Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability

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Pacific herring (*Clupea pallasii*), a foundation of coastal social-ecological systems, is in decline throughout much of its range. We assembled data on fish bones from 171 archaeological sites from Alaska, British Columbia, and Washington to provide proxy measures of past herring distribution and abundance. The dataset represents 435,777 fish bones, dating throughout the Holocene, but primarily to the last 2,500 y. Herring is the single-most ubiquitous fish taxon (99% ubiquity) and among the two most abundant taxa in 80% of individual assemblages. Herring bones are archaeologically abundant in all regions, but are superabundant in the northern Salish Sea and southwestern Vancouver Island areas. Analyses of temporal variability in 50 well-sampled sites reveals that herring exhibits consistently high abundance (>20% of fish bones) and consistently low variance (<10%) within the majority of sites (88% and 96%, respectively). We pose three alternative hypotheses to account for the disjunction between modern and archaeological herring populations. We reject the first hypothesis that the archaeological data overestimate past abundance and underestimate past variability. We are unable to distinguish between the second two hypotheses, which both assert that the archaeological data reflect a higher mean abundance of herring in the past, but differ in whether variability was similar to or less than that observed recently. In either case, sufficient herring was consistently available to meet the needs of harvesters, even if variability is damped in the archaeological record. These results provide baseline information prior to herring depletion and can inform modern management.

historical ecology | fisheries | forage fish | Northwest Coast | archaeology

Low trophic-level fish ("forage fish") are experiencing global declines, with increasing recognition of widespread and cumulative ecological, cultural, and economic impacts (1–3). Both indigenous and nonindigenous peoples on the Northwest Coast of North America recognize Pacific herring (*Clupea pallasii*) as a foundation species in coastal food webs (4) that serve an essential role in maintaining social-ecological systems (e.g., refs. 5 and 6). Herring and its roe are critical prey for a host of fish (e.g., hake, Pacific cod, dogfish, salmon), birds, and marine mammal predators (7–9). Herring is also central to the social, cultural, and economic relations of coastal indigenous communities, many of which seek to continue their traditional fisheries for herring and herring roe on kelp or other substrates (10–12). Since 1882 and continuing into recent decades, industrial fishing of herring has helped support many communities across the Northwest Coast (13, 14).

Populations of this once highly abundant forage fish have been dramatically reduced across much of its North Pacific range relative to levels seen in the mid 20th century (14–16). Fisheries scientists have proposed various factors accounting for these declines and sustained low abundances even after reductions of fishing pressure. These factors include climate-induced ecological changes in distribution of predators and prey (7), disease (17), overfishing (18), and the rebound of marine mammal populations that prey on herring (15). Assessing these potential drivers and moving forward with conservation requires baseline information on herring abundance and distribution before its depletion. However, current knowledge of Pacific herring distribution and abundance is based on biomass estimates that date back only to the mid 20th century, well after the onset of industrial fishing.

Most modern ecological data lack sufficient time depth for establishing baselines for marine ecosystem management and recovery (19); this has the potential to dramatically underestimate the degree of population loss [the "shifting baseline" problem (20)] and inhibit recovery efforts. As a result, traditional and local ecological knowledge, as well as paleoecological and archaeological data, are increasingly important for informing these baselines (21). Such data provide both the long-term perspective needed to assess preindustrial ecological states, and ecologically and culturally salient baselines for conservation (22–24).

Here, we compile the archaeological record of fisheries in the Northeast Pacific from Alaska, British Columbia, and Washington (Fig. 1) to assess the spatial and temporal distribution of

Significance

Over the last century, Pacific herring, a forage fish of tremendous cultural, economic, and ecological importance, has declined in abundance over much of its range. We synthesize archaeological fisheries data spanning the past 10,000 y from Puget Sound in Washington to southeast Alaska to extend the ecological baseline for herring and contextualize the dynamics of modern industrial fisheries. While modern herring populations can be erratic and exhibit catastrophic declines, the archaeological record indicates a pattern of consistent abundance, providing an example of long-term sustainability and resilience in a fishery known for its modern variability. The most parsimonious explanation for the discrepancy between herring abundance in the ancient and more recent past is industrial harvesting over the last century.

Fig. 1. Percent abundance of herring bones in archaeological sites with >50 identified fish bones (*n* = 171 sites). Only two sites lack herring bones. Herring is abundant (>60% of total fish NISP) in sites throughout the Strait of Georgia in southern British Columbia. In 71% of sites, herring makes up at least 20% of the site's total assemblage of fish bones.

preindustrial herring abundance. The abundance and spatial distribution of archaeological fish bones reveals the widespread importance of herring to indigenous peoples throughout the region, and indicates the abundance of herring in coastal ecosystems over the past several thousand years. Herring were superabundant along southwest Vancouver Island and in the Salish Sea. The archaeological record indicates that places with abundant herring were consistently harvested over time, and suggests that the areas where herring massed or spawned were more extensive and less variable in the past than today. Although archaeological data are expressed over different spatial and temporal scales than modern fisheries population estimates, archaeological data highlight both a disjunction between preindustrial and contemporary herring abundances and distribution, and the need to revise and expand the data on which current fisheries management and conservation are based.

History of Herring and Herring Roe Fishing
For many First Nations and Native American groups from Alaska to Washington, the nutritionally valuable and readily harvested herring and its roe were integral to daily lives and worldviews (e.g., refs. 25–27). This importance is reflected in photographs, interviews, oral histories, and indigenous place names: for example, *Teeshoshum*, "milky waters from herring spawn"; *K'i:na?a*, "herring guts on rocks" (28); *Yaaw Teiyi* "Herring Rock," the sacred place where the first herring arrived; *Shaan Daa* "White Island," also known as "Fish Egg Island," named for the whiteness created by the spawning activity each spring; and "Silver Bay," because in the winter, there were so many herring "if you looked at it in the moonlight you'd see the backs of the herring ... and it would look silver" (29). Many coastal groups maintained family-owned locations for harvesting herring and herring roe from anchored kelp fronds, eelgrass, or boughs of hemlock or cedar trees (12, 30). Herring was harvested at other times of the year than the spawning period when massing in local waters (31–34), but most ethnohistorical observations identify late winter and springtime spawning as a key period of harvest for both roe and fish. Processed herring and roe were consumed in large quantities and traded widely among coastal First Nations (26, 35). Sustainable harvests were

encouraged by building kelp gardens (27), wherein some roe-covered fronds were not collected, by minimizing noise and movement during spawning events, and by elaborate systems of kin-based rights and responsibilities that regulated herring use and distribution (12, 26, 29, 36, 37).

Industrial commercial fishing of herring began in earnest on the Northwest Coast in the late 19th century, primarily using beach and drag seines to catch fish and then render ("reduce") oil and meal (13, 29, 38, 39). In British Columbia, officials prohibited the reduction of herring into oil and fertilizer in 1910 (40) and noted that the larger bays were "being gradually deserted by the larger schools where they were formerly easily obtained" (13). In 1927 (23 y before the current management baseline for estimating historical biomass), the fishery on eastern Vancouver Island, British Columbia, processed 31,103 tons of herring (41), which is roughly two times the annual harvest rate in 2012 and ~38% of the 2013 biomass estimate for the entire Strait of Georgia (42, 43). In Alaska, the herring reduction industry began in 1882, with statewide harvests reaching a peak of 75,000 tons in 1929 (14). By the 1930s, the effects on population numbers and behavior caused fisheries scientists to express deep concern about the effects of overfishing on herring (38, 40, 44), as the fishery shifted to deeper water harvest technology (13) and underwent a considerable spatial expansion in search effort (38).

By the late 1960s, as a result of increased fleet efficiency, reduction fisheries, and poor recruitment, the herring populations of British Columbia and Washington collapsed (45). This collapse led Canada to permanently close its reduction fishery in 1968 (46), followed by the closure in Washington state in the early 1980s (39). In the early 1970s, the herring industry in Japan collapsed (47), which increased East Asian demand for herring eggs taken from North American waters. As a result, a Sac Roe Fishery began throughout the Northeast Pacific, targeting female herring just before spawning. In the last decade, coast-wide declines in herring numbers (39, 48) have led to a greatly reduced Sac Roe Fishery, now limited to a few regions, such as the Strait of Georgia (Salish Sea) and Sitka and Togiak, Alaska (14). In addition to these larger ventures, a relatively small food-and-bait fishery has persisted since the early 20th century. Since the

1970s, licenses and legal judgments have been issued to First Nations in Canada (10, 12), Native Americans in Washington (49), and Alaskan Natives (29) that support food, social, and ceremonial fisheries, and in some cases commercial fishing.

Government fishery managers, scientists, and local and indigenous peoples lack consensus on the cumulative consequences of ongoing commercial fisheries on herring populations. Many First Nations, Native Americans, Alaska Natives, and other local fishers, based on personal observations and traditional knowledge, hypothesize that local herring stocks, on which they consistently relied for generations, have been dramatically reduced and made more difficult to access following 20th century industrial fishing (29, 36, 50, 51). In contrast, fisheries managers (15, 52) identify commercial fishing as only one of several potential causes for the coast-wide decline in herring and persistent lack of recovery since implementing conservation measures (53). In the Strait of Georgia (British Columbia), managers hypothesize that populations have in fact not been depleted, but rather have shifted spatially because of climatic factors and predator abundance (7, 53). The unresolved nature of these alternative hypotheses regarding the primary factors responsible for temporal and spatial shifts in herring populations represent a barrier to achieving consensus on the need and strategies for improving herring conservation and management. Zooarchaeological data offer a record of the preindustrial abundances and distribution of herring, providing a longer-term perspective that can illuminate and contextualize these debates.

Herring and the Archaeological Record

On the Northwest Coast, stratified, shell-bearing archaeological sites ("shell middens") provide long-term records of human–animal interactions. Although animal bones can enter archaeological sites through a range of cultural and noncultural processes (54), the majority of fish bones in coastal middens are associated with human processing or consumption of fish. Even though animal products were widely traded in the past, the bulk of zooarchaeological remains in shell midden deposits tend to be composed primarily of resources harvested nearby (55–57). Thus, in most cases, zooarchaeological remains, including marine fish bones, can be used as proxies for local distribution and abundance.

This synthesis of zooarchaeological fisheries records builds on the increasing number of recent analyses using rigorous methods of fish bone recovery and quantification, particularly the use of column sampling and fine-screen mesh (≤3.2 mm) that is critical to ensuring adequate proportional representation of small-bodied fish, such as herring (58). Our estimates of herring relative abundance and rank order are based on a standard zooarchaeological measure of "number of identified specimens" (NISP), which is not equivalent to biomass or meat weight. Rather, NISP is correlated with numbers of individual animals (59) and thus can be used as a culturally and taphonomically filtered proxy of past local fish populations (60). Most archaeological deposits, including the zooarchaeological data presented here, have relatively low chronological resolution, as calibrated radiocarbon age-range estimates often span more than a century; thus, specific deposits incorporate a degree of time averaging (61, 62).

Despite interpretive challenges, ancient fish bone records provide long-term and spatially explicit data on past use and abundance of herring and other fish. Our dataset compiles rigorously screened data from numerous sites across the Pacific Northwest Coast that represent multiple temporal and regional scales. This is the largest available dataset of fine-screened archaeological fish assemblages from the Northwest Coast and offers new insight into the taxonomic composition of indigenous fisheries.

Results

In the study area, 171 coastal archaeological sites have been sufficiently sampled to evaluate the past distribution and archaeological abundance of herring (Fig. 1 and Table S1). These sites span the early Holocene (10,700 cal B.P.) to the contact-era

(A.D. 1740–1860), with the bulk of sites dating to within the past 2,500 y (76%). The dataset contains 435,777 fish bones confidently identified to family, genus, or species. These specimens represent a wide range of taxa, with each site containing a minimum of 50 identified bone specimens. Coast-wide similarities in the taxonomic richness of assemblages and relative abundance of numerically dominant fish taxa indicate that the archaeofaunal sample sizes are adequate to assess the distribution and relative abundance of herring (Table S1).

Within this dataset, herring is the single-most ubiquitous fish taxon in archaeological sites throughout the Northwest Coast, occurring in 169 of the 171 assemblages (99%) representing various physiographic settings. Herring is also the single-most numerically abundant taxon in the dataset, representing 49% of all identified fish bones, with a site average of 47% (±33% NISP). Herring is similarly the first ranked taxon by NISP in over half (56%) of the 171 assemblages and is among the two most numerous taxa in 80% of assemblages (Fig. 2). Herring comprises more than 20% of fish bones in 71% of the assemblages (NISP). The high ubiquity, rank order, and relative abundance of herring in most sites is remarkable given the many other taxa present in each site (mean n of fish taxa = 10.2, SD = 3.2) and that some ubiquitous genera, such as *Oncorhynchus* spp. (salmon and trout) and *Sebastes* spp. (rockfish) comprise many species (7 and 36, respectively). The occurrence and relative abundance of herring in the majority of sites surpasses any other fish taxon, and demonstrates a pervasive and previously underrecognized role for this species in indigenous economies spanning the Holocene.

Geographically, nearly half the sites in the database (46%) are concentrated around the Salish Sea, reflecting more intensive archaeological investigation in this region. Only two assemblages, both in the northern portion of the study area, do not contain herring bones (Table S1). The occurrence of sites with significant proportions of herring throughout the study area (Fig. 1) indicate that the spatial gaps in the distribution of analyzed sites reflect gaps in archaeological sampling, rather than gaps in the ancient distribution of herring. Thus, as a proxy for the number of fish harvested in coastal waters, these data reflect a widespread abundance of herring in marine ecosystems in the deep past.

Archaeological sites numerically dominated by herring occur throughout the study area. Sites in the Central Coast, West Coast Vancouver Island, and Salish Sea areas are consistently dominated by herring bones with median abundance values representing over 40% of the assemblage (Fig. 3). Most sites where herring represents less than 20% of NISP (n = 50) are in the northernmost portion of the study area (Haida Gwaii, northern British Columbia coast, and southeast Alaska) or in the
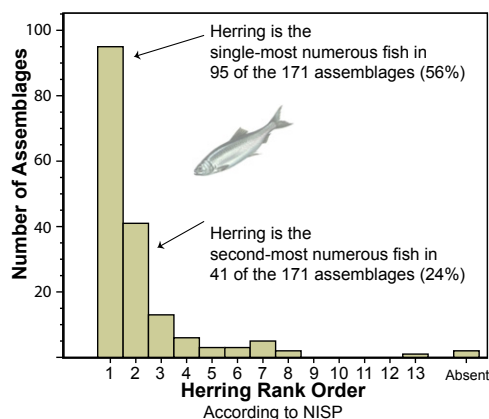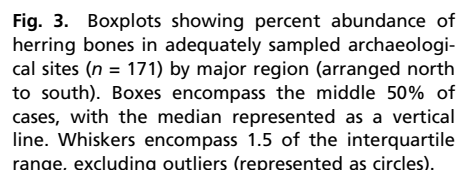

Fig. 2. Rank order of herring bones in 171 adequately sampled archaeological sites. Herring is among the top three most abundant fish taxa in 88% of the sites and is absent in only two sites.

Herring is the single-most numerous fish in 95 of the 171 assemblages (56%)

Herring is the second-most numerous fish in 41 of the 171 assemblages (24%)

Fig. 3. Boxplots showing percent abundance of herring bones in adequately sampled archaeological sites ($n = 171$) by major region (arranged north to south). Boxes encompass the middle 50% of cases, with the median represented as a vertical line. Whiskers encompass 1.5 of the interquartile range, excluding outliers (represented as circles).

southernmost portion of the study area (Puget Sound and the lower mainland of British Columbia) (Figs. 1, 3, and 4). Even in the northern portion of the study area, herring still ranks among the three most ubiquitous and abundant fish in 75% of sites (Table S1). The proportion of herring in Haida Gwaii exhibits high variability among nearby sites, with salmon, rockfish, and dogfish (*Squalus acanthias*) representing the other dominant fish taxa. On the northern British Columbia coast, sites around Prince Rupert and on the Dundas Islands tend to be dominated by salmon and oil-rich smelts (Osmeridae). In southeast Alaska, salmon tends to dominate, followed by herring, Pacific cod (*Gadus macrocephalus*), and sculpins (Cottidae).

The Salish Sea region exhibits exceptionally high archaeological abundance of herring, but with substantial variation among subregions (Figs. 3 and 4). Sites along the northwestern and northeastern Strait of Georgia (eastern Vancouver Island, eastern Strait of Georgia, respectively), the southwestern Strait of Georgia (southern Vancouver Island) and the Gulf Islands, have the highest mean relative abundances for herring (Fig. 4). These high numbers contrast with sites in Puget Sound ($n = 10$, $\bar{x} = 20.6\%$) and along the Fraser Delta ($n = 10$, $\bar{x} = 33.7\%$), which tend to have abundance values less than 40%. This spatially variable distribution of herring across broad regions of the Northwest Coast and around the Salish Sea suggests that although herring was a ubiquitous component of coastal ecosystems, herring biomass (vis-à-vis other fish taxa) was relatively greater in some regions than others.

The sites in the dataset span the past 10,700 cal y. The majority of the sites (78%) have temporal components that fall within the past 2,500 y, whereas much smaller numbers of sites have components that date before this period and only a handful that date before 5,000 y ago (Table S1). This temporal distribution broadly corresponds to the proportion of dated archaeological sites in the region (63), and is a product of site

taphonomy, relative search effort, and geographically variable Holocene sea levels and shoreline locations (64).

Of the 171 sites, 50 (29%) meet our criteria for examining detailed intrasite temporal patterning (Figs. 5 and 6; see also *Materials and Methods*). Similar to the overall dataset, over half of these sites are from the Salish Sea region ($n = 27$, 54%) and the majority date to within the past 2,500 y. Collectively, the 50 sites are comprised of 569 vertically distinct levels, each with sample sizes of ≥ 50 NISP (Table S2).

Herring occurs in the overwhelming majority of the 569 individual levels (99.3%) and the mean relative abundance of herring exceeds 20% in the majority of the 50 sites (88%). Variance in the relative abundance of herring is less than $\pm 10\%$ within 96% of individual sites (Fig. 6 and Table S2), further supporting an interpretation of broad consistency over time. Variance is correlated with sample size, however (Spearman's $\rho = 0.303$, $P = 0.032$, $n = 50$), which reflects the influence of several thoroughly sampled sites from a single region with moderate variability (Barkley Sound) (Fig. 5D). Herring ranks as the first or second-most numerous fish taxon in the majority (92.1%) of the 569 stratigraphic levels. Seven sites exhibit mean abundances lower than 20% and low rank orders (less than 3) for herring over time (Fig. 6). Herring is only absent from four individual levels in four sites that also have consistently low mean abundance values (<4% NISP) (Fig. 5).

The broad consistency in abundance through time is particularly striking, considering these archaeological deposits likely represent a variety of cultural and ecological contexts, seasons of occupation, and depositional processes over multiple temporal scales (55, 62). Of the two sites in our sample that exhibit the highest intrasite variability (more than $\pm 10\%$ variance), one (Burnaby Narrows) (Fig. 5A5) spans a key period of subsistence change (65) and sea-level change (64). In the other (Spring Cove) (Fig. 5B10), dramatic increases in anchovy in two of five occupational levels reduce the relative abundance of herring,

Fig. 4. Percent abundance of herring bones in archaeological sites by subregions (arranged north to south) within the Salish Sea region ($n = 78$). Note the lower abundance of herring in the Fraser Delta and Puget Sound. Note: Gulf Islands includes the Canadian Gulf Islands and the US San Juan Islands. Circles represent outliers and stars represent extreme outliers.
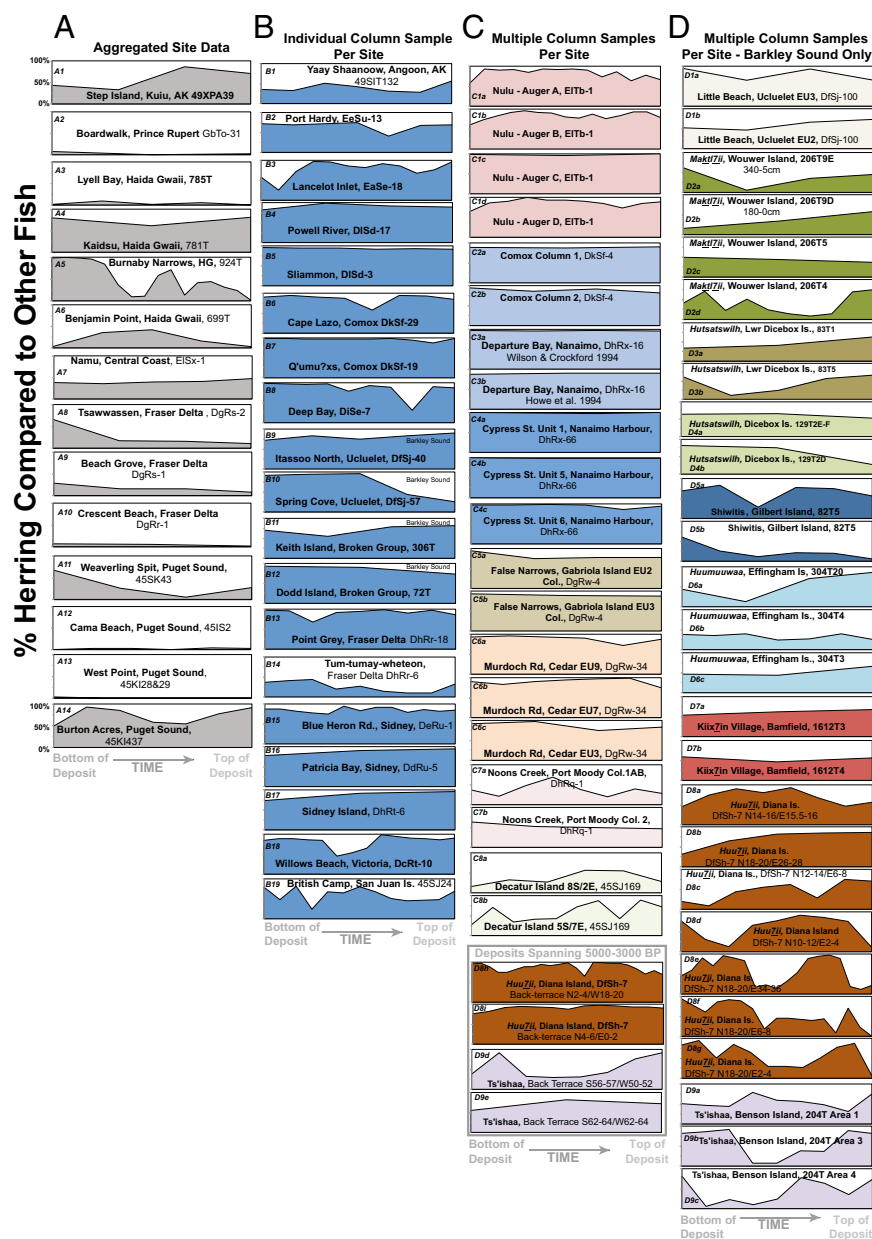
Fig. 5. Percent abundance of herring bones over time in sites with dated samples (n = 50) (Table S2). Sites are arranged into four groups: (A) multiple samples within a site aggregated into broad temporal groupings (ca. 500–2,000 y per stratigraphic layer, n = 14 sites); (B) sites with a single vertical "column" of contiguously sampled levels (n = 19); (C) sites with multiple column samples from multiple site areas (n = 8); and (D) sites with multiple column samples from multiple site areas in Barkley Sound (n = 9). Each site is associated with one or more radiocarbon dates and/or contains historic-era artifacts in the upper levels indicating they date ca. A.D. 1778–1850 (Table S1).

which correspondingly increases variance. As with modern fisheries landing data, social, economic, and environmental circumstances, as well as analytical resolution and ecological drivers, need to be considered when interpreting fine-scale variability within a specific site.

Sites in close proximity and which are broadly contemporaneous display similar patterns of herring abundance over time [e.g., Tsawwassen, Beach Grove, and Crescent Beach around Boundary Bay (Fig. 5 *A8–A10*); Cape Lazo, Q'umu?xs, and DkSf-4 in Comox Harbour (Fig. 5 *B6, B7,* and *C2*); and the Nanaimo Harbour/Departure Bay area (Fig. 5 *C3* and *C4*)]. This similarity suggests subregional coherence in herring abundance over time and indicates that the formation processes associated with each site assemblage (either human harvest of herring or natural taphonomic processes within a site) do not obscure the overall ability of the zooarchaeological data to accurately estimate abundance of herring in these settings. Furthermore, the observations of similar herring abundance values from multiple columns from spatially separate but temporally overlapping deposits within a single site (Fig. 5C and Table S2) strengthens the inference

that single-column samples can document site-wide patterning for such abundant and ubiquitous taxa (33). These overall patterns thus support the value of zooarchaeological data as a proxy for past herring abundance.

Collectively, these multiple analytical scales (Figs. 3–6) and abundance measures indicate a pattern of relatively low temporal variability and broad consistency in herring use as represented among and within archaeological sites distributed across a large coastal region. In areas where herring was archaeologically abundant, it appears to be consistently available and abundant throughout the mid-to-late Holocene. Given the limits of radiocarbon dating and calibration, we cannot determine the extent to which the temporal resolution of our data may inhibit our ability to detect finer-scale (e.g., annual, decadal, multidecadal) variation in herring abundance through time. If high variation in the local availability of herring over time was characteristic for this region, however, we hypothesize this would be apparent in more of our site sequences. Overall, this large-scale archaeological dataset indicates that herring was a desired and
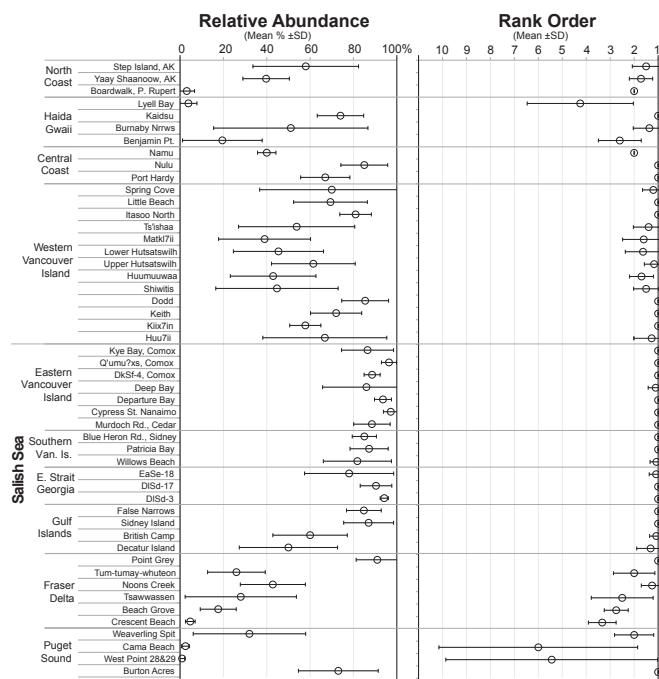
Fig. 6. Mean abundance and rank order of archaeological herring bones from levels in adequately sampled and dated sites (*n* = 50; arranged north to south). Error bars represent ±1 SD (see Table S2 for additional information).

reliable source of food in coastal waters in most locations across the Northwest Coast.

To evaluate the ecological longevity of herring spawning habitat and the extent that herring spawning areas have changed historically, we determined the proximity of archaeological sites to herring spawning areas documented as a result of federal fisheries monitoring efforts that support stock assessment in British Columbia (66). We limited our analysis to archaeological deposits dating within the last 2,500 y (late period sites) and located within areas annually monitored for spawning activity since the mid 20th century (*n* = 79 sites). We observe that archaeological sites with greater than 80% herring are significantly closer (Mann–Whitney *U* test = 475, *Z* = −3.314, *p* = 0.001) to documented spawning locations than archaeological sites with less than 80% herring (Fig. 7 and Table S3). The significance of this difference is strengthened when we include data from nine sites with traditional and local ecological knowledge (50, 67) on the British Columbia Coast (Mann–Whitney *U* test = 444, *Z* = −3.731, *p* = 0.000). The strong correspondence between high archaeological abundance of herring bones and the multidecade monitoring record of modern spawning sites is a compelling argument for the long-term site fidelity of herring spawning.

In British Columbia, 30% (*n* = 34) of the 113 late-period archaeological study sites are in areas that have not been monitored for herring spawn by the Department of Fisheries and Oceans (DFO) (mean distance from closest monitored shoreline is 7.7 km, SD = 8.0 km). Of these, 12% (*n* = 4 sites) have herring abundance values over 80%. Based on the close proximity between the 32 sites with >80% herring bone abundance and documented spawning sites (Fig. 7), we hypothesize that these four sites were also close (i.e., within ±2 km) to former herring spawn locations. Thus, archaeological sites can be used to expand the ecological baseline for spawning populations and identify localities that may no longer support spawning or are missed by modern monitoring efforts.

We also note a general correspondence between six abundance categories used by federal fisheries monitoring in British Columbia (*Materials and Methods* and Table S3) to characterize the cumulative location and intensity of herring spawning, and

six ordinal categories of archaeological abundance of herring. That is, just over half of the late-period archaeological assemblages (43 of 79 sites; 54%) have similar categorical abundance values to the fisheries monitoring dataset (±2 km). However, 34% of these archaeological sites (*n* = 27 sites) contain a categorically greater abundance of herring than fisheries monitoring records, whereas only 11% have substantially lower abundance values than cumulative spawning records (*n* = 9 sites).

Collectively, these comparisons both provide information on the longevity of spawning habitats as well as the potential depletion of spawning habitats in historic times. The predominant correspondence between ordinal categories in the ancient and modern data indicates correspondence between ancient productivity of herring and the productivity of contemporary spawning habitats in a given location. This finding, in turn, indicates consistency in the geography of spawning habitats from the distant to the more recent past. Furthermore, the 34% of archaeological sites that have higher abundances of herring than is predicted by the federal cumulative spawn records provides a basis for expanding our estimate of potentially productive spawning habitat beyond what is indicated by historic census records.

Discussion

This broad compilation of zooarchaeological data provides a previously unconsidered record of the past abundance and distribution of fisheries along the Northwest Coast of North America. The compilation establishes herring as among the most important marine fish on which coastal indigenous people relied in the past. These data expand greatly upon the extant paleoecological fisheries record (68–70) and indicate that herring was both widespread across the coast and a mainstay of ecological and socio-economic systems over the Holocene. Herring occurred in abundance (>40% NISP) in numerous sites across all areas of the coast but exhibited superabundance (i.e., >60% NISP) in a few regions, such as the central and northern Strait of Georgia and the west coast of Vancouver Island. Spatially clustered sites reflect similarly consistent abundance values and a few sites exhibit modest trends over time that may relate to physically driven habitat change, such as the geomorphological evolution of the Fraser Delta (e.g., Beach Grove and Tsawwassen). Only a small number of sites exhibit high variability whereas the more common pattern is of broadly sustained abundance over space and time (Figs. 5 and 6).

Could the contrast between the consistency seen in the archaeological record and patterns in recent fisheries showing overall decline and increasing fluctuation in spawning distribution arise from insufficient temporal resolution in the archaeological data? Even though modern population fluctuations are observed at interannual to decadal timescales, and the likely
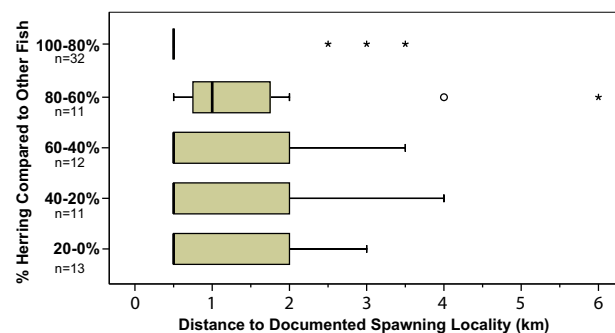

Fig. 7. Boxplot showing variability in the archaeological abundance of herring bones in relation to proximity by water to historically surveyed spawning locations (±500 m). Distance data calculated only for sites in British Columbia within monitored areas (*n* = 79) and with components dating to within the last 2,500 y (Table S3). Archaeological data are grouped into relative abundance categories as per Fig. 1.

resolution of the archaeological record is at the centennial scale, it is unlikely that the temporal consistency in the archaeological record is an artifact of insufficient chronological resolution for several reasons. First, if extreme fluctuations in abundance and periodic absences were common in the past (for example, such that sites with great abundance in some periods commonly declined to low levels), we would expect to see this reflected in our data, even if we couldn't resolve the actual temporal trajectory in an individual population. Alternatively, our data may also represent subannual temporal variability, which is masked by the coarseness of existing calibrated radiocarbon records. Both scenarios indicate that in our sample of 569 levels, across 50 sites and representing approximately 7,000 y of harvesting data, we should observe some indication of absences and wide fluctuations in herring abundance if they were present. However, these data show a remarkably consistent presence of herring with 99.3% of the 569 levels containing herring and a mean relative abundance exceeding 20% in 86% of the sites, with within site variance of less than ±10% in 48 of 50 sites (Fig. 7 and Table S2).

Second, because of the regularity with which ancient peoples "sampled" their marine environments, the archeological record should be a sensitive indicator of marked declines in local abundance of herring, as harvesters would conceivably switch to alternative prey when a target species declines to low levels. Such resource switching is observed in the regional zooarchaeological record, but is expressed over centennial scales and among a limited range of animal species other than herring (e.g., refs. 65 and 71). In contrast, even substantial variability around a high mean abundance might not be reflected in our data if herring populations never declined to a threshold where people could meet their needs for consumption, storage, and trade. Similarly, another factor potentially contributing to consistency in the archaeological abundance of herring may be multiseason herring harvests, where fish, fish oil, and roe were processed for longer-term storage and extended consumption within a year (e.g., refs. 33 and 34). This scenario may further dampen fluctuations in abundance over decadal or centennial time scales but also depends on consistent interannual availability of herring.

We envision three alternative hypotheses to account for the difference we observe between archaeological and modern data in the apparent variability and abundance of herring populations (Fig. 8). The first hypothesis asserts that the modern pattern of interannual dynamics is an accurate reflection of the past and that the archaeological record overestimates abundance and underestimates variability in ancient herring populations (Fig. 8, hypothesis 1). For the reasons advanced above, we argue that this hypothesis can be rejected.

Our data seem most consistent with hypotheses that ancient herring populations had a higher mean abundance than in the last century (Fig. 8, hypotheses 2 and 3). Variability could have been damped relative to the industrially exploited populations of the 20th century (Fig. 8, hypothesis 2), or it could have been similar to those harvested populations (Fig. 8, hypothesis 2). In either case, abundance in the more distant past was sufficiently high to meet the needs of harvesters, leading to consistency in the archaeological record.

Although the archaeological record shows consistency through time, the paleooceanographic record for the Northwest Coast illustrates considerable variability (e.g., ref. 72). Both ocean temperature and productivity vary throughout the late Holocene at different spatial and temporal scales, with some periods of interregional convergence (70, 73, 74). If ancient herring populations fluctuated in response to high-frequency oceanographic variability (e.g., ref. 75), the fluctuations were not of sufficient amplitude to influence the overall catch of ancient fishers (cf. ref. 76); the substantial variability in the paleooceanographic record is not matched by the archaeological record of herring. Moreover, it seems unlikely that climatic change alone is sufficient to account for substantial declines in Pacific herring populations and spawning distribution over the last 100 y (cf. refs. 77 and 78).

The most parsimonious explanation for the difference between the modern pattern of variability in herring abundance and the long-term archaeological record is the onset of industrial-scale commercial fishing. Dramatic reductions and spatial shifts in herring populations were observed by fisheries managers in British Columbia and Alaska in the 1930s (13, 14, 38, 40, 41, 44). A period of decline between A.D. 1910 and 1970 is evident in the well-dated sediment cores from southeast Vancouver Island (68). Since the 1970s, further population constrictions have been observed by non-Native bait fisherman in the Georgia and Johnstone Straits (British Columbia), including the widespread absence of herring in over 170 locations that previously supported spawning (16).
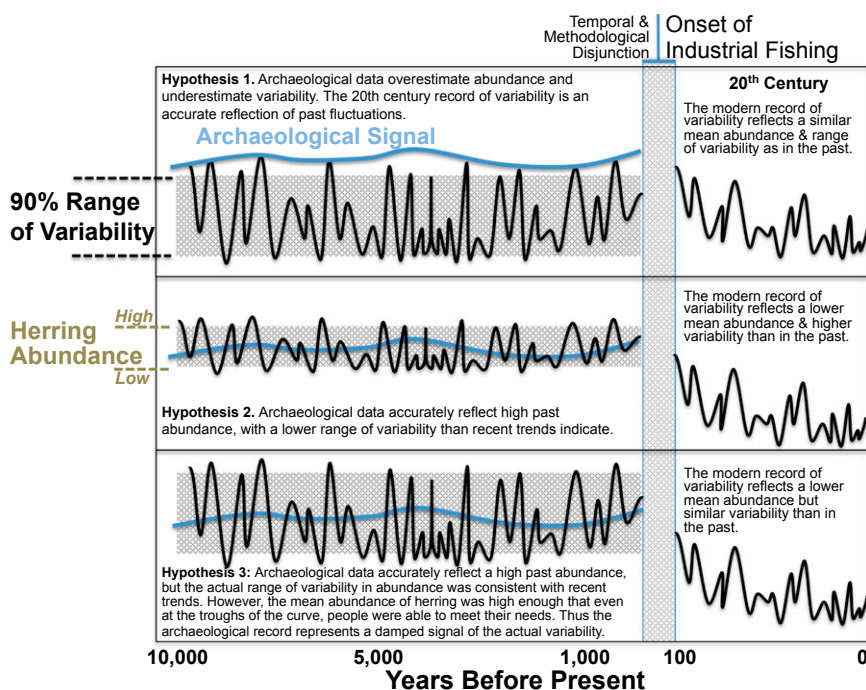
Fig. 8. Schematic representing three alternative hypotheses regarding the relationship between modern and archaeological abundance and variability of herring populations. The left side of the figure combines the smooth archaeological signal (blue lines) with three hypothesized trajectories for actual populations (black lines), each shown with its 90% range of variability (gray stippled rectangles). In each case, the end of the timeline following the onset of industrial fishing represents a caricature of the recent pattern of herring population dynamics, characterized by great variability, an overall decline in abundance, and some periods of very low abundance.

Modern declines and contractions of the spawning range of Pacific herring are supported by recent syntheses of the traditional ecological knowledge of indigenous peoples in Alaska and British Columbia (50, 51, 67). These syntheses document quantifiable reductions in the magnitude of spawning events and loss of spawning locations in living memory. Furthermore, this shift in abundance is reflected in indigenous place names, which highlight locations of formerly abundant herring, but where few herring are found today (e.g., *Ch'axa'y* or "Sizzling [with herring] Water") (79). Archaeological abundance of herring is additionally mirrored in indigenous place names and origin narratives. For example, the 2,400-y-old site of Nulu on the Central British Columbia Coast, where herring made up 85 ± 11% of the fish assemblage (80), is the place where, according to Heiltsuk oral tradition, Raven first obtained herring (25). Conversely, a culturally affiliated site at the Koeye River 25-km away from Nulu (Table S1), is not associated with herring or herring spawn either in ethnographic or modern ecological data, and exhibits low archaeological herring abundance (10% NISP). In the northeastern Salish Sea in southern British Columbia, the place name of *Teeshoshum* ("waters white with herring spawn") is associated with an approximately 800-y-old assemblage comprised of 93% herring bones (Table S1). However, extensive herring spawning in this ecologically suitable location have not been documented since 1998 (66).

Collectively, these sources of historical and ethnobiological data reinforce the contrast between the archaeological record and the dynamics of the modern fishery. In response to locally reduced or absent spawning populations, the current herring fishery in British Columbia has contracted from its mid-20th century coast-wide focus and is now concentrated along the east coast of Vancouver Island, overlapping an area in which herring were superabundant archaeologically (9, 42). Although other factors are also responsible for range contraction of harvested fish populations, range contractions are recognized as one of the effects of overfishing (81, 82).

Historical baselines in natural resource management serve as reference conditions for understanding the context for modern population or ecosystem dynamics, providing both assessments of abundance and ranges of natural variability (83, 84). Our archaeological data, in combination with traditional ecological knowledge and early historic observations (14, 40, 41), suggest that late 20th century census data alone do not provide a sufficient baseline for assessing the abundance, distribution, and dynamics of Pacific herring in relation to industrial fishing since the 1880s. This discrepancy between recent and past dynamics is expressed in both temporal and spatial domains. In the temporal domain, the archaeological data challenge the notion that large fluctuations in abundance, including extremely low levels of abundance, are a regularly occurring component of population variability. In the spatial domain, our data argue against the idea that spawning was spatially erratic in the past, with little site fidelity (53). The archaeological data, in combination with the oral historical knowledge and early historic observations, suggest that industrial fishing already had a significant ecological impact on herring abundance and spawning location well before the initiation of coast-wide spawning censuses in British Columbia in 1938. Moreover, the historical baseline currently used for annual stock assessments that underpin current harvest allocations in British Columbia began only in 1951 (43).

The recent history of erratic population fluctuations, declines, and shifting spawning distributions exhibited by Pacific herring populations are not unusual among industrially harvested populations of forage fish worldwide (1–3, 78). What is unique is our ability to provide a long-term temporal context for these recent dynamics. This ability is particularly relevant because these data reflect sustained continuous harvesting of herring populations for millennia before more than a century of modern industrial exploitation. Similar to historical research on the impacts of early industrial-era fishing on Atlantic cod (84) and herring in northern Europe (85, 86), and the long-term effects of human use of coral reefs (87), the archaeological analyses synthesized here critically extend the temporal depth of ecological baselines for contemporary fisheries management.

Conclusion

Spatially and temporally extensive archaeological data on the relative abundance of herring bones in coastal archaeological sites along the Northwest Coast provide insight into the past distribution and abundance of Pacific herring and long-term human–herring interactions. Herring bones exhibit a remarkable degree of dominance within the archaeofauna across space and time in the majority of these records. Over the period represented well by the archaeological record (ca. 2,500–200 y B.P.), Pacific herring populations also appear to have exhibited higher abundance and greater consistency in their distribution than is indicated by the dynamics of industrially harvested populations over the past 50–100 y. The archaeological data indicate that in most parts of the study area, and particularly in the Strait of Georgia, herring remained consistently available to harvesters over thousands of years. Of the hypotheses posed in Fig. 8, we reject hypothesis 1, that the archaeological data misrepresent the actual abundance and variability of herring. At present, we cannot distinguish between hypotheses 2 and 3: herring abundance appears to have been consistently high, but we cannot resolve the magnitude of variability in abundance. The archaeological record, in combination with local and traditional knowledge, early historical records, and paleoecological records, suggest that spawning locations were formerly more abundant and geographically extensive than is recorded by modern surveys. These data, particularly in the context of high harvest levels during the early industrial fishery and the subsequent contraction of effective spawning range, indicate that the currently used ecological baseline of the mid 20th century is inadequate for modern management.

Our data support the idea (Fig. 8, hypotheses 2 and 3) that if past populations of Pacific herring exhibited substantial variability, then this variability was expressed around a high enough mean abundance such that there was adequate herring available for indigenous fishers to sustain their harvests but avoid the extirpation of local populations. These records thus demonstrate a fishery that was sustainable at local and regional scales over millennia, and a resilient relationship between harvesters, herring, and environmental change that has been absent in the modern era. Archaeological data have the potential to provide a deep time perspective on the interaction between humans and the resources on which they depend. Furthermore, the data can contribute significantly toward developing temporally meaningful ecological baselines that avoid the biases of shorter-term records.

Materials and Methods

Data Sources. To examine the distribution and abundance of herring represented in archaeological sites of the Northwest Coast (southeastern Alaska, British Columbia, Washington), we compiled a database of all well-sampled sites with adequately recovered and identified fish bone assemblages located within 1 km of the current marine shoreline (Table S1). This compilation entailed an extensive literature review of published and gray literature on zooarchaeological analyses completed over the past 40 y. Given the small size of herring bones (e.g., vertebral centra are generally less than 4 mm in diameter), we only included sites where the zooarchaeological remains were systematically recovered using a fine-screen mesh (equal to or less than 3.2 mm). All zooarchaeological remains were identified by established analysts or students working under the analysts' direct supervision using comparative collections (Table S1).

Only sites containing a minimum of 50 fish bone specimens identified to at least family level were included. Over 91% of the 171 sites have more than 100 fish bones. This is a reasonable threshold for assessing the relative abundance of the three-most ubiquitous and abundant taxa at a site (71). For the site-based analyses presented in Fig. 1 and the regional analyses presented in Figs. 3–6, we combined zooarchaeological data from sites with multiple excavated subassemblages to ensure adequate sample sizes (Tables S1 and S2).

We used the relative abundance of herring bones among all identified fish (NISP) as a proxy for the relative abundance of herring in archaeological sites. We did not convert herring bone NISPs to estimates of "meat-weight" or

biomass because suitable taphonomic, allometric, and stratigraphic data are lacking for the majority of sites. We judge our assessment of the abundance of identified herring bones as a proportion of all fish bones to be conservative given that herring have fewer vertebrae than some larger fish taxa that can fracture into numerous identifiable fragments (e.g., *Oncorhynchus* spp., *Squalus acanthias*). Although quantitative data on herring bone-density measurements have not been conducted, their bones are notably smaller and more delicate relative to most other measured fish species (88). Moreover, the cellular structure of herring bone likely makes them more susceptible to microbial degeneration relative to other fish (89), indicating this species would likely be less well-preserved in the archaeological record.

Chronological Assessments. To assign age ranges to archaeological assemblages, we used stratigraphic and chronological information provided in the original research reports and in subsequent published archaeological research (Table S1). The majority of sites contain at least one radiocarbon date (88%) and the remainder contain temporally diagnostic artifacts and are on landforms consistent with late Holocene sea levels (*n* = 21 sites). Radiocarbon age estimates were assigned age categories based on dates recalibrated using the Intcal09 curve (90) and represent the 2-σ calibrated range. Most radiocarbon samples were taken from the basal layers of individual site deposits.

Time Series Analysis. To examine within-site temporal patterns at the finest possible depositional scale, we identified a subset of 50 sites that report chronologically distinct vertical levels or stratigraphic layers (Figs. 6 and 7, and Table S2). We included only those sites that have been dated in their basal and terminal levels either by radiocarbon dating or the presence of historic artifacts of European manufacture. Assemblages had to have 50 or more identified fish bones per vertical level or stratigraphic layer and three or more levels in sequence. To ensure each datapoint had 50 or more specimens, some assemblages from contiguous strata or levels with less than 50 identifiable specimens were combined (Table S2).

Because of differences in how assemblages were collected in situ, and the level of detail in which they are reported, we present these data in four analytically separate categories in Fig. 5. These categories are: (*i*) assemblages collected from multiple areas within a site according to temporally distinct strata (ca. 500–2000 y per stratigraphic layer, *n* = 14 sites); (*ii*) sites with a single column sample of contiguous levels (*n* = 19 sites); (*iii*) sites with multiple column samples with multiple contiguous levels spanning broad temporal intervals (*n* = 8 sites); and (*iv*) sites with multiple column samples with multiple contiguous levels spanning broad temporal intervals in Barkley Sound (*n* = 9 sites).

Comparison with Modern Spawning Records. To evaluate archaeological data in relation to historic and contemporary herring spawning records from British Columbia (Fig. 7), we calculated the distance between our archaeological study sites and historically documented herring spawning localities (Table S3). We restricted this analysis to sites within areas with modern herring spawning observations as these represent a long-term ecological record of cumulative spawning activity and are derived from annual surveys of spawning length, thickness, timing, and other variables collected by the DFO (66) since 1937 (91). Where available, we also documented the proximity to spawning areas identified in traditional and local ecological knowledge studies in British Columbia (50, 67). These studies are based on interviews with knowledgeable indigenous and nonindigenous local residents with lifetimes of perspective on the fisheries in their traditional territories. Distance to closest documented spawn was determined by placing geo-rectified maps of cumulative spawning localities into *Google Earth* and measuring the shortest route by water (±500 m) to an archaeological site.

To assess the potential disjuncture between archaeological data and the cumulative record of historical spawning activity, we compared the six quantitative categories used by the DFO [ranging from "vital" to "minor" (91)] to correspondingly ranked archaeological abundance categories (e.g., 100–80% NISP = vital, 1–20% = minor). If there was more than one record of cumulative spawning within a distance of 2 km, we chose the most abundant ranking for the comparison. If the ordinal grouping in the two records differed by more than one category, we considered the two records to represent a disjuncture in abundance (Table S3).

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