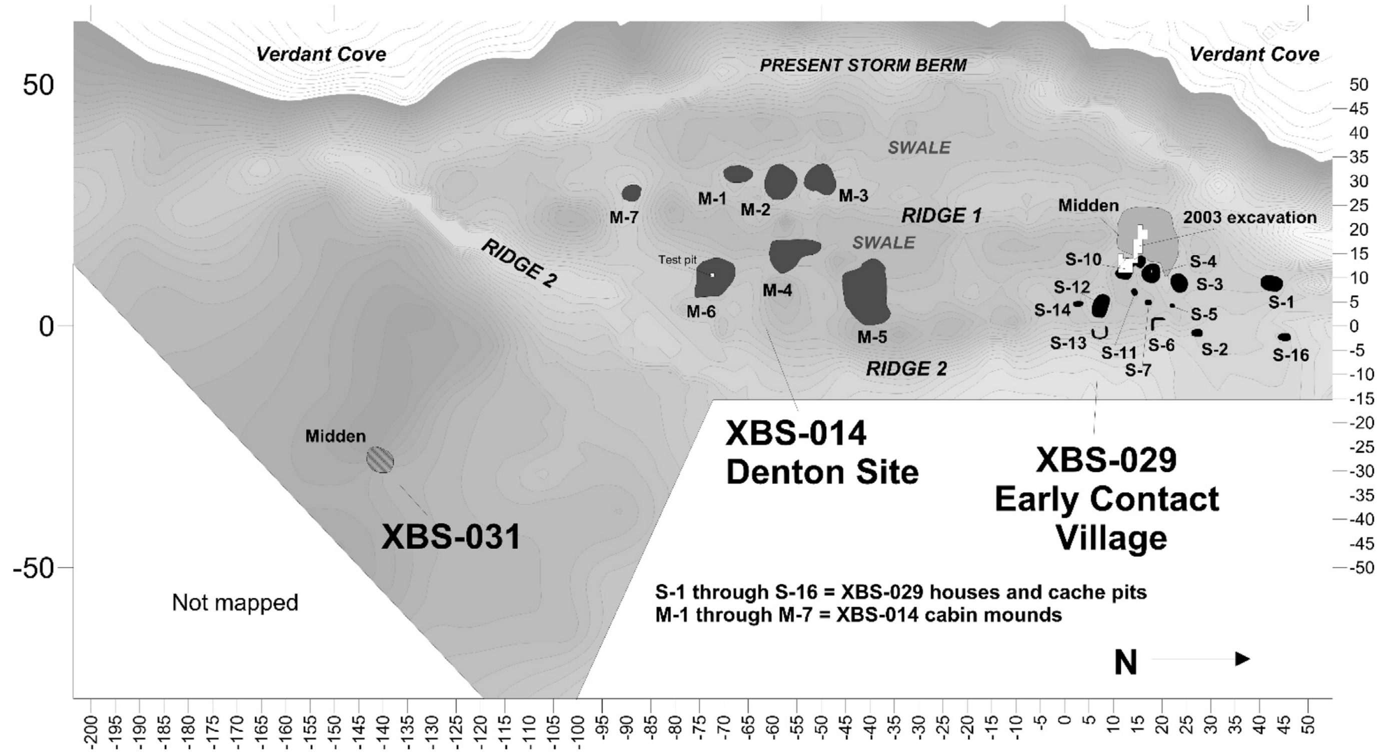

Fig. 2. Feature and topographic map of the Early Contact Village Site (XBS-029) and Denton Site (XBS-014) in Verdant Cove on the west side of Aialik Bay, Kenai Fjords National Park, Alaska. Pacific cod (*Gadus macrocephalus*) otolith samples were taken from the midden area at XBS-029, and from cabin mounds M-2 and M-3 at XBS-014. Excavations at the two sites were conducted in 2003–2004. Both x- and y-label axes are in meters.

The ion microprobe (secondary ion mass spectrometer, SIMS) parameters (settings) we used for $\delta^{18}O$ analysis are the same as in Matta et al. (2013) who sampled otoliths from yellowfin sole (*Limanda aspera*), which are similar in composition to the Pacific cod otoliths analyzed here. The relevant parameters and a description of analytical conditions for our study are summarized in the following description, and more detail can be found in Matta et al. (2013) and Ferry et al. (2010). The primary beam of $^{133}Cs^{+}$ ions was focused a spot diameter of ~10 μm on the surface of the thin section. The analysis of each sample spot took 4 min and resulted in a pit ~1 μm deep. For carbon isotope analysis, a $^{133}Cs^{+}$ ion beam with a diameter of ~7 μm was used, with a total analysis time of 6 min per spot. The secondary ions were analyzed in the mass spectrometer set up for high secondary-ion transmission (Kita et al., 2009). Groups of 10 to 15 sample spots were bracketed, before and after, by 4–5 analyses of the calcite standards. In 2007 the standard was UWC-1 ($\delta^{18}O = 23.36‰$ Vienna Standard Mean Ocean Water (VSMOW) and $\delta^{13}C = 2.03‰$ Vienna Pee Dee Belemnite standard (VPDB)) and in 2011 and 2012 the standard was UWC-3 ($\delta^{18}O = 12.49‰$ VSMOW, $\delta^{13}C = -0.91‰$ VPDB) (Bowman et al., 2009; Kozdon et al., 2009). Analysis of the standard was used to correct for instrumental bias and to estimate precision in spot sampling (Kita et al., 2009; Valley and Kita, 2009; Kozdon et al., 2009; Matta et al., 2013; Orland et al., 2009). After the ion microprobe analyses, we imaged each spot by scanning electron microscopy to be sure that the pits did not include otolith irregularities or contaminants. In two otoliths, one from ~100 YBP (XBS-014-5) and the other 0 YBP (MOD-14) a full life history transect was measured for both $\delta^{13}C$ and $\delta^{18}O$ to evaluate the relationship between these isotopes and possibly infer potential differences in coastal productivity. Variability in $\delta^{13}C$ can be related to marine productivity, fish metabolic rates, fish diet, and fish growth rate. Results from both measurement methods are reported in $\delta^{13}C$ ‰ and $\delta^{18}O$ ‰ VPDB. To check for diagenesis, the sample spot analyses were

Table 1
Modern and archaeological Pacific cod (*Gadus macrocephalus*) otoliths recovered from the Early Contact village (~200 YBP) and Denton (~100 YBP) sites on Kenai Peninsula. Summary data include sample age (YBP), fish ages estimated from growth zone counts, otolith weight, fish length, details of the ion probe SIMS analyses, core region $\delta^{18}O$, and average nearshore surface water temperatures predicted from $\delta^{18}O$ values (Ion probe spot-specific temperatures were predicted from $T°C = 6.198–2.195 * \delta^{18}O$, and averaged).

	Calibrated	Estimated	Otolith	Fish	Number	Transect	Transect	Core $\delta^{18}O$		Ave. water
Sample ID[a]	Age (YBP)	Age (years)	Weight (g)	Length (mm)[b]	SIMS spots	Oreintation	Distance (mm)	Mean	SD	Temp (°C)[c]
XBS-029-10	200	5–6	0.445	564	37	Dorsal	4.43	− 0.80	0.806	7.95
XBS-029-11	200	4–5	0.454	571	32	Dorsal	3.03	− 0.66	0.436	7.89
XBS-029-19	200	6–7	0.529	629	25	Proximal	3.49	− 1.34	0.394	9.14
XBS-014-1	100	6–7	0.537	635	44	Dorsal	4.43	− 1.44	0.370	9.36
XBS-014-4	100	4–5	0.728	782	60	Ventral	4.15	− 1.50	0.432	9.49
XBS-014-5	100	5–6	0.534	633	31	Dorsal	4.72	− 1.07	0.455	8.55
MOD-14	present	4–5	0.531	630	50	Dorsal	3.68	− 3.07	0.265	12.94
MOD-17	present	5–6	0.482	593	28	Dorsal	4.94	− 3.11	0.283	13.10
MOD-18	present	5–6	0.679	744	32	Ventral	4.67	− 1.29	0.472	9.03

[a] XBS-029 refers to the Early Contact Village site, XBS-014 refers to the Denton Site.
[b] Pacific cod length is predicted from: $L = 221.5 + 769.97 * Otolith\_weight$, $r^{c} = 0.91$ (IPHC trawl data from Gulf of Alaska, 1964).
[c] Temperature predicted from: $T°C = 6.198–2.195 * \delta^{18}O$.

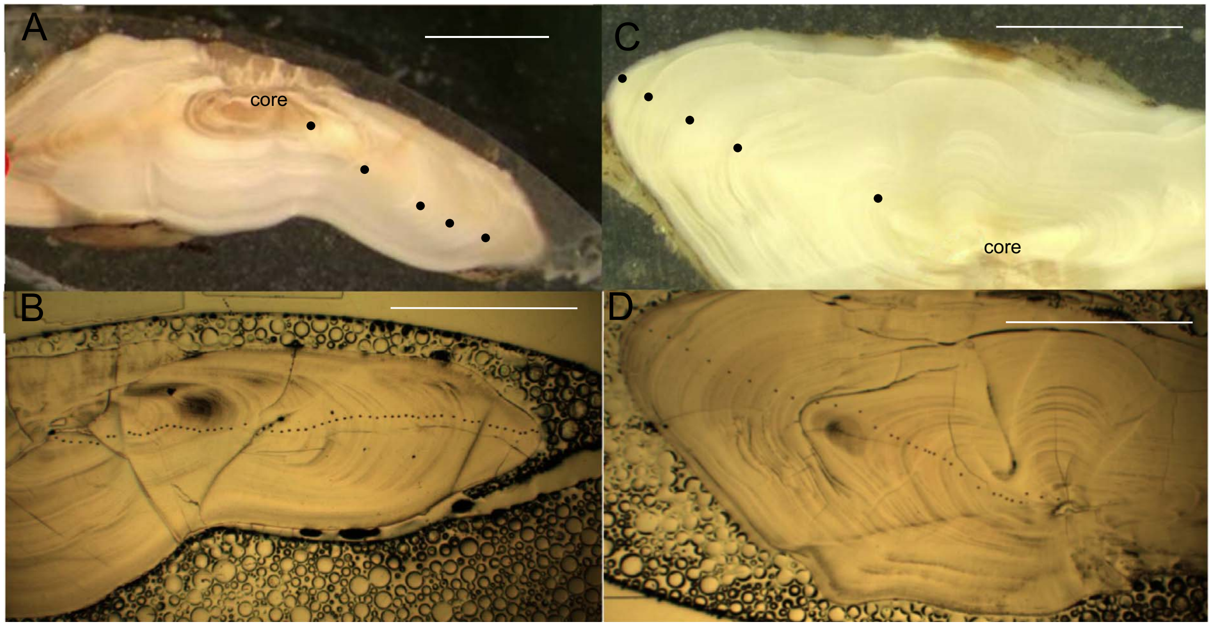

Fig. 3. Images of transverse thin sections from Pacific cod (*Gadus macrocephalus*) otoliths recovered from the archaeological sites in Aialik Bay, Alaska. Panels A and B are ~200 year before present (from XBS-029-11) and panels C and D are ~100 year before present (from XBS-014-4). Panels A and C show locations of the core and the approximate region of translucent annual winter growth zones (black dots). Panels B and D show the ion microprobe spot samples along dorsal-oriented (B) and ventral-oriented (D) transects from otolith core to edge. White bars represent 1 mm.

evaluated using the ion yield (^{16}O or ^{12}C count rates/primary beam intensity) to recognize irregular data. Based on dispersion of ion yields of the standard calcite in the same session, irregular (altered) data were defined if the C ion yield is 10% higher than average value or if the O ion yield is 5% lower than the average value, and omitted from analysis.

We developed an empirical fractionation equation between δ^{18}O and temperature from the 7 electronic archival tagged Pacific cod (Nichol et al., 2007). Each time series of instrumental temperatures was divided into quarters and averaged. The re-captures occurred during the winter or spring, and most fish were at liberty for nearly a year. Quarterly average δ^{18}O values were then obtained using a rough proportional distance between the otolith margin and inner annulus; which we took to represent the period the fish was at liberty. Ion microprobe samples at the margin spanned the most recent winter period. As such, if a Pacific cod was at liberty for 1 year, then we obtained 4 averaged data points of δ^{18}O and temperature. One Pacific cod (sample 1169) was at liberty for 716 days and given roughly 8 data points. Then the average quarterly δ^{18}O representing the aragonite material accreted during the period at liberty were regressed with average quarterly *in situ* instrumental temperatures; $\delta^{18}\mathrm{O} = \alpha + \beta\, T$°C, where α and β is the intercept and slope of the linear response of δ^{18}O to temperature (T). However, we regressed temperature on δ^{18}O to derive a predictive equation ($T°\mathrm{C} = \alpha' + \beta'\delta^{18}\mathrm{O}$), and then applied that to estimate the thermography of Pacific cod's life history from ion probe spot samples over the entire transect, shown as a loess smoothed time series. We also reconstructed the presumed average nearshore Gulf of Alaska surface temperatures from spot samples taken within the 1st growth zone near the otolith core of archaeological and modern samples. *In situ* nearshore temperature data (2000–2006) from an oceanographic monitoring mooring station, GAK1, at 59°50.7′N, 149°28.0′W (http://www.ims.uaf.edu/gak1/) was used to ground truth the surface (< 25 m) water temperature with those inferred from δ^{18}O measured in the contemporary Pacific cod otoliths.

3. Results

Archaeological Pacific cod annual growth zones, visible from stereomicroscopic examination of otoliths were sufficiently preserved for analysts to assign age within +/− 1 year (Table 1, Fig. 3). Ages ranged between 4 and 7 years of age (Table 1). In selected samples shown in Fig. 3A–B (XBS-014-4) and 3C-3D (XBS-029-11), the otolith core was generally apparent as an ellipse within the first year's growth, followed by a number of concentric wide opaque and thin translucent material identified as annual growth zones from which age (count of translucent zones) was estimated. Based on our knowledge of contemporary Pacific cod growth, the opaque, material represents aragonite accretion during fast summer growth periods and translucent material forms during slower winter growth periods. The fish lengths, estimated with the relationship between Pacific cod fish length and otolith weight, ranged from 562 to 782 mm (Table 1). In general, lengths and ages of Pacific cod inferred through otoliths did not show differences between archaeological recovered and contemporary specimens.

While maximization was not a goal, the number of spots from the ion microprobe varied between 22 and 58 per otolith, with the greatest density made in or near the otolith core in the first year of the animal's life (Table. 1, Fig. 3). This was largely because the aragonite linear accretion rate is greatest during the first year allowing for a greater sampling density. The greatest number of analyses ($n = 58$) were taken in specimen XBS-029-11 with about sixteen 10 μm-diameter spots within each of the first and second years of life, followed by approximately 8–10 samples in each of the remaining growth zones (Fig. 3D). Transect lengths ranged from about 3 to 4.9 mm with sample densities ranging from 5 to 19 spots per mm (Table 1). This provided multiple spots per annulus which allowed an assessment of seasonal trends in the δ^{18}O values.

In all otoliths, the lowest δ^{18}O value was generally observed within or near the core, which is considered the early juvenile stage of life (Fig. 4). Depending upon the era from which otoliths were recovered the δ^{18}O value ranged from a low of approximately −2.0‰ to a high of 1.5‰ (XBS-029-10) among the 200 YBP group, −3.0‰ to 1.0‰ (XBS-014-4) among the 100 YBP group, and −3.5‰ to 1.0‰ (MOD-18) in the 0 YBP group. In most samples, the δ^{18}O value increased considerably during the first or second year and showed a sinuous pattern of peaks and troughs. The observed sinuous pattern indicated a strong seasonal variation in temperature. Given the inverse relationship between δ^{18}O values and temperature, the increase in ^{18}O during the first

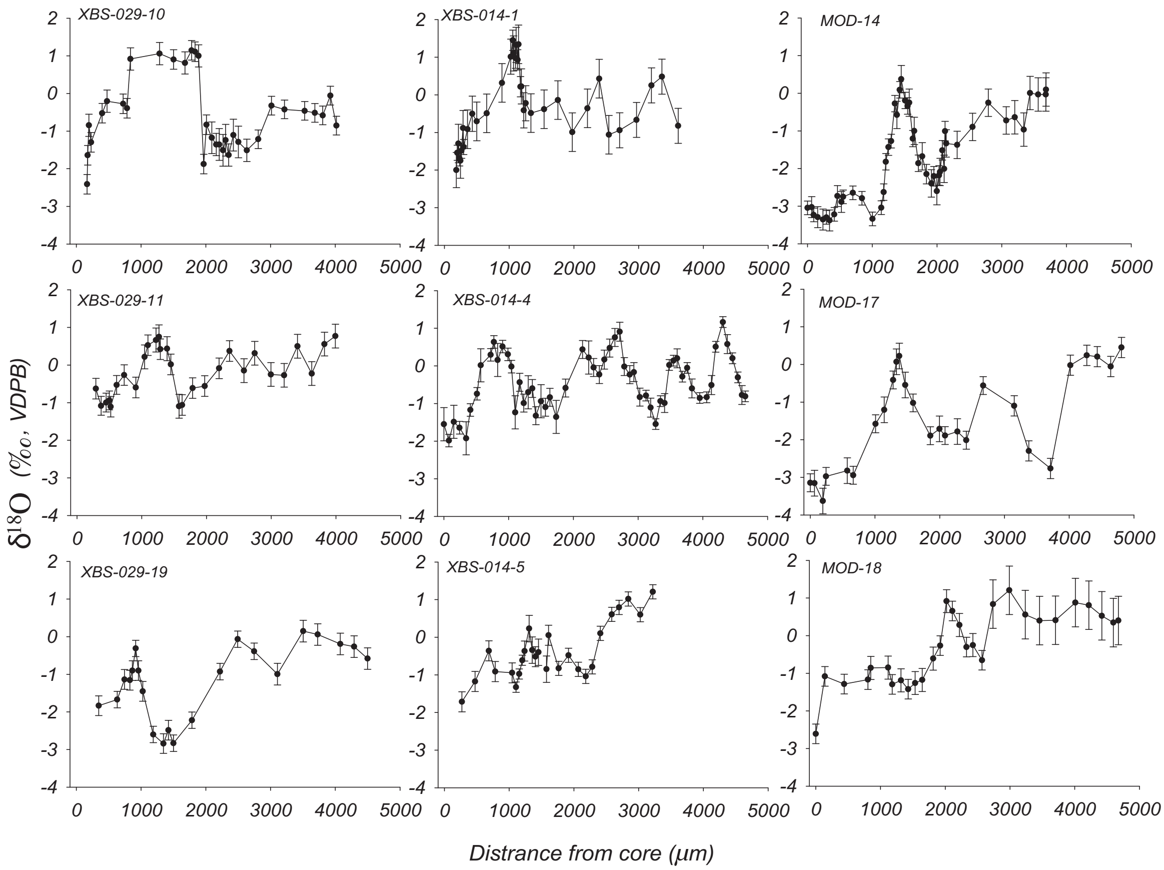

Fig. 4. Sequences of measured δ^{18}O (‰ VPDB, ± 2 S.D.) in Pacific cod (*Gadus macrocephalus*) otoliths, in μm from the core region to the margin. The left column is samples with a calibrated age of ~200 + years before present (YBP), the middle column is samples with an age of ~100 + YBP, and the right column is samples with an age of 0 YBP.

1 or 2 years indicated that individual Pacific cod in the Gulf of Alaska experienced an overall decrease in water temperature through their life. This possibly reflects an ontogenetic migration from warmer nearshore costal water to cooler deeper shelf water. Another interesting feature, particularly for otoliths with high sampling density such as XBS-014-4, is that the 5 peaks in δ^{18}O are consistent with the estimated age of the fish (Table 1, Fig. 4).

We found that water temperature was a dominant factor affecting the δ^{18}O (aragonite) of Pacific cod otoliths (Fig. 5). The estimated functional relationship between Pacific cod otolith aragonite (δ^{18}O) and water temperature showed a statistically significant inverse linear relationship ($\delta^{18}O = 2.13–0.25T$°C, $r^2 = 0.75$, $p < 0.001$). This was based on the 7 Pacific cod which had instrumental temperature measured during the time at liberty with archival tags and the corresponding otolith δ^{18}O measured with ion microprobe analyses. The estimated regression from all 7 fish shows that there is approximately a 3–4 °C temperature change for each per mil change in the δ^{18}O concentration. This is also demonstrated with sample 1169 where the *in situ* bi-hourly temperature sequence, over the 716 day period at liberty, corresponds in an inverse relationship to the ion microprobe samples of δ^{18}O (Fig. 5). This relationship (reanalyzed for temperature as the response variable and δ^{18}O as the independent variable, Table 1) was used to reconstruct the life history temperature profile in the archaeological and contemporary Pacific cod (Fig. 6). For selected specimens, Fig. 6 shows the general and consistent pattern where Pacific cod experience higher thermal habitat in nearshore areas as early stage juveniles, but as they grow into later stages of development the temperature experienced or preferred becomes gradually cooler as they move to deeper depths.

Ion microprobe analyses taken within the first growth zone near the otolith's core, were used to reconstruct nearshore Gulf of Alaska temperatures experience by Pacific cod during ~200 +, ~100 + and 0 YBP. Here we assumed that the average of these near-core δ^{18}O samples represent the first summer of life when the Pacific cod were in nearshore coastal water and most affected by surface temperature changes. A decline in average δ^{18}O from otolith cores in archaeological (~200 +, ~100 + YBP) to modern samples suggest increasing sea surface temperatures from the late Little Ice Age to present. Predicted average sea surface temperatures from δ^{18}O in Pacific cod otoliths was roughly 8.5 °C during the ~200 YBP period with a slight temperature increase to 9.0 °C in the ~100 YBP period (Fig. 6). The δ^{18}O in otoliths from contemporary Pacific cod suggest an average 2–3 °C rise over the last 100 years in coastal sea surface temperatures in the Gulf of Alaska (Fig. 6). Two of the modern Pacific cod otoliths indicated a nearshore summer temperature of ~13 °C (Fig. 7). Normally, when making such a prediction, an estimate of water δ^{18}O (itself a function of salinity) is necessary (Hoie et al., 2004a). We do not have an estimate of surface water δ^{18}O, however, the GAK1 mooring surface temperature consistently reached 11–13 °C during the early to mid-2000s. This agreement provided a way to ground truth the δ^{18}O based temperature estimates. In one Pacific cod otolith (MOD-18) the average near-core δ^{18}O (− 1.29‰) was considerably higher, and hence predicted lower temperature than the other two contemporary fish (Fig. 7).

Average values of δ^{13}C and δ^{18}O from sample XBS-014-5 (100 YBP) were − 2.87‰, and − 0.35‰, respectively (Fig. 8A). For sample MOD-14 (0 YBP), δ^{13}C was similar with an average of − 2.77‰, but by comparison, δ^{18}O had a substantially more negative concentration of − 1.69‰ (Fig. 8A). Both samples show a measure of linear relationship between δ^{13}C and δ^{18}O concentrations, however, sample XBS-014-5 (100 YBP) has a much stronger correlation between the two isotopes ($r = 0.77$). Variability in δ^{13}C from XBS-014-5 was also observed to be greater than in MOD-14. Both otolith chronologies of δ^{13}C, over the entire

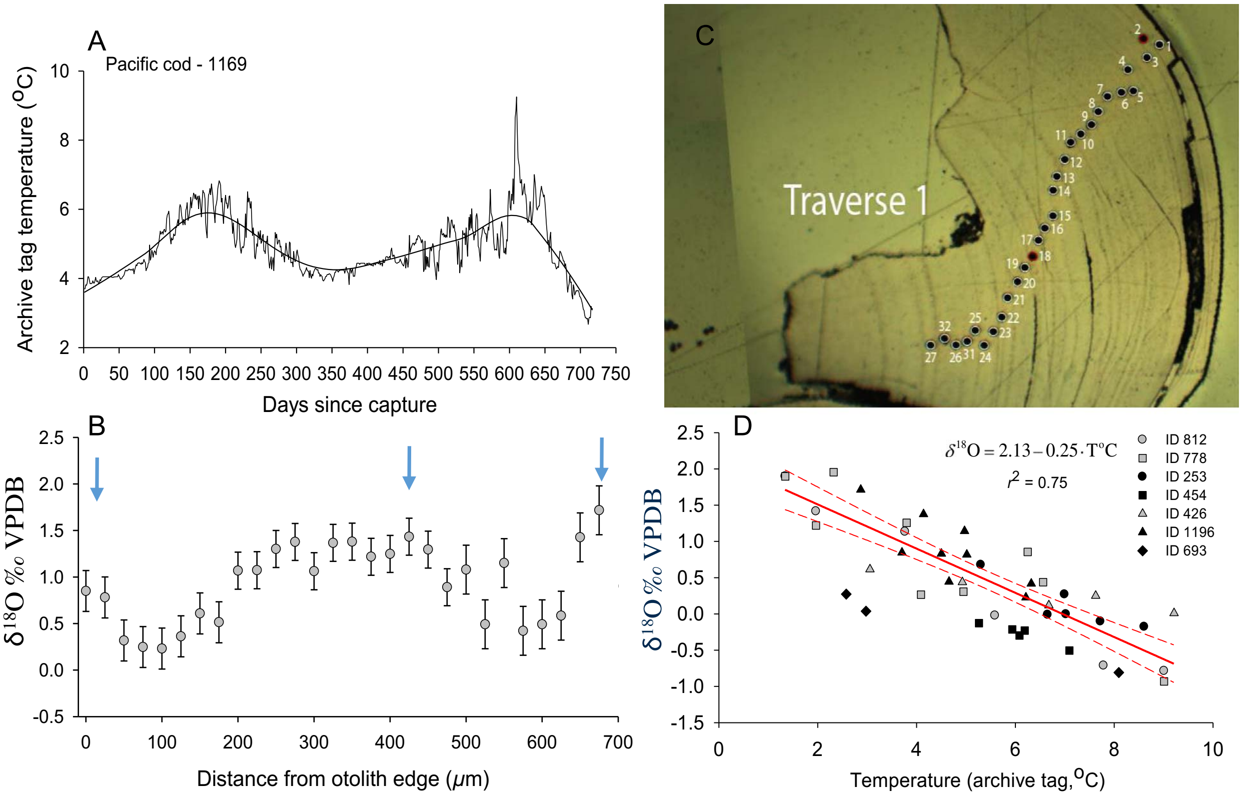

Fig. 5. A) Temperature recorded by an archival recording tag on Pacific cod (*Gadus macrocephalus*) ID 1169 during the time at liberty, 716 days. C) Image of a Pacific cod otolith thin section showing the location of ion microprobe spot samples which were near the outer edge of the otolith in material representing time at liberty. B) The δ^{18}O (‰ VPDB, ± 2 S.D.) values measured as distance (μm) from the otolith edge. D) Empirical fractionation equation of otolith aragonite (δ^{18}O) to water temperature from 7 archival tagged Pacific cod, showing a statistically significant inverse linear relationship (r = 0.75, p < 0.001).

life history transects, appear on the whole to show similar increasing trends (Fig. 8B). One principal difference is the average δ^{13}C values in the core areas; XBS-014-5 is significantly lower than in MOD-14.

4. Discussion

High resolution sampling for δ^{18}O, using tools such as the ion microprobe, provides a unique perspective on Pacific cod biogeography and migratory behavior, showing habitat preference for warmer nearshore water during early life stages followed by migration to cooler deeper water. First year juvenile Pacific cod (age 0 years) have been documented to exhibit associations with shallow, nearshore coastal areas in the Gulf of Alaska (Laurel et al., 2007; Stoner et al., 2008). As the juveniles grow they move gradually to offshore cooler coastal water as sub-adult and adults (Laurel et al., 2009). These movement patterns are confirmed by population level research survey data which shows the greatest concentration of juvenile Pacific cod are in shallower, warmer shelf water until 4 years old (Nichol et al., 2007; Nichol et al., 2013). During the transition to maturity, between ages 4–5 years (Stark, 2007), there is a tendency for animals to move toward deeper cooler waters of the continental shelf where they find suitable habitat for spawning. Matta et al. (2013) conducted a similar high-resolution ion microprobe study of yellowfin sole in the Eastern Bering Sea and found δ^{18}O chronologies reflecting similar seasonal and biogeographic movements. Similar patterns in the δ^{18}O chronologies in the archaeologically obtained otoliths and those of contemporary Pacific cod point to an ontogenetic migratory life history strategy that does not appear to have changed over the past 200 years. Migratory behavior such as this could be an adaptive response to advance and retreat of glacial reorganizations throughout evolutionary time scales.

The Pacific cod ages estimated from archaeologically obtained otoliths in this study (4–6 years) are indeed consistent with the most numerous age classes in the Gulf of Alaska population (A'mar et al., 2012). Fish lengths predicted from otoliths are also consistent with typical sizes of Gulf of Alaska Pacific cod taken in recent fishery-independent resource surveys, and there is also no indication that the length estimated from the archaeological specimens are any different from those of contemporary fish. Ethnohistoric descriptions of Alutiiq fishing technology, presented in the Introduction, indicate a focus on larger fish taken near bottom depths, often over 100 m. Based on current information such fish could clearly be fully grown adult Pacific cod. Interestingly, in some specimens the number of δ^{18}O concentration peaks roughly corresponds to the estimated fish age based on visual interpretations of otolith growth zone counts. Several recent studies of δ^{18}O signatures in otoliths have been used to age both Pacific cod (Kastelle et al., 2017) and Atlantic cod (Weidman and Millner, 2000). Kastelle et al. (2017) found that from a sample of 40 Pacific cod otoliths aged by growth zone counts, nearly 70% were assigned the same age or 90% were assigned an age +/− 1 year different from estimates derived from counts of δ^{18}O peaks. In both the above studies, the goal was to use δ^{18}O chronologies in fish otoliths to validate ages estimated by interpreting and counting growth zones. These studies relied on the well-established relationship between an otolith's oxygen isotopic fractionation and water temperature (Valley and Kita, 2009; Hoie et al., 2004a; Thorrold et al., 1997). The study by Kastelle et al. (2017) was the first to give a δ^{18}O – temperature fractionation relationship based on Pacific cod otoliths from the North Pacific Ocean. The fractionation relationship reported here (Fig. 5) is consistent with that reported in Kastelle et al. (2017); we found a both a comparable slope and intercept. Similar studies on otoliths from other regions and species report consistent expected temperature-driven variation in δ^{18}O of aragonite, close to 0.2‰/°C (Hoie et al., 2004a; Grossman and Ku, 1986; Thorrold et al., 1997; Kim et al., 2007; Wang et al., 2013). Not surprisingly, this well studied property has led investigators to use δ^{18}O in biogenic

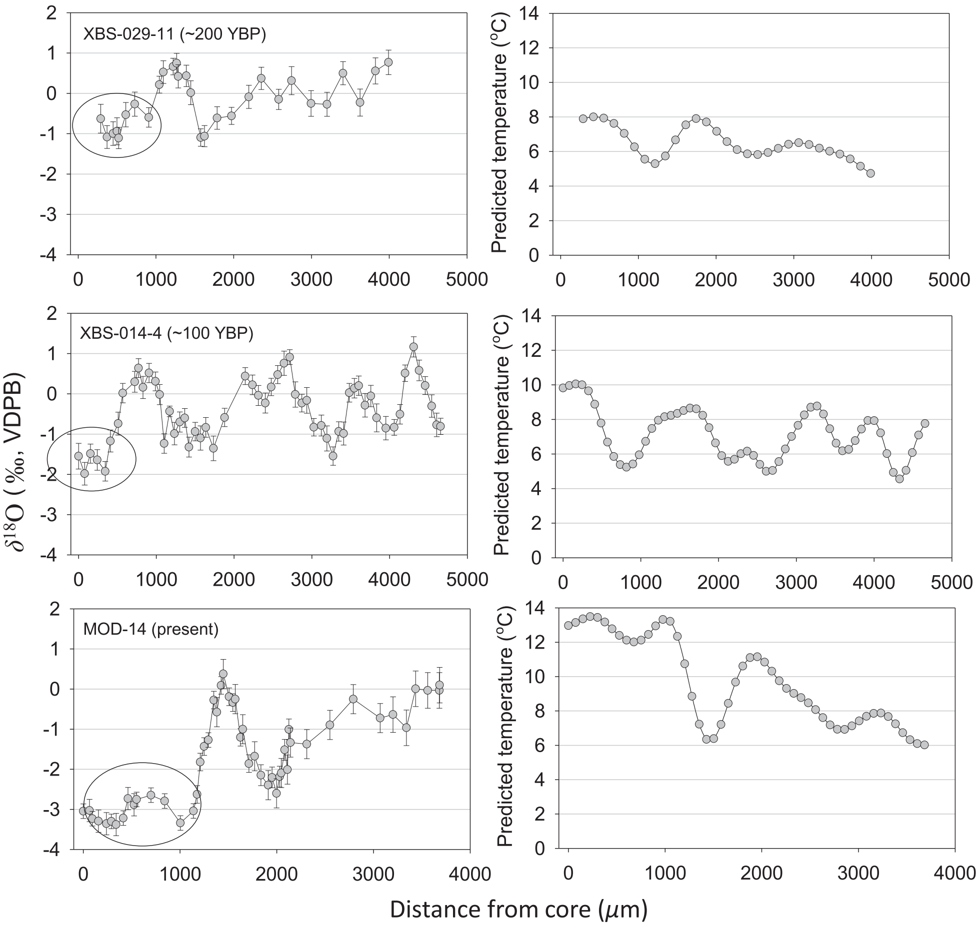

Fig. 6. Left column: Three example sequences of ion microprobe spot samples measuring δ^{18}O (‰ VPDB, ± 2 S.D.) from the otolith core to edge. The right column shows the temperatures estimated from the equation, T°C = 6.198–2.195 ∗ δ^{18}O (Fig. 5) shown as Loess smoothed time series. The large circles in the δ^{18}O sequences indicate spot samples which were in the otolith core region and used to reconstruct nearshore surface temperature change since Little Ice Age.

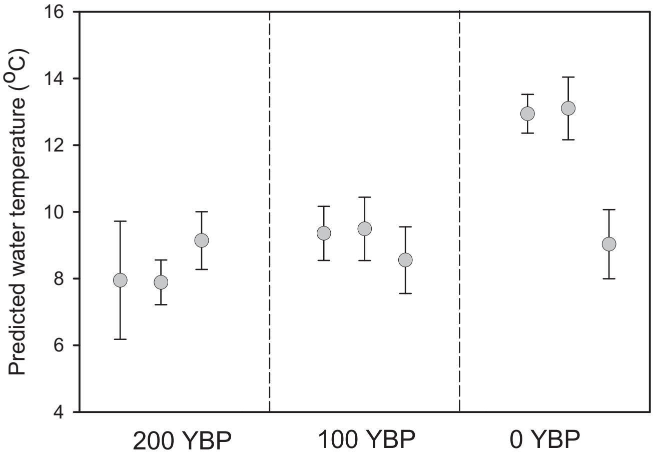

Fig. 7. Average predicted nearshore surface water temperature since the Little Ice Age, 200 + years before present (YBP), to modern times, 0 YBP. The predictions were from 9 Pacific cod otoliths (*Gadus macrocephalus*) (6 recovered from archaeological sites dated to ~200 + and ~100 + YBP, and 3 from 0 YBP) sampled for stable oxygen isotopes δ^{18}O in the core of the otolith (refer to Fig. 6). Ion probe spot-specific temperatures were predicted from T°C = 6.198–2.195 ∗ δ^{18}O, and averaged. Error bars show 2SD of the mean.

structures as a proxy for reconstructing palaeotemperatures (Wierzbowski and Rogov, 2011; West et al., 2012), and examining seasonal fluctuations of δ^{18}O signatures in otoliths (Thorrold et al., 1997; Matta et al., 2013).

Nearshore surface temperatures in the Gulf of Alaska, estimated here using the δ^{18}O of otolith core regions from archaeological and modern Pacific cod, appears to have increased 2–3 °C since the late Little Ice Age. We only sampled three fish from each era, although many ion probe analyses were taken in the core, nevertheless we emphasis that this estimate represents an implied average sea surface temperature. Nor do the results of this analysis provide a large geographical inference because Pacific cod inhabit a diversity of nearshore habitat during their first year of life throughout the Gulf of Alaska. West et al. (2012) found a period of ocean warming around 400 + YBP in the Gulf of Alaska, with a gradual decrease in temperature to about 190 + YBP based on archaeological recovered Pacific cod otoliths from archaeological sites on Kodiak Island, AK; West et al. (2012) did not analyze modern otoliths. Similar findings from δ^{18}O chronologies of Atlantic cod otoliths show cooler ocean water temperatures during the Late Little Ice Age (Geffen et al., 2011). Samples in West et al. (2012) were obtained partly by micro-drilling and averaging ^{18}O measurements (from conventional acid digestion/gas-source mass spectrometry) across the entire life history transect. This method of sampling would obscure both seasonal and age-related ontogenetic movements. Further, they used a different analytic technique of measuring δ^{18}O, which may make comparisons with our study difficult. Nevertheless, a difference of about 2–3 °C cooler around the decade of 1800 CE from otolith δ^{18}O demonstrated in these multiple studies are consistent with tree-ring derived estimates of cooler summer air temperatures during the same period (Barkley et al., 1999; D'Arrigo et al., 2005; Wiles et al., 2014). We "ground truthed" contemporary temperatures estimated from otolith core δ^{18}O. The temperature- δ^{18}O curve was used to generate predictions of nearshore temperatures from the cores of modern Pacific cod otoliths which were consistent with < 25 m surface water temperatures from the GAK1 mooring during the early 2000s. Both indicated temperatures up to about 13 °C during summer months within nearshore habitat. Other recent studies have corroborated these temperature estimates; high densities of age-0 and age-1 Pacific cod occupy a diversity of nearshore embayments in the Gulf of Alaska where annual

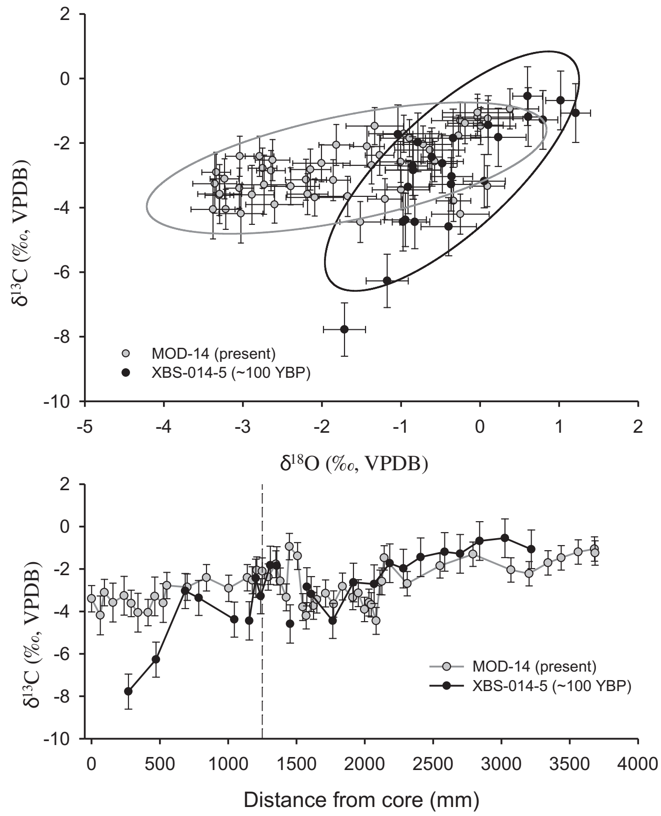

Fig. 8. Upper panel: Relationship between δ^{13}C and δ^{18}O (‰ VPDB, ± 2 S.D.) measured by ion microprobe at WiscSIMS, in two specimens. Lower panel: Sequences from the otolith's core to its margin of measured δ^{13}C and δ^{18}O (‰ VPDB, ± 2 S.D.) in the same two specimens as above.

summer water temperatures reach 13–15 °C (Ormseth et al., 2016), and are important nursery areas during the early juvenile stage (Abookire et al., 2007; Laurel et al., 2007; Stoner et al., 2008). Further, Pacific cod growth and activity is maximized at 12 to 15 °C (Laurel et al., 2016); so this temp range is reasonable.

Carbon isotope chemistry in fish otoliths is complex and the fractionation in precipitated aragonite is thought to be mediated possibly by biological, diet, and kinetic effects (Thorrold et al., 1997; Weidel et al., 2007). Isotopes of carbon ^{13}C/^{12}C and oxygen ^{18}O/^{16}O have commonly been reported to be highly correlated in numerous animal taxa (Patterson et al., 1993; Thorrold et al., 1997; Vanhove et al., 2011). Kalish (1991) also reported a positive correlation between δ^{13}C and δ^{18}O in marine fish otoliths and proposed that δ^{13}C levels are a function of metabolic rates increasing with temperature. Considering a freshwater fish species, Wurster and Patterson (2003) similarly suggested that δ^{13}C levels are controlled by changes in metabolic rates. Since aragonitic δ^{13}C has been shown to be inversely related to water temperature across different taxa of biogenic carbonates (Kalish, 1991; Grossman and Ku, 1986; Wurster and Patterson, 2003), the positive relationship between δ^{13}C and oxygen δ^{18}O is not at all surprising. While the precise mechanism is unknown, evidence from laboratory and field studies point to diet and metabolic effects rather than physical temperature dependence of δ^{13}C in otolith aragonite precipitation (Thorrold et al., 1997; Romanek et al., 1992). In our study only two otoliths were analyzed for δ^{13}C and δ^{18}O so proposing a mechanism for their relationship is not possible. However, roughly similar trends between δ^{13}C over the life history transects in these otoliths might suggest the δ^{13}C disequilibria is associated with temperature related increased metabolic activity, which is accompanied by enhanced demands for growth and reproduction (Thorrold et al., 1997).

We found the core region of specimen XBS-014-5 (~100 YBP) to be lower in δ^{13}C relative to MOD-14 (0 YBP). Assuming somewhat similar metabolic functioning of these two Pacific cod in their first year of life, it might be postulated that concentrations of inorganic carbon (DIC) in the nearshore marine waters in the Gulf of Alaska were lower during 100 YBP period compared to the present. Depletion of DIC could be attributed to lower marine productivity associated with advancing glaciers into nearshore Pacific cod habitat as well as overall lower water temperatures limiting plankton production. Growth of juvenile Pacific cod in laboratory studies is shown to be depressed in ambient water temperatures of less than the optimum of 11.5 °C (Laurel et al., 2016). Based on δ^{18}O predicted historic temperatures of 8–9 °C in our study, metabolic limitations of carbon incorporation into otoliths from either poor growth or reduced marine productivity seem within the realm of plausibility. We should caution that predicted temperature histories from otolith δ^{18}O aragonite from archaeological specimens assumes that the δ^{18}O of the water (hence salinity) has remained unchanged, which is a difficult assumption to verify. Other factors can also affect the δ^{18}O fractionation seen in otoliths (Campana, 1999; Horn et al., 2012) such as changes in seawater δ^{18}O due to glacier ice melt and river runoff (Coachman, 1986; Stabeno et al., 2005). These geophysical processes must have undoubtedly changed over the past 200 years affecting coastal glacier retreated and freshening of the continental shelf waters, so it is difficult to ascertain the extent to which they have affected our temperature reconstructions. Further research is needed to understand and correct for the δ^{18}O concentration of coastal waters. Despite these uncertainties, the fact that δ^{18}O predicted nearshore temperatures from contemporary otoliths are quite reasonable based on real time mooring data and other studies, including ones that use tree rings, and suggest a similar finding of increased coastal temperatures lends credence to the findings presented in this study.

Colder SSTs during the late LIA are likely to have affected the abundance of Pacific cod and other fish species in the GOA, necessitating adjustments in the subsistence economies and settlement patterns of human coastal populations. Considering modern short-cycle climate data first, commercial catches and recruitment of GOA Pacific cod rose (although with high annual variability) during the strong warm phase of the Pacific Decadal Oscillation (PDO) from 1977 to 1988 and declined during the weaker cooling phase from 1989 to 1998, as did flatfish and other gadids including walleye pollock and hake (A'mar et al., 2012; Benson and Trites, 2002; Hare and Mantua, 2000; McGowan et al., 1998; Overland et al., 2008). Catches of all salmon stocks and species increased, in some cases substantially, during 1977–1988, and most increased again or showed weak declines after 1989 (Hare and Mantua, 2000: Table 1).

Because gadids and/or salmonids are the numerically predominant fish in most GOA archaeofaunal assemblages (based on the number of identified specimens), the present discussion focuses on the relative abundance of these two important taxa during the Neoglacial interval (5000 BCE - 900 CE), the Medieval Warm Period (900–1350 CE), and the Little Ice Age (1350–1900 CE). Over this span Pacific cod and salmon populations appear to have decreased and increased in response to climate changes but in opposing directions rather than in phase as during recent PDO regimes. In the examples below, archaeological abundance (high numbers of bones in middens) serves as a proxy for species abundance in the natural environment, although this relationship is indirect and mediated by human behavior.

On Sanak Island in the western GOA, Pacific cod were the dominant species harvested at eight archaeological sites from 2550 BCE through 520 CE (Neoglacial), then declined in dominance relative to other species (salmon, flatfish, greenlings, sculpins) during the MWP (sample date = 1030 CE) and increased again during the LIA (sample date = 1540 CE) (Maschner et al., 2008). At four sites in the Kodiak archipelago (Rice Ridge, Uyak, Crag Point, and Settlement Point), Pacific cod were the dominant fish species during the Neoglacial from 5000 BCE through about 1100 CE, but were superseded by salmon at about 1300 CE in the late MWP (Kopperl, 2003). Pacific cod and other marine species exceeded salmon in some stratigraphic levels at Karluk-1 on Kodiak Island, an LIA site dated to about 1400–1750 CE, despite the site's location at the mouth of one of the GOA's most productive salmon rivers, suggesting salmon decline during the LIA (West et al., 2012). This is confirmed by a study of oceanic ^{15}N sampled from 2200 years of bottom sediments in Karluk Lake, a sockeye salmon spawning site at the head of the Karluk River (Finney et al., 2002). Spawning in the lake was at low levels from 100 BCE to 800 CE during the Neoglacial, increased to high levels during the MWP and early LIA, and dropped sharply in 1700–1850 CE during the late LIA. The two Kenai Peninsula LIA sites discussed in the present paper – the Early Contact Village (1790–1820 CE) and the Denton Site (1850–1920 CE) – are dominated by Pacific cod with only minor representation of salmon, and so conform to the regional trend. In southeastern Alaska, gadids (primarily Pacific cod) alternate with salmonids as the dominant taxon in 26 archaeological sites ranging in age from 6200 BCE to 1900 CE, but clear temporal trends or association with climatic cycles have not been discerned (Moss, 2011). Overall, the GOA archaeological record suggests that cod were most abundant and important to subsistence during the Neoglacial and LIA, while salmon peaked during the MWP.

Major shifts in GOA water temperatures and biological regimes have been correlated with cultural transitions and altered settlement patterns. With the onset of the MWP, interior Dena'ina groups migrated to the coast of Cook Inlet and initiated a subsistence economy based on intensive salmon harvesting (Reger, 2013). On Kodiak Island, the Late Kachemak phase with its emphasis on Pacific cod and other pelagic fish gave way at the start of the MWP to the Koniag phase when large salmon fishing villages were established on the Karluk, Ayakulik and other rivers along the southwestern side of the island (Finney et al., 2002; Knecht, 1995; Kopperl, 2003; Steffian et al., 2015). During the late LIA but before Russian contact in the late 18th century, many of the western Kodiak villages were abandoned and the Koniag population shifted to the northern and eastern coasts of the island where cod and other offshore resources are more abundant (Clark, 1987).

A GIS-based factor analysis of all known archaeological sites (n = 1959) along 17,000 km of coastline in the central GOA demonstrated that sites cluster in areas of highest food resource diversity and that two factors – Factor 1 indicating access to cod, halibut, herring, and sea lions and Factor 4 to salmon – together explain over 60% of the variance in site count per 2.5 km shoreline segment (Crowell et al., 2013). In part, this result is likely to reflect seasonal rotation between fall-winter-spring villages and summer salmon camps, but on a larger scale Factor 1 may represent subsistence emphasis and corresponding site choice during cooler phases when salmon were reduced but gadids, flatfish, forage fish, and sea mammals increased, whereas Factor 4 represents the alternative warm phase strategy when coastal residents moved to major salmon rivers and relied on mass production of this resource. Of the 1959 GOA sites in the sample, 41% were estimated from radiocarbon dates, artifacts, and features to have been occupied since 900 CE; 10% were older than 900 CE; and 49% were of indeterminate age but likely to be post-900 CE in the same proportion. Therefore, the analysis primarily represents changes in settlement patterns and resource use during the MWP and LIA.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.jasrep.2017.06.037.

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