

Late Holocene Anthropogenic Depression of Sturgeon in San Francisco Bay, California

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*Prehistoric resource depression has been widely documented in many late Holocene contexts characterized by expanding human population densities, and has been causally linked to a wide range of other significant changes in human behavior and biology. Some of the more detailed records of this phenomenon have been derived from the San Francisco Bay area of California, including a possible case of anthropogenic sturgeon depression, but evidence for the latter was derived from limited fish-bone samples. We synthesize and analyze a massive ichthyoarchaeological data set here, including over 83,000 identified fish specimens from 30 site components in the central San Francisco Bay, to further test this hypothesis. Allometric live weight relationships from selected elements are established to reconstruct size change in white sturgeon (*Acipenser transmontanus*) through time, and—collectively—the data show significant linear declines over the last 3,000 years in the relative abundance of sturgeon compared to all other identified fishes, as well as declines in the maximum and mean weights of the harvested fish. Both these patterns are consistent with resource depression and do not appear to be related to changes in the estuarine paleoenvironment. Variation in sturgeon abundances also declines through time, in a pattern that reflects the single local source of this resource. These data have implications for both late Holocene regional human settlement systems and modern management of sturgeon populations, which are among the most imperiled animal populations on earth.*

The history of sturgeon fisheries throughout most of the world has been one of overexploitation resulting in severe population reduction. The large size and sluggish nature of sturgeon make them vulnerable to netting and snagging and their valuable caviar...and flesh have made them very lucrative—while they last.

[Moyle 2002:106]

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APPEARING FIRST IN THE TETHYS SEA DURING the lower Jurassic 200 million years ago, sturgeons (*Acipenseridae*) radiated across the former Laurasian landmasses and would come to occupy many of the largest rivers and inland lakes and seas of Eurasia and

North America. Representing one of the oldest lineages of ray-finned fishes, these so-called “living fossils” are characterized by large spindle-shaped bodies covered by five rows of bony scutes, tubular mouths equipped with sensory barbells, and cartilaginous post-cranial

endoskeletons. As a group, they are slow-maturing, long-lived fishes, and many follow an anadromous life-history pattern where they migrate from marine or estuarine environments to freshwater lakes and rivers to spawn (Bemis et al. 1997; Pikitch et al. 2005).

Twenty-five species of sturgeon exist in these settings today but, unfortunately, nearly all of them are considered threatened or endangered, making them among the most imperiled groups of animals on Earth. Although overfishing is implicated as a primary cause in many cases of historic population declines, as Moyle alluded to above, pollution, blockage of access to habitats by dams and dikes, and elimination or alteration of backwater areas or spawning habitats have also played significant roles (Birstein et al. 1997; Boreman 1997). Given their susceptibility to harvest pressure and habitat degradation owing to their exceptionally slow life history and their “large size and sluggish nature,” it is somewhat surprising that documented cases of prehistoric human impacts on sturgeon populations are so few in number.

In Eurasia, the strongest evidence of fishing pressure on ancient sturgeon has emerged from medieval contexts in the southern Baltic region (Poland, Germany). In this case, declines in common sturgeon (*Acipenser sturio*) bone frequencies are evident from sites during the eighth through the thirteenth centuries. Because the declines are not synchronous in time, but instead occur across the occupational histories of individual sites, they are argued to reflect human-induced population reductions, rather than climate-based environmental changes (Bartosiewicz et al. 2008; Benecke 1986:10). Recent syntheses of prehistoric sturgeon fishing in eastern Europe, however, are more cautious, suggesting that the “sporadic archaeological data cannot be used in studying the depletion of stocks” (Bartosiewicz and Bonsall 2008; Bartosiewicz et al. 2008:52).

The most detailed analyses of prehistoric sturgeon harvest pressure have occurred recently along the Pacific Coast of North America. Butler (2000) and Broughton (1994a; Broughton et al. 2010), for instance, have documented significant late Holocene declines in the relative abundance of sturgeon (*Acipenser* spp.) and salmon (*Onchorhynchus* spp.) from inland contexts along the Columbia and Sacramento rivers, respectively. While in both cases the declines were attributed to human fishing pressure, in neither context was region-specific

paleoenvironmental data arrayed against the changing relative frequencies of sturgeon—to assess the influence of climate change—nor was demographic evidence (e.g., age/size structure) provided to corroborate a harvest-based cause for the declines. However, declines in both sturgeon abundances and element (dentary) size were documented at the Emeryville Shellmound on the San Francisco Bay in the absence of correlated changes in estuarine salinity, but from a fish-bone sample of only ~2,000 specimens derived from a single site locality (Broughton 1997, 1999, 2002).

In the present analysis, we synthesize a massive ichthyoarchaeological data set from the central San Francisco Bay and examine trends in sturgeon relative abundances from 30 site components, including over 83,000 identified fish specimens. We also develop allometric live weight-element size regression formulae, based on analyses of modern white sturgeon (*Acipenser transmontanus*), to document trends in sturgeon size from measured elements from the Emeryville sample. This dataset, much of it generated over the last decade by multiple analysts (e.g., Gobalet and Hardin 2002; Simons and Carpenter 2009; Wake and Gobalet 2000), represents the largest collection of archaeological sturgeon material assembled anywhere in the world and allows a rigorous test of the sturgeon depression hypothesis for this region. Our analysis also has implications for substantive issues in regional prehistory, the methodology of prehistoric resource depression studies, and the modern management of sturgeon populations.

PREHISTORIC RESOURCE DEPRESSION STUDIES IN CALIFORNIA

Resource depression refers to the reduction in prey encounter rates that results from predator activities (Charnov et al. 1976), and rigorous assessments of the potential for resource depression on California vertebrate faunas began in earnest with the emerging approach of evolutionary ecology and foraging theory in the late 1970s and 1980s. Ironically, it was an apparent trend in the dietary use of a plant resource—acorns—that led to many studies devoted to understanding human impacts on local faunas.

Widely recognized as a staple for many native California groups at contact, acorns produced very

low return rates, to judge from considerations of the available data on their handling costs and caloric gains (Basgall 1987; Bettinger and Baumhoff 1982). The late inclusion of the acorn resource in human diets and its increasing importance across the late Holocene was interpreted as suggesting that expanding human populations drove the process of resource intensification and declining foraging efficiency (Basgall 1987; Bettinger and Baumhoff 1982). Insofar as acorns—a low-ranking resource—were increasingly utilized as foraging efficiencies steadily declined across the late Holocene, it seemed to follow that absolute or per capita abundances of other higher-return resources—such as larger fish and game taxa—must have declined (Broughton 1994a).

With this background in place, a small industry of fine-grained archaeofaunal tests of late Holocene resource depression and associated declines in human foraging efficiency in prehistoric California has emerged over the last three decades. Geographically, the studies encompass a wide range and diversity of habitats and specific locations: from the alpine tundra of the White Mountains to pelagic marine contexts off the coast of southern California. Taxonomically, the resources involved are also diverse and include waterfowl (Broughton 2004; Broughton et al. 2007; Goshen 2013), cormorants (Broughton 2004; Broughton et al. 2007; Whitaker 2010), artiodactyls (Broughton et al. 2010, 2013; Grayson 2001), pinnipeds (e.g., Gifford-Gonzalez et al. 2004; Hildebrandt and Jones 2002), and marine and anadromous fishes (e.g., Braje et al. 2012; Broughton 1997; 2002; Broughton et al. 2010; Salls 1992; see also Erlandson and Braje 2013 and other papers in that volume for a discussion of prehistoric human environmental impacts on a global scale).

On balance, these studies document the fact that if not ubiquitous (e.g., see Codding et al. 2010; Whittaker 2009), the geographic and taxonomic extent of late Holocene resource depression and declining foraging efficiency in California was clearly widespread. In addition, this work has produced important insights into various analytic and taphonomic factors that influence our ability to detect prehistoric resource depression. Important non-anthropogenic environmental considerations include, for example, controlling for variation in the spatial structure of prey abundances, prey behavior, and climatic changes that can affect temporal

trends in prey densities. Of course, underlying variation in faunal sample sizes, the quantification units and statistical methods used, and variation in the methods used to recover faunas—including screen-size and intra-site spatial sampling—have each been recognized as playing important roles in deciphering trends (e.g., Cannon 2001; Goshen 2013; Schollmeyer and Driver 2013; Whitaker 2009).

We address all of these issues below in our evaluation of the evidence for prehistoric sturgeon depression in the central San Francisco Bay region. After introducing the ecological and archaeological context of the San Francisco Bay region, we assess the evidence for sturgeon depression at Emeryville, focusing on relative abundance data from the 1999 excavations and recent analyses of sturgeon size changes from materials collected from the early twentieth-century projects. We then synthesize the available data and examine quantitative trends in sturgeon abundances from three other San Francisco Bay regions, including bayshore sites from (1) Contra Costa County, (2) southeast Marin County, and (3) the San Francisco Peninsula.

THE SAN FRANCISCO ESTUARY AND ITS FISH RESOURCES

The San Francisco Estuary

The San Francisco Estuary (Fig. 1) is the largest estuary on the Pacific coast of North America, and including the contiguous Sacramento-San Joaquin Delta, covers roughly 4,100 km². The estuary is formed by the confluence of ocean water and freshwater inflow, largely from the Sacramento-San Joaquin watershed, and drains 40% of the land area of the state of California (Josselyn 1983; Sommer et al. 2007).

The San Francisco Estuary consists of three subembayments: the North Bay, which includes both San Pablo and Suisun bays, the Central Bay, and the South Bay. The bays are characterized by large areas of open water, encircled by intertidal mudflats and tidal marshes (Chin et al. 2004). Although the basin supported at least three ephemeral estuaries over the past million years, the current one began to form toward the end of the Pleistocene and reached close to its modern extent and levels about 4,000 to 3,000 years ago (Atwater et al. 1977).

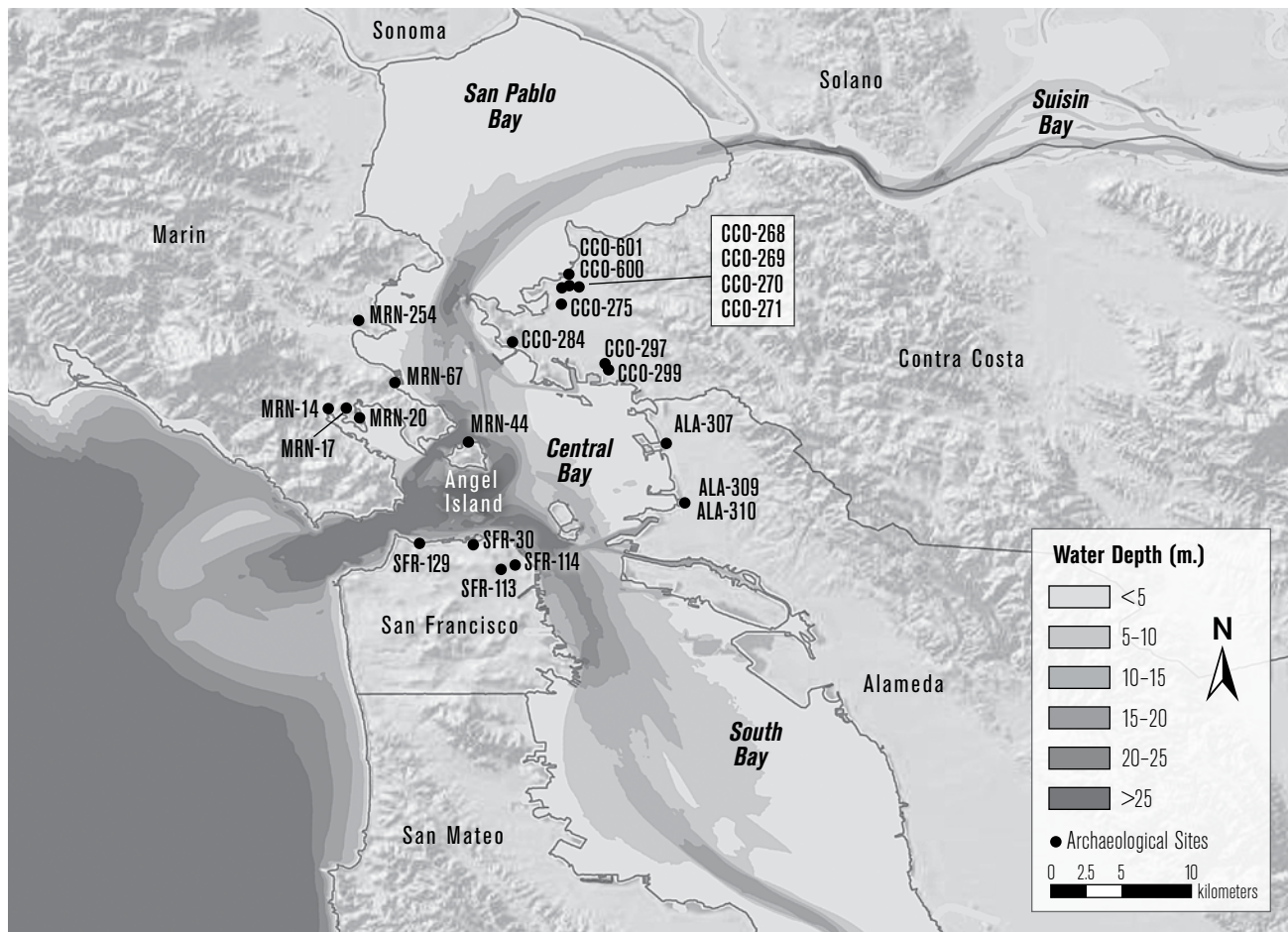


Figure 1. Map of San Francisco Bay showing location of archaeological sites discussed in the text and variation in water depth.

Considerable variation in salinity occurs within the estuary, with marine water dominance in the Central and South bays, and freshwater dominance in the Sacramento-San Joaquin Delta. Intermediate areas, such as in the North Bay, exhibit the greatest salinity variation, which is influenced by diurnal tidal currents, seasonal variation in freshwater inflow, and longer-term trends related to regional climate and moisture history (Ingram et al. 1996; Sommer et al. 2007).

Substantial variation in depth also occurs in different areas of the bay (Fig. 1). As a whole, the average depth is about 6 m., mean lower low water (MLLW; the average elevation of the lower of the two daily tides). Areas near the Golden Gate and the San Francisco Peninsula are the deepest, and attain maximum depths of 100 m. Powerful tidal currents scour the bay floor clean, leaving more coarse-grained and rocky substrates in these areas. Other areas of the bay are much shallower,

with average depths of about 3–4 m. MLLW (Chin et al. 2004), and have softer, mud bottoms. These abiotic factors have important implications for the nature of the San Francisco Bay ichthyofauna and the accessibility of sturgeon resources to indigenous foragers of the region.

Fish Resources of the San Francisco Estuary

The rich fish community of San Francisco Bay is a unique mosaic of freshwater, anadromous, marine, and euryhaline taxa—including over 90 native species (Moyle 2008; Moyle et al. 2010). However, the vast majority of fishes utilized by past peoples of the region fall into six major groups: (1) sturgeon, (2) salmon and steelhead, (3) hound sharks (Triakidae), (4) bay rays (*Myliobatis californica*), (5) surfperch (Embiotocidae), and (6) herrings and silversides (Clupeiformes, Atheriniformes; taxonomic nomenclature follows Nelson et al. 2004). The fishes in each of these taxonomic groups have distinctive

sizes, mobility and life history characteristics, and seasonal occurrence patterns in the bay that influence the energetics associated with their use and susceptibility to depression (see reviews in Broughton 1997; Gobalet and Hardin 2002).

Two species of sturgeon, white (*A. transmontanus*) and green (*A. medirostris*), occur in the San Francisco Estuary—but of the two, white sturgeon has overwhelmingly dominated the sturgeon assemblage in historic times (Miller 1972; Moyle 2002; Skinner 1962). And although distinguishing these species osteologically is exceedingly difficult and most previous analysts have provided only genus-level identifications, Gobalet and Hardin (2002) describe consistent differences in scute surface morphology and made 1,023 species-level sturgeon identifications in the 1999 Emeryville collection. Consistent with historic abundances, white sturgeon were represented in 91% (930 of 1,023) of the sturgeon scute material from Emeryville.

The white sturgeon of San Francisco Bay are anadromous and iteroparous, but spend most of their lives in the estuary—they move up the Sacramento-San Joaquin river system to spawn between March and June but return to the bay shortly thereafter. Sturgeon exhibit an exceedingly slow life-history pattern—females do not reach sexual maturity until they are 12 to 16 years of age and have attained weights of about 30–40 kg. Sexually mature fish only spawn about once every five years, and thus only a small fraction of the population is involved in the spawning migration during any given year (Moyle 2002). Green sturgeon exhibit a similar life history pattern, but spend relatively more time in the marine environment (Kelly et al. 2007; Moyle 2002).

Within the estuary, white sturgeon are most abundant in brackish portions of the bay that are characterized by extensive shallow mudflats that become partially exposed at low tides. These locations provide access to a variety of benthic prey, such as opossum shrimp (*Neomysis mercedis*) and amphipods (*Corophium* spp.). In dry years, with reduced freshwater inflow, white sturgeon follow brackish waters upstream—movements toward the Central Bay occur during wet years (Kohlhorst et al. 1991; Moyle 2002). Minimal data exist on green sturgeon distributions and movements within the bay (Kelly et al. 2007).

Previously reported data (updated in Table 1) and analyses have suggested that sturgeon would have likely

Table 1
BODY SIZE AND FAT CONTENT FOR MAJOR TAXONOMIC GROUPS OF SAN FRANCISCO BAY FISHES^a

Taxonomic Group	Max. Weight, kg. (Rank)	Mean Weight (kg.)	% Fat (Rank)
Sturgeon	816.0 (1)	18.40	4.04–12.50 (2)
Salmon/Steelhead	39.0 (3)	9.00–10.00	2.20–19.00 (1)
Surfperch	2.0 (5)	0.40	1.18 (6)
Bat rays	95.0 (2)	3.64–11.45	.20–2.00 (5)
Hound sharks	32.0 (4)	4.00–4.09	.90–4.50 (4)
Herrings and Silversides	0.6 (6)	0.05–0.40	10.45 (3)

^aData on maximum weight and fat content are from Broughton (1997), Eschmeyer et al. (1983), and USDA (2014).

provided among the highest post-encounter profitability (e/h , energy over handling), or return rates, of the San Francisco Bay fishes based on considerations of their large body size and high fat content (Broughton 1997). As a result, decreasing relative abundances of sturgeon at Emeryville were read to reflect overall declines in the efficiency of fish use across the occupational history of this locality. This argument is supported by a recent survey of the available empirical data on the relationships between prey body size and post-encounter return rates for vertebrate resources. These data, derived from both experimental and ethnographic contexts, document significant and positive body size–return rate correlations in the vast majority of cases—including the three that are focused exclusively on different size classes of fishes (Broughton et al. 2011).

These data notwithstanding, it is possible that substantial differences in prey mobility might influence the handling costs enough to alter a ranking based on energetic value estimates alone (Bird et al. 2009; Codding et al. 2012). Variation in handling costs associated with extracting fish resources from the San Francisco Estuary was likely quite variable and context dependent as a wide variety of fishing methods were employed by aboriginal groups of the region, including netting, seining, angling, harpooning, spearing, snaring, and gaffing (Bennyhoff 1950; Follett 1975; Kroeber and Barrett 1960). Artifacts indicative of these fishing methods—including net weights, fishhooks, harpoons, and spear points—have been recovered from numerous regional bayshore shellmounds (e.g., Follett 1975; Schenck 1926; Uhle 1907). Gill netting operations targeting sturgeon, in particular, were employed by native

peoples and described by historic explorers in the San Francisco Estuary (Follet 1975). As we discuss in more detail below, sturgeon gill netting was apparently limited to shallow water contexts of the bay, and water depth adjacent to sites might thus influence the accessibility of sturgeon resources to past human foragers.

While direct evidence of the time costs associated with harvesting different fish prey types in archaeological contexts is obviously unobtainable, species characteristics that are correlated with prey mobility and pursuit costs are available. Most notably, the pursuit costs of the various fish prey types in this system would likely scale positively with their maximum swimming speeds—whatever the particular fishing methods and contexts that may have characterized fish harvesting in the past.

Published data are available on the maximum swimming speeds for representatives of all the major San Francisco Bay taxonomic fish groups (e.g., Adams et al. 2003; Bell 1996; Collins et al. 2008; Graham et al. 1990; Videler and Wardle 1991; Webber et al. 2007). In general, salmon and steelhead are the most powerful swimmers in this assemblage, with the three species represented each attaining speeds of over 600 cm./sec. Different sturgeon species fall near the low or middle end of the range (37–252 cm./sec.) and well below that of the salmonids. The disparity in swimming performance between salmon and sturgeon, it has been suggested, is due to substantial morphological differences—sturgeon are constrained by increased pressure drag associated with the multiple dermal scute rows, and decreased thrust from the reduced tail depth and nonossified vertebral skeleton (Webb 1986; Webber et al. 2007).

In sum, the extremely large potential size and high fat content of sturgeon, coupled with a comparatively low swimming performance and hence modest pursuit costs, suggests that they would have been among the highest return fish prey types available to prehistoric foragers of the San Francisco Bay. Temporal decreases in sturgeon abundances relative to all other estuarine fishes should thus reflect reductions in the encounter rates with sturgeon, in addition to declining overall foraging returns from the estuarine fishery.¹

In addition to representing the most attractive fish resource to human consumers of the region, sturgeon exhibit other habits and life history characteristics that make them more susceptible to resource depression

as compared to the other fish groups that occur in San Francisco Bay. First, compared to other larger fishes—bat rays, salmon, and hound sharks—sturgeon are more or less resident within the bay itself. The other fishes use the bay as part of seasonal breeding-spawning migrations, and are thus available to human foragers for a shorter duration in the annual cycle. Second, and most importantly, sturgeon have an exceptionally slow life-history pattern, with slow growth rates, exceedingly late ages of first (age 12–16) and full (age 35) female sexual maturity, with extended periods (3–5 years) between successive spawnings. These characteristics make them highly vulnerable to human activities, especially harvest mortality (Birstein et al. 1997; Boreman 1997; Kohlhorst et al. 1991).

SAN FRANCISCO BAY SHELL MOUNDS

In the first decade of the twentieth century, Nels C. Nelson surveyed the shoreline of San Francisco Bay and recorded over 400 “earth mounds and heaps,” the largest of them measuring nearly 180 m. in diameter and 9 m. in height. Over the next century, the mounds would fall prey to residential and commercial development, and even to direct mining for the shells that were converted to fertilizer, topsoil, or road base (Nelson 1909, 1910; Uhle 1907; Wallace and Lathrap 1975). Fortunately, many of the large mounds were excavated during the early and mid twentieth century, and substantial artifact and faunal assemblages recovered from them reside in local museums. As a result, although intact shell mound deposits are occasionally still encountered and subjected to systematic archaeological investigations (e.g., Bieling 1998; DeGoergey 2013; Wake 2012), much of the recent research on San Francisco Bay shell mounds has focused on the curated collections (e.g., Beasley et al. 2013; Broughton 1999; Finstad et al. 2013; Schweikhardt et al. 2011).

Most of the mounds were situated adjacent to where freshwater streams emptied into the bay, and many occurred in clusters composed of four to six separate sites. Most of mounds formed by accretion over hundreds or thousands of years, preserving rich collections of dietary refuse including animal bone and shell, artifacts, architectural features, and numerous human burials (Lightfoot and Luby 2002; Nelson 1909; Uhle 1907). Their varied contents and compositions, and their large size and number, attest to a substantial human population

that used the raised sites as mounded villages where a diverse array of sacred and domestic activities took place (Lightfoot and Luby 2002), in some cases year-round (Broughton 1999). It has also been suggested that the “intentional construction of mounded space” would not only have kept residents dry during wetter winter months, but would have become highly visible symbolic cultural features in an otherwise flat, bayshore landscape (Lightfoot and Luby 2002).

The oldest known mounds began to form around 4,500 years ago, with substantial increases and a peak in mound formation and occupation between about 2,500 and 1,200 B.P. Analyses of the available radiocarbon dates and other time-sensitive artifacts indicate a dramatic reduction in shell mound sites dating after about 1,000 B.P., a reduction that some suggest may represent an abandonment of bayshore residential occupations during the Late Period. Possible explanations for the apparent reduction in the late prehistoric human occupation of the bayshore include environmental degradation resulting from either climate change or resource depression, human population movements, and changes in social/settlement organization (Lightfoot and Luby 2002). However, there may also be a bias in the representation of Late Period occupations of San Francisco Bay shell mounds since the tops of many were shaved off at the turn of century, as was noted above. This has in fact been documented for many of the larger sites in the East Bay area, including Emeryville, West Berkeley, Ellis Landing, and some of the mounds in the Stege complex (Broughton 1999). However, a full record of human occupation extending through the Late Period has been recovered at some mounds horizontally, even though their tops (and vertical depositions) are missing (e.g., DeGeorgey 2013). In any case, our analyses of diachronic trends in fishing efficiency, presented here, will provide a test for hypotheses that suggest declines in Late Period site occupation of the San Francisco Bay shoreline resulted from resource depression. We begin with the single largest Bay Area shell midden site, the Emeryville Shellmound.

THE EMERYVILLE SHELLMOUND

Previous analyses of the fish remains from the early twentieth-century excavations at Emeryville provided evidence for a decline in both the relative abundance and

size of sturgeon across the occupational history of this site (Broughton 1997, 1999, 2002). The analyses were based on a sample of 2,004 fish specimens that were recovered from the excavations of Uhle (1907), Nelson (1909), and Schenck (1926)—the precise recovery methods employed in these projects are unknown, but the curated fauna is consistent with the use of large-mesh screens (1/2-in.) or no screens at all (Broughton 1999). Clearly, the analysis was limited to the upper end of the size range of fish represented in the mound, but the patterns were consistent with a wide range of other faunal indices of intensification—from fragmentation patterns as it relates to processing, to artiodactyl body part representations reflecting increasing distant patch use.

Although the Emeryville Shellmound was demolished to the level of the surrounding plain in 1925 to make way for a Sherwin-Williams paint factory, intact deposits remained within the original footprint of the site and at nearby CA-ALA-310, a mound directly adjacent to Emeryville. In 1999, major excavations at Emeryville led by URS Corporation were initiated in the context of regulatory compliance prior to the commercial development of the area. This work produced an enormous corpus of vertebrate faunal remains, with much of it collected with fine-mesh (1/8" [3.2 mm.], and 1/16" [1.6 mm.]) screens, thus allowing for more refined tests to be carried out, especially those related to small-sized vertebrates that were not recovered from the earlier projects (Wake 2012).

Extensive radiocarbon dating of materials derived from the 1999 project indicates a deposition between 2,800 and 800 cal B.P. for the main Emeryville mound, while dates from ALA-310 indicate a later occupation from 550 to 300 cal B.P. Based on 86 radiocarbon dates and stratigraphy evident within the deposits, Wake (2012:10) assigned approximate deposition date ranges to 60 excavation units, which we use here in our temporal analyses of the massive fish faunal collection that was originally identified and reported by Gobalet and Hardin (2002).

Sturgeon Abundance Change from the 1999 Collection

The fish assemblage from the 1999 Emeryville project includes 58,000 specimens identified to at least the order level (Gobalet and Hardin 2002). For the assemblage as a whole, bat rays, silversides and herrings, salmon and

steelhead, and sturgeon are the most abundant fish taxa, representing 42%, 19%, 16% and 14% of the total fish NISP, respectively. As expected from the larger sample size and finer-grained recovery methods, taxonomic richness (NTAXA = 35) far surpasses that from the earlier collection (NTAXA = 8), as does the relative abundance of small-sized fishes, namely silversides and herrings, which were extremely rare in the early twentieth-century sample.

Most importantly, this work produced the largest assemblage of sturgeon (NISP = 8,431) for any San Francisco Bay site, including, as noted above, identifications of both white and green sturgeon. Since our interest here is in measuring change in the relative

abundance of sturgeon compared to all other fishes though time, only those excavation units with secure chronological assignments (from Wake 2012) are included in this analysis. This subset of the assemblage is represented by a total of 47,183 fish specimens, with 7,087 of those belonging to sturgeon (Table 2).

The Sturgeon Index (NISP Sturgeon/NISP Total Fishes) is plotted by midpoint (cal B.P.) dates for the 1999 Emeryville excavation units (ALA-309 and ALA-310) in Figure 2. This trend shows considerable variability in sturgeon abundances across these units, with both more variability and higher values associated with earlier occupation dates. Since the fish-specimen sample sizes per unit that make up these index values vary

Table 2

NUMBERS OF IDENTIFIED STURGEON, OTHER FISHES, AND STURGEON INDEX VALUES FOR THE 1999 EMERYVILLE EXCAVATIONS^a

Unit ^b	NISP	Sturgeon NISP	Other Fish NISP	Sturgeon Index	Midpoint Date Cal B.P. ^c	Associated ¹⁴ C Dates (Conventional Radiocarbon Age)
75 ("310")	1,865	47	1,818	0.025	400	300±60, 420±60
"310" ^d	17,082	684	16,398	0.040	450	220±60, 330±60, 340±80, 400±60, 440±60, 330±60, 520±40
50	117	7	110	0.060	1,025	1,220±70, 1,290±70
58	843	155	688	0.184	1,050	1,030±60
65	262	56	206	0.213	1,200	1,020±60
23-25	362	88	274	0.243	1,400	1,080±40, 1,680±70
72	3,105	100	3,005	0.032	1,650	1,080±40, 1,680±70, 1,930±70
43	284	7	277	0.025	1,700	1,860±40, 1,940±60
67	1,090	45	1,045	0.041	1,750	1,860±40, 1,940±60
37, 44	666	280	386	0.420	1,925	2,010±90
27-57	7,574	2,470	5,104	0.326	2,000	1,920±60, 1,950±60, 1,990±40, 2,000±80, 2,010±90, 2,010±120, 2,140±40, 2,220±70, 2,250±40, 2,470±80, 2,530±40, 2,640±40
32, 66, 71	5,758	1,314	4,444	0.228	2,100	2,030±70, 2,050±60, 2,160±70, 2,180±70
33, 34, 33/34	795	166	629	0.210	2,150	2,410±±60, 2,470±±40
61	812	187	625	0.230	2,175	2,360±40
69	172	35	137	0.203	2,200	2,070±70, 2,250±60, 2,330±60, 2,430±70, 2,430±40, 2,520±80, 2,530±60, 2,740±70
68	3,391	653	2,738	0.193	2,400	2,070±70, 2,250±60, 2,330±60, 2,430±70, 2,430±40, 2,520±80, 2,530±60, 2,740±70
33/34/59 & 60	2,653	668	1,985	0.252	2,450	2,010±130, 2,540±50, 2,550±40
59	352	125	227	0.355	2,500	2,010±130, 2,540±50, 2,550±40
Total	47,183	7,087	40,096			

^aData from Gobalet and Hardin 2002.

^bExcavation units with identical date ranges are combined here.

^cFrom Wake 2012.

^dIncludes units 13, 45, 46, 52, 62, 74, 74 urs, DD, and EE, from CA-ALA-310—all have same date range.

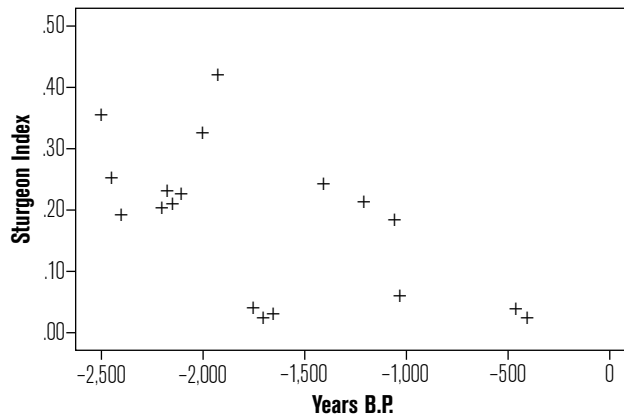


Figure 2. Distribution of the Sturgeon Index through time for the 1999 Emeryville collection (all dated units).

substantially, statistical evaluation of a temporal trend must take this into account. Cochran's X^2 test of linear trends is a statistical method that does just that (Cannon 2001; Zar 1996).

Cochran's test is a chi-square-based method that evaluates trends in relative abundances of samples while directly controlling for variation in their underlying sample sizes. The test is analogous to a form of regression analysis in which relative abundance values are weighted according to their associated sample sizes (Cannon 2001). The test isolates from a total Chi-square statistic that which is associated with a linear trend in proportions across samples, and that which is associated with other factors or noise in the data. A Cochran's test comparing the numbers of identified sturgeon (including both species- and genus-level identifications) and all other fishes across the Emeryville excavation units reveals a highly significant linear decline in sturgeon abundance ($X^2_{\text{trend}} = 3,222.19$, $P < 0.001$). Bat rays, salmonids, and silversides and herrings assume greater proportionate abundances as sturgeon decrease through time in this deposit.

In their meticulous work with the 1999 Emeryville fish materials, Gobalet and Hardin (2002) cautioned appropriately that deciphering meaningful temporal trends with these data is complicated by the fact that different recovery methods (1/16"-, 1/8"-, and 1/4"-mesh screens) were used to collect the materials from the different excavation units. Although it is not evident that different screen mesh-sizes were used systematically for the older and younger deposits, we address this issue

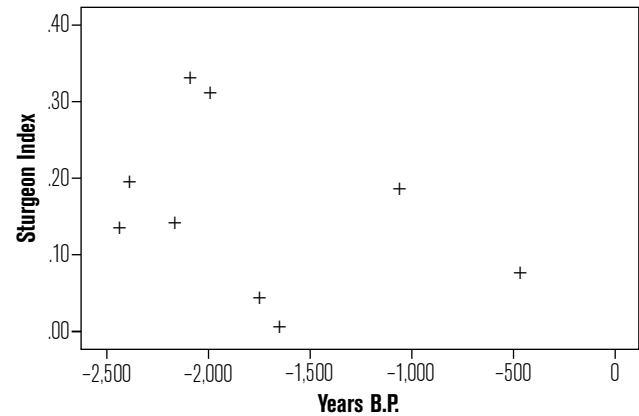


Figure 3. Distribution of the Sturgeon Index through time for the 1999 Emeryville collection (units collected with 1/16" screens).

directly by repeating the analysis but controlling for recovery method.

Figure 3 displays the Sturgeon Index through time using only the Emeryville excavation units collected with 1/16"-mesh screens (Table 3). While the sample size is reduced (Fish NISP=16,147), the overall pattern is very similar to the one using the entire collection, and a Cochran's test again reveals a highly significant decline through time in sturgeon abundances ($X^2_{\text{trend}} = 336.30$, $P < 0.001$). A similar pattern is indicated if only units collected with 1/4" screens are included. Considering both the early twentieth century and 1999 samples, variation in recovery method does not appear to be a key factor influencing the temporal decline in the relative abundance of sturgeon. Finally, data from the other notable northern Alameda County bayshore site, the West Berkeley Shellmound (CA-ALA-307), is consistent with this overall pattern. With an early occupational range (4,264 to 2,300 B.P.), sturgeon represent 136 of the 341 identified specimens, or 40%, at West Berkeley (Follet 1975)—a value that approaches those derived from the oldest units that date near this range at Emeryville.

Size Analysis

We turn now to an update of previous work with sturgeon size changes, following the logic that increasing harvest rates and depressed fisheries are commonly signaled by declines in the average size and age of fishes (Beverton and Holt 1956; Jackson et al. 2001; King 1995). Again, Broughton (1997) documented a significant decline in dentary width as a proxy for sturgeon age and size from

Table 3

**NUMBERS OF IDENTIFIED STURGEON, OTHER FISHES, AND STURGEON INDEX VALUES
FOR THE 1999 EMERYVILLE EXCAVATIONS (1/16" MATERIALS)^a**

Unit	Sturgeon NISP	Other Fish NISP	Sturgeon Index	Midpoint Date Cal B.P. ^b	Associated ¹⁴ C Dates (Conventional Radiocarbon Age)
62, 74	301	3,715	0.075	450	400±60, 440±60, 470±60, 480±70, 550±60, 820±60
58	155	688	0.184	1,050	1,030±60
72	4	969	0.004	1,650	1,080±40, 1,680±70, 1,930±70
67	45	1,045	0.041	1,750	1,860±40, 1,940±60
57	687	1,519	0.311	2,000	2,470±80, 2,640±40,
71	615	1,263	0.330	2,100	2,050±60, 2,060±60, 2,130±70, 2,190±60, 2,320±60
61	214	1,318	0.140	2,175	2,360±40
68	653	2,738	0.193	2,400	2,070±70, 2,250±60, 2,330±60, 2,430±70, 2,430±40, 2,520±80, 2,530±60, 2,740±70
33/34/59	29	189	0.133	2,450	2,010±130, 2,550±40, 2,540±50
Total	2,703	13,444			

^aData from Gobalet and Hardin 2002.

^bFrom Wake 2012.

the early twentieth-century collections. However, the sample size was small (n=39 dentaries), and although several other elements were measured (dermopalatine n=17; palatopterygoid n=20), they have different ranges of absolute size and were not incorporated within the dentary size trend. We build on this work here by using an allometric methodology that converts measurements from the three elements into a common metric, live body weight. Not only does it provide deeper insight into the demographic structure of past San Francisco Bay sturgeon populations, it nearly doubles the earlier sample size by incorporating the data from the two other measured elements.

The allometric analyses were based on live weight and skeletal measurements taken by one of us (B. McEneaney) from 21 white sturgeon of various sizes. Fifteen of these were collected from the Stolt Sea Farm, Elverta, California; six others were housed in the comparative osteological collections at University of California, Davis, and the California Department of Parks and Recreation, Sacramento. The three bony elements used in the allometric analyses were the dentary, dermopalatine, and palatopterygoid.² These three bones, together with the ectopterygoid, ceratohyal, and hyomandibular, form the primary elements of the protrusible mouth (Findeis 1997; Hilton et al. 2011; Jollie 1980). Measurement locations on these bones are from Broughton (1999).

As demonstrated in previous fish allometry research (Leach and Boocock 1995; Leach and Davidson 2001; Leach et al. 1996a, 1996b), the collected sturgeon live weights show strong power-law relationships with element size of the form $live\ weight\ (kg.) = a * element\ size^b$. Both estimated live weights and corresponding element measurements were log transformed in order to assess the relationships by translating them into the form of a general linear regression $ln(live\ weight) = a + b * ln(element\ size)$. The equations were then transformed back to normal space in the manner of $live\ weight = e^{a * element\ size^b}$ to produce the formulae presented in Table 4. All three equations proved to be statistically significant ($P < 0.0001$) robust predictors of live weight.

These regression equations were used to predict the live weights from the three sets of sturgeon elements from Emeryville (Table 5). Based on stratigraphic relationships and 13 radiocarbon assays on bone and charcoal, the faunal samples from Emeryville, including

Table 4

**REGRESSION FORMULAE DESCRIBING RELATIONSHIPS
BETWEEN WHITE STURGEON ELEMENT MEASUREMENTS
AND LIVE WEIGHT (KG.)**

Element type	Formula	P-value	R ²
Dentary	.0406 * X ^{2.9972}	<0.0001	0.9546
Dermopalatine	.2823 * X ^{2.4745}	<0.0001	0.8872
Palatopterygoid	.0056 * X ^{3.0397}	<0.0001	0.8848

Table 5

WHITE STURGEON LIVE WEIGHT ESTIMATES FROM SELECTED ELEMENTS FROM THE EMERYVILLE SHELLMOUND

Cal B.P. Midpoint (Stratum)	Element Size (mm.)			Weight (kg.)
	Dentary	Dermopalatine	Palatopterygoid	
2,590(10)	11.68			64.319
2,590(10)	9.75			37.432
2,590(10)	12.88			86.226
2,590(10)	12.55			79.772
2,590(10)	8.76			27.156
2,590(10)	12.21			73.469
2,590(10)	10.32			44.381
2,590(10)	6.34			10.304
2,590(10)	15.44			148.461
2,590(10)		6.82		32.661
2,590(10)		8.06		49.381
2,590(10)		6.01		23.887
2,590(10)		6.87		33.257
2,590(10)		5.03		15.377
2,590(10)		6.43		28.233
2,590(10)		3.62		6.813
2,590(10)		5.83		22.155
2,590(10)			24.77	96.508
2,590(10)			15.50	23.211
2,590(10)			12.60	12.366
2,590(10)			22.06	67.858
2,590(10)			17.01	30.790
2,397(9)	9.37			33.227
2,397(9)	8.27			22.853
2,397(9)	12.08			71.149
2,397(9)	13.92			108.821
2,397(9)	9.27			32.176
2,397(9)	9.39			33.440
2,397(9)	12.32			75.470
2,397(9)	8.60			25.697
2,397(9)		4.46		11.419
2,397(9)		4.96		14.853
2,397(9)			15.35	22.535
2,397(9)			22.66	73.626
2,397(9)			13.43	15.013
2,397(9)			14.52	19.032
2,397(9)			15.05	21.223
2,105(8)	11.35			59.024

Table 5 (Continued)

WHITE STURGEON LIVE WEIGHT ESTIMATES FROM SELECTED ELEMENTS FROM THE EMERYVILLE SHELLMOUND

Cal B.P. Midpoint (Stratum)	Element Size (mm.)			Weight (kg.)
	Dentary	Dermopalatine	Palatopterygoid	
2,105(8)	7.02			13.984
2,105(8)	8.23			22.523
2,105(8)	10.9			52.284
2,105(8)	12.58			80.345
2,105(8)	7.24			15.339
2,105(8)	10.09			41.482
2,105(8)	14.42			120.962
2,105(8)		5.13		16.144
2,105(8)		3.33		5.541
2,105(8)		4.78		13.554
2,105(8)		7.52		41.594
2,105(8)			16.18	26.447
2,105(8)			14.25	17.976
2,105(8)			18.14	37.439
2,105(8)			19.3	45.202
2,105(8)			20.62	55.270
2,105(8)			17.33	32.585
2,105(8)			22.68	73.823
2,105(8)			21.42	62.049
2,105(8)			32.92	229.122
1,891(7)	9.72			37.088
1,891(7)	13.45			98.176
1,891(7)	5.84			8.055
1,891(7)	10.96			53.152
1,891(7)	9.71			36.974
1,891(7)	7.96			20.380
1,891(7)			14.61	19.392
1,690(6)	7.89			19.848
1,457(5)	7.47			16.847
1,457(5)	11.01			53.882
1,457(5)		7.18		37.095
1,310(4)	10.45			46.078
1,310(4)	9.73			37.202
1,310(4)	8.97			29.155
1,310(4)		5.90		22.820
1,152(3)	9.65			36.293
1,152(3)	6.65			11.889
1,152(3)		7.36		39.439

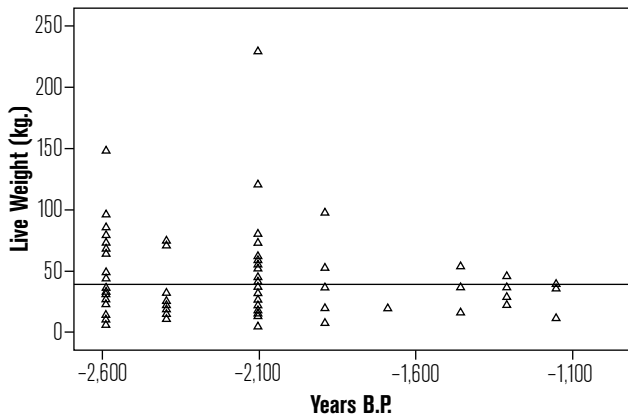


Figure 4. Distribution of live weight estimates of white sturgeon from Emeryville (early 20th century collections). The horizontal line indicates the size of reproductively mature female white sturgeon.

the sturgeon elements studied here, were assigned to ten primary stratigraphic units that span the period from 2,600 to 700 B.P. (Broughton 1999). Live weights varied considerably across these strata, with a large outlier of 245 kg, in Stratum 8, to smaller fish weighing less than 10 kg. As suggested by the visual impression of the sturgeon size distribution by stratum (Fig. 4), statistically significant declines through time are demonstrated in the calculated mean ($r_s = -0.738$, $P = 0.046$), maximum, ($r_s = -0.786$, $P = 0.028$), and variance ($r_s = -0.786$, $P = 0.048$) of white sturgeon live weight. These trends are consistent with a harvest-based depression of the sturgeon fishery, and most importantly do not follow from a climate-based deterioration of the estuarine environment. A *reduction* in recruitment rates and the proportion of subadult individuals in the population is generally anticipated from the latter (e.g., Houde 1987; Rijnsdorp et al. 2009).

These absolute size estimates are especially interesting in light of modern white sturgeon age and growth features. The reproductive potential of sturgeon, like that of most fish, is strongly correlated with fish size, and female sexual maturity is not attained in white sturgeon until 12 to 16 years of age, when individuals reach about 30–40 kg. in weight—the point where the horizontal line is drawn in Figure 4. Full sexual maturity, however, is not reached until about 35 years of age, when females typically exceed about 80 kg. (Boreman 1997; Chapman et al. 1996; Kohlhorst et al. 1991; Moyle 2002). The data from Emeryville thus indicate that after the deposition of Stratum 7 (a context with a

midpoint calibrated date of 1,891 B.P.) few fish were living long enough to reach full sexual maturity. Not only is the overall trend consistent with an anthropogenic depression of sturgeon, the absolute size estimates reveal a substantial reduction in the population growth and maintenance potential of this important fish resource.

CENTRAL SAN FRANCISCO BAY: REGIONAL ANALYSES OF STURGEON DEPRESSION

To examine trends in sturgeon use on a broader regional scale, we synthesize previously reported and some new ichthyoarchaeological data from three San Francisco Bay regions where considerable work with fish remains has taken place: the Contra Costa County coast, southeast Marin County, and the San Francisco Peninsula. In these inter-site analyses, we consider only assemblages that contain total fish NISP values greater than 50, and draw upon previously published chronological information to assign date ranges and midpoints to site components as determined from radiocarbon dating, obsidian hydration, and artifact typologies. We stress that only a very coarse-grained assessment of sturgeon depression in these settings is possible given the uneven dating both within and between sites, the long occupation spans of several localities included, different fish-bone recovery methods, and the fact that identifications are often presented at the site level (e.g., CA-MRN-67), rather than by finer stratigraphic subdivisions. Indeed, these features make it more difficult to discern temporal patterning in fish use but do not compromise the significance of any consistent broad-scale trends should they be documented.

Contra Costa County

A total of 12 site components from Contra Costa County bayshore sites have produced a composite fish NISP of 16,532 (Table 6). Gobalet identified almost all of the fish remains from these assemblages, and similar screen mesh-sizes were used to collect them so as to minimize biases that can be introduced by interanalyst variation (Gobalet 2001) and differential recovery. Sturgeon are well-represented in this region, comprising 39% of the total sample of identified fishes (total NISP 6,406). In some localities, such as at CCO-269, CCO-271, and CCO-275, they in fact dominate the ichthyofaunas. Most noteworthy, sturgeon represent 92% of the total

Table 6
NUMBERS OF IDENTIFIED STURGEON, OTHER FISHES, AND STURGEON INDEX VALUES
FOR CONTRA COSTA COUNTY SHELL MOUNDS

Site	Screen Size	Years B.P. Midpoint	Sturgeon NISP	Other Fish NISP	Total Fish NISP	Sturgeon Index	Reference (fauna)	Reference (dates)
CCO-297 (II) ^a	1/4", 1/8", 1/16"	287	87	4,979	5,066	0.017	Simons & Gobalet 2013	DeGeorgey 2013
CCO-297 (I)	1/4", 1/8"	678	160	2,245	2,405	0.071	Gobalet 1990	Banks and Orlins 1981
CCO-299	1/4", 1/8"	750	5	49	54	0.096	Gobalet 1990	Banks and Orlins 1981
CCO-284	1/4", 1/8"	1,398	124	497	621	0.200	Wake 1999	Wiberg et al. 1999
CCO-600	1/4", 1/8", 40 mm.	1,600	970	223	1,193	0.810	Gobalet 1994	Holson et al. 2000
CCO-270	1/4", 1/8"	1,683	190	276	466	0.408	Gobalet 1990	Banks and Orlins 1981
CCO-601	1/4", 1/8"	1,925	37	39	76	0.487	Gobalet 1994	Holson et al. 2000
CCO-269a ^b	1/4", 1/8", 40 mm.	2,083	1,908	1,305	3,213	0.594	Gobalet 1990	Banks & Orlins 1981; Holson 2000
CCO-269b	1/4", 1/8", 40 mm.	2,083	2,702	246	2,948	0.917	Gobalet 1994	Banks & Orlins 1981; Holson 2000
CCO-268	1/4", 1/8"	2,103	40	123	163	0.245	Gobalet 1990	Banks and Orlins 1981
CCO-271	1/4", 1/8"	2,140	71	69	140	0.507	Gobalet 1990	Banks and Orlins 1981
CCO-275	1/4", 1/8"	2,175	112	75	187	0.599	Gobalet 1990	Banks and Orlins 1981
Total			6,406	10,126	16,532	0.387		

^aCCO-297(II) and CCO-297(I) represent different excavations and fish bone samples at this site.

^bCCO-269a and CCO-269b represent different excavations and fish bone samples at this site.

fish NISP at CCO-269b,³ leading to the suggestion that these materials may represent the residues of a sturgeon-processing locality for gill-netting operations that occurred in the shallow waters of San Pablo Bay directly adjacent to the site (Gobalet 1994).

As is the case at Emeryville, the relative abundance of sturgeon varies considerably across different spatial and temporal contexts, and much of this variation is related to the time period of deposition (Fig. 5). Sites occupied earlier (before 1,500 B.P.) exhibit not only more variation in sturgeon abundances, but higher values in general. Later sites, those with midpoints after 1,000 B.P., have consistently low (<0.10) Sturgeon Index values. A Cochran's test of linear trends documents that this decline in the proportional abundance of sturgeon relative to other fish is astronomically significant ($X^2_{\text{trend}}=7,266.79$, $P<0.001$). In this setting, sardine and herring, salmon, and bat rays, collectively, comprise greater proportionate abundances through time as sturgeon numbers dwindle.

Southeast Marin County

Bayshore sites along the southeast margin of Marin County have produced a composite fish NISP of 8,185 derived from 11 distinct site components (Table 7). More variation in the methods used to recover, and

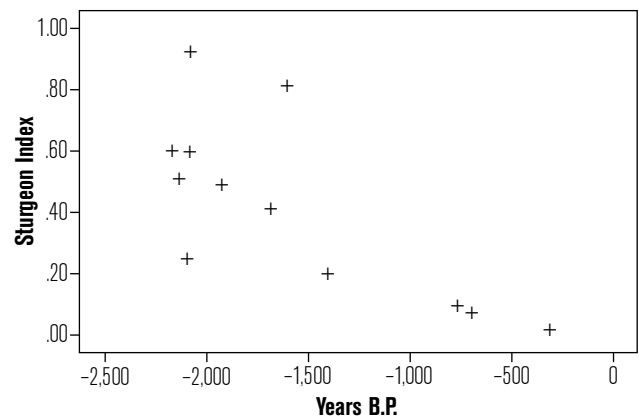


Figure 5. Distribution of the Sturgeon Index through time for shell mound sites from Contra Costa County.

the faunal analysts employed to identify, the fish materials in this context potentially introduces more bias or noise into the temporal analysis of sturgeon depression here. Representing 20% of the total fish NISP (Table 7), sturgeon are generally less abundant, relative to other fishes, compared to the Contra Costa County sites, although they dominate (72%) all three components of the older MRN-254 locality. Salmon, bat rays, silversides, or requiem sharks are the most abundant fish in the assemblages of other Marin County bayshore shellmounds.

Table 7
NUMBERS OF IDENTIFIED STURGEON, OTHER FISHES, AND STURGEON INDEX VALUES
FOR SOUTHEAST MARIN COUNTY SHELL MOUNDS

Site	Screen Size	Years B.P. Midpoint	Sturgeon NISP	Other Fish NISP	Total Fish NISP	Sturgeon Index	Reference (fauna)	Reference (dating)
MRN-44/H-b ^a	1/8", 1/16"	500	24	415	439	0.055	Simons & Carpenter 2009	DeGeorgey 2006
MRN-44/H-c	1/8", 1/16"	800	0	889	889	0.000	Simons & Carpenter 2009	DeGeorgey 2006
MRN-20	?	850	12	151	163	0.074	Follett 1957	McGeekin & Meuller 1955; Moratto 1984
MRN-44/H-a	1/8", 1/16"	1,000	60	2,435	2,495	0.024	Simons & Carpenter 2009	DeGeorgey 2006
MRN-254b ^b	1/8"	1,150	233	67	300	0.777	Scott 1998	Bieling 1998
MRN-14	1/4"	1,300	4	126	130	0.031	Follett 1974	Moratto 1984; Moratto et al. 1974
MRN-254d	1/8"	1,575	349	179	528	0.661	Scott 1998	Bieling 1998
MRN-254c	1/8"	1,750	85	16	101	0.842	Scott 1998	Bieling 1998
MRN-17(upper) ^c	1/8"	1,775	98	570	668	0.147	Scott & Millerstrom 2003	Pahl 2003
MRN-67	1/8"	2,750	731	1,586	2,317	0.316	Simons et al. 2014	Simons et al. 2014
MRN-17(lower)	1/8"	3,950	37	118	155	0.239	Scott & Millerstrom 2003	Pahl 2003
Total			1,633	6,552	8,185	0.196		

^aMRN-44/H was excavated at three primary loci: a, b, and c.

^bMaterials from MRN-254 were separated into four temporal components, three of which (b, c, and d) produced fish assemblages >50 NISP.

^cMRN-17 included a substantial Middle Period component (2,500–1,050 B.P.) but also several dates suggesting deposition beginning over 5,000 B.P. In this analysis, fish remains were separated into upper (above 300 cm.) and lower (below 300 cm.) components.

The temporal pattern in this region is also characterized by early variability, with the highest Sturgeon Index values occurring in deposits with midpoints older than 1,000 B.P., and with all sites post-dating 1,000 B.P. consistently showing extremely low sturgeon numbers (Fig. 6). Here, a Cochran’s test of linear trends again documents the fact that this apparent decline in sturgeon proportionate abundances is indeed highly significant ($X^2_{trend} = 740.621, P < 0.001$). This result is duplicated in an analysis that includes only faunas in the study sample that were excavated after the mid-1990s and that were recovered with 1/8"- and/or 1/16"-mesh screens ($X^2_{trend} = 642.017, P < 0.001$).

The San Francisco Peninsula

The San Francisco Peninsula is represented by a total of six site components with a total ichthyofaunal sample of 11,238 identified specimens—all were recovered with 1/8" screens (Table 8). In this setting, sturgeon remains are poorly represented regardless of a site’s occupation date. Collectively, they represent a mere 0.2% of this region’s fish specimen total and in no single site component do they comprise more than 1% of the total fish NISP (Fig. 7). Other common San Francisco Bay fishes—salmon, hound sharks, and silversides—

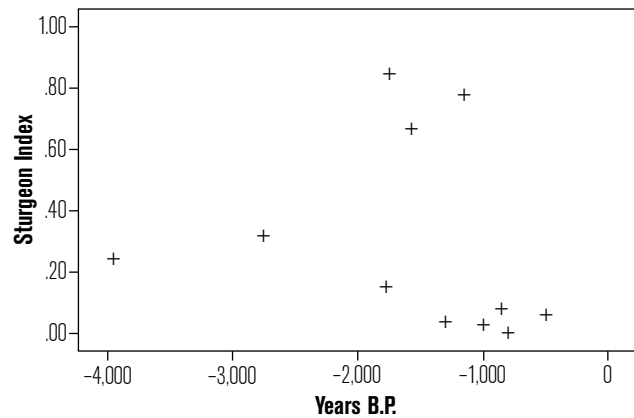


Figure 6. Distribution of the Sturgeon Index through time for shell mound sites from southeast Marin County.

fill the void, but most noteworthy is the exceptional abundance of surfperch, with species preferring rocky or sandy-bottom surf-zone contexts dominating depending on the site (Eschmeyer and Shonewald 1981; Wake and Gobalet 2000). Indeed, extensive mud-bottom, shallow water habitats, within which sturgeon are most abundant and were apparently harvested with nets, do not occur in close proximity to the San Francisco Peninsula. This pattern is, in fact, readily evident in San Francisco Bay bathymetric maps (Fig. 1). Thus, no evident temporal trend in sturgeon relative abundances

Table 8
NUMBERS OF IDENTIFIED STURGEON, OTHER FISHES, AND STURGEON INDEX VALUES
FOR SAN FRANCISCO PENINSULA SHELL MOUNDS

Site (Component)	Screen Size	Years B.P. Midpoint	Sturgeon NISP	Other Fish NISP	Total Fish NISP	Sturgeon Index	Reference (fauna)	Reference (dating)
SFR-129	1/8"	450	7	6,882	6,889	0.0010	Wake and Gobalet 2000	Wake and Gobalet 2000
SFR-114 (WT) ^a	1/8"	1,146	2	383	385	0.0052	Broughton 1991	Hattori and Pastron 1991
SFR-30	1/8"	1,350	8	2,537	2,545	0.0031	Eschmeyer & Shonewald 1981	Baker 1978; Breschini et al. 1990
SFR-114 (ET)	1/8"	1,587	4	255	259	0.0150	Broughton 1991	Hattori and Pastron 1991
SFR-113	1/8"	1,896	2	1,158	1,160	0.0020	Gobalet 1988	Pastron and Walsh 1988
		Total	23	11,215	11,238	0.0020		

^aWT and ET refers to the West Trench and East Trench excavation units, respectively, at SFR-114.

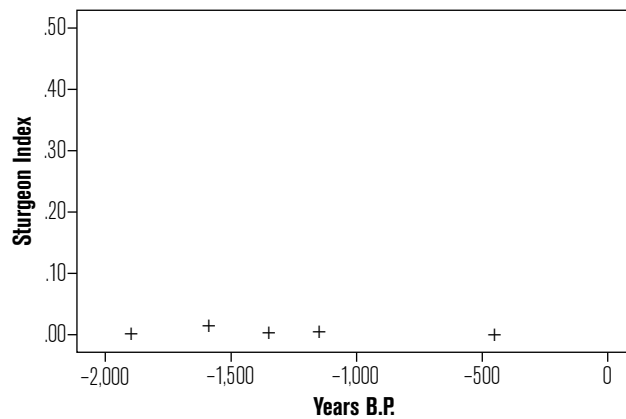


Figure 7. Distribution of the Sturgeon Index through time for shell mound sites from the San Francisco Peninsula.

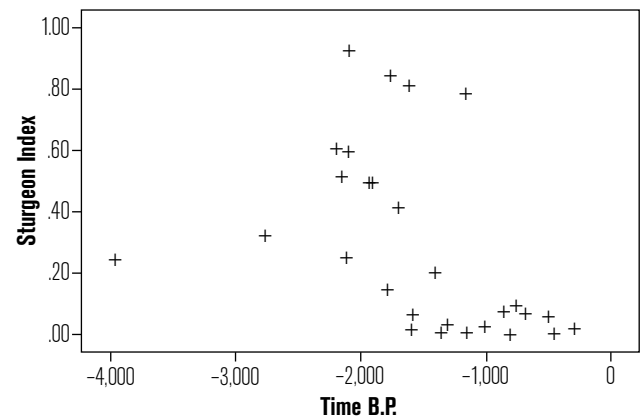


Figure 8. Distribution of the Sturgeon Index through time for shell mound sites from Contra Costa County, southeast Marin County, and the San Francisco Peninsula.

in the San Francisco Peninsula appears to reflect the fact that these fishes were never sufficiently abundant in adjacent waters.

Central San Francisco Bay: Regional Synthesis

The distribution of the Sturgeon Index through time, including the entire sample from the three regions examined separately above—Contra Costa County, southeast Marin County, and the San Francisco Peninsula—is displayed in Figure 8 and illustrates the prevailing trends in these data. The overall pattern is for sturgeon abundances to decline, relative to all other fishes, through time in a linear trend that is astronomically significant ($X^2_{\text{trend}}=11,049.85$, $P<0.001$), but with substantial variability (high and low values) occurring during the earlier period before 1,200 B.P. In Contra Costa county, for instance, sturgeon attain their highest recorded abundances (e.g., ~90% at CCO-269)

in sites dating before 2,000 B.P., but other more or less synchronously occupied localities produce much lower frequencies (e.g., 25% at CCO-268). This dramatic early variation may reflect issues related to differential intra-regional access to productive sturgeon waters or even taphonomic factors related to the inter- and intra-site spatial structure of sturgeon processing and carcass deposition.

This variability all but vanishes during the later occupations as Sturgeon Index values plummet and the collective percentage of sturgeon bone abundance for sites dating after 1,000 B.P. is only 1.9% (355 of 18,400 total fish NISP). These data are consistent with the detailed intra-site analyses at Emeryville that showed all of these same features as well as a significant decline in the average age and size of exploited sturgeon and the eventual loss of sexually mature fish. The collective signal provides strong support for the resource depression

hypothesis in this context. However, population declines can stem from other factors, most importantly climate-based environmental change, and we explore that potential cause below.

CLIMATE CHANGE AND SAN FRANCISCO BAY STURGEON

The distribution and abundance of white sturgeon populations in San Francisco Bay are strongly influenced by fluctuations in estuarine salinity and freshwater inflow (Fish 2010; Kohlhorst et al. 1991). Greater winter and spring inflow and reduced salinity positively influences year-class strength by improving conditions for successful spawning, hatching, rearing, and increased downstream transport of juveniles into the estuary (Fish 2010). In addition, white sturgeon move upstream (eastward), out of the central San Francisco Bay, and from San Pablo Bay into Suisun Bay, during years with low inflow. Insofar as the late Holocene declines in sturgeon abundances were driven, in whole or in part, by climate-based environmental change, significant linear declines in freshwater inflow and increases in salinity should be evident over this period of time.

Several late Holocene records of change in San Francisco Bay salinity and temperature have been generated over the last several decades from bay and tidal marsh core samples based on pollen, plant macrofossil, diatom and foraminiferal relative abundances, and trace element and isotope ratios from foraminifera, organic detritus, and molluscs (e.g., Ingram et al. 1996; Malamud-Roam et al. 2006; McGann 2008). While it is not possible to securely align these records to our archaeological fish data in order to provide direct quantitative correlations (owing to the coarse-grained dating methods available for the latter data), evidence for temporal trends within the salinity records themselves can provide useful tests.

In general, temporal patterns in the various paleo-environmental proxies vary in the details, but none suggest linear increases in San Francisco Bay estuarine salinity over the past 3,000 years. For example, recent fine-scale salinity analyses from $\delta^{18}\text{O}$ in the carbonate of foraminifera tests show that salinity has varied substantially across the late Holocene, with nearly a 7-psu (practical salinity unit) range over the last 3,900 years archived in the core, but (most notably) there is

no linear trend toward either increases or decreases in salinity levels over this period ($r^2=0.02$, $P=.46$; data from McGann 2008: Table 4).

Finally, we observe that an environmentally-based cause for a decline in sturgeon populations is inconsistent with the trend in age/size structure that was documented above from sturgeon elements at Emeryville. Declining sturgeon populations resulting from long-term decreases in freshwater inflow and increases in salinity should be associated with depressed recruitment rates, as well as shifts to higher proportions of *larger*, older individuals (an aging population)—which is the opposite of the pattern evident in the data.

DISCUSSION AND CONCLUSIONS

Analysis of over 83,000 identified fish specimens from 30 site components from the central San Francisco Bay region shows linear declines in the relative abundance of sturgeon compared to other fishes across the late Holocene occupational history of the region, with exceptions occurring only in the San Francisco Peninsula region—a setting that lacked accessible sturgeon resources to begin with. The declines are accompanied by a significant decrease in the average size of exploited sturgeon, but not associated with trends in paleoestuarine conditions that might suggest a climate-based cause for the ever-dwindling sturgeon numbers.

The declines in sturgeon abundances are unaffected by variation in the underlying sample sizes of the fishes represented as they were determined using a statistical approach that takes such variation into account. Nor do the trends appear to be related to variation in the recovery methods used to retrieve the fish materials from these sites, since holding recovery method (screen size) constant produces the same general trends. Finally, since sturgeon remains are highly distinctive osteologically at the genus-level, and our primary taxonomic comparisons involved the abundance of sturgeon compared to all other fishes, it is unlikely that interanalyst variation was related to this trend. Indeed, in several contexts (e.g., 1999 Emeryville collection, and Contra Costa Co.), the same analyst (Gobalet) provided all of the taxonomic identifications. Our analysis is thus most consistent with the hypothesis that human foragers depressed the prehistoric sturgeon fishery in this region.

But beyond that, the analysis shows at both regional and site-based scales a pattern of high early variation, with later deposits characterized by consistently low sturgeon relative frequencies. This pattern of declining *variation* in high-ranked prey is noteworthy insofar as it has not been clearly identified in previous resource depression studies that have, nonetheless, documented increasing complexity in how this phenomenon plays out on regional spatial scales.

Rather than simple, region-wide, tightly linear declines in high-return prey, a range of patterns now seems apparent in the context of resource depression that reflects a host of variables related to disparate factors ranging from changes in human socioeconomic and settlement systems to variation in prey spatial structure and behavior. In the first explicit foraging theory-based analysis of prehistoric resource depression, Bayham (1982, 2010; Szuter and Bayham 1989), for instance, revealed broadscale, region-wide declines in high-ranked artiodactyl prey from the Archaic through the Hohokam period in south-central Arizona. At the same time, he also documented increases through time in the intra-site *variation* in artiodactyl abundances—later periods showed higher variability. He attributed the increase in variation to organizational shifts in the socioeconomic system, with increased lowland food storage and sedentism, and greater logistical hunting of large game at upland site localities.

Similar trends have been documented in many other contexts in the American Southwest more recently, with variation in artiodactyl abundances linked to settlement history but also to site elevation and the position of sites within settlement clusters (e.g., Badenhorst and Driver 2009; Cannon 2000, 2003; Schollmeyer and Driver 2013). Other things being equal, higher elevation and more mesic sites located on the periphery of settlement clusters yield higher artiodactyl abundances, as they are closer to “source” areas of deer populations. Indeed, Schollmeyer and Driver (2013) argue that despite a significant rapid depression of artiodactyls in areas with substantial human settlements—the “sinks”—a long-term regional resilience of deer populations is maintained by these source areas being located in the lightly-populated hinterlands.

Returning to the San Francisco Bay area, similar arguments were proposed to account for increases in

black-tailed deer abundances in the upper strata of the Emeryville Shellmound, after initial substantial declines in deer bones were documented in the early phase of occupation. Source populations were suggested to have existed in the oak woodlands far to the east of the site, which were eventually tapped as returns from local patches progressively declined (Broughton 1999, 2002). This site-specific pattern has not yet been documented at other San Francisco Bay localities that generally show declines in deer abundances through time (Broughton 1994b), so that the overall pattern of increasing variability thus appears to fit deer in this setting, just as it does for these animals in the Southwest.

The case of sturgeon depression documented here shows both interesting similarities to, as well as marked differences from, the patterns of artiodactyl depression. First, it is readily apparent that a site’s location in relationship to the proximity of sturgeon habitat plays a strong role in influencing sturgeon abundances and the site’s ability to provide evidence of temporal patterns of resource depression. The San Francisco Peninsula sites show this very clearly. Second, the sturgeon populations in San Francisco Bay can only be appropriately considered the regional “source” for these fish—the bay represents the primary location of annual residence, growth, and population recruitment. There is thus no sturgeon hinterlands to re-supply declining local populations or to which human consumers could travel to reach a less exhausted resource. Hence, the pattern of increasing late-period variation in the context of regional prey depression documented for deer is not apparent with sturgeon and does not seem likely given the spatial characteristics of this resource.

The more geographically-circumscribed spatial structure of the sturgeon resource may also influence the pattern of high early-period variation. Insofar as sturgeon populations were robust early on, yet not all people at different site locations surrounding the bay had equal access to productive sturgeon harvesting areas, sturgeon bone deposition rates should exhibit considerable inter-assemblage variability. Early variability may also, of course, reflect vagaries of site function, fish carcass depositional factors, and post-depositional taphonomic factors that we have not attempted to explore here. Further, more detailed spatial analyses of sturgeon abundances in relationship to site function and proximity

to habitat productivity for sturgeon and other estuarine resources may shed additional light on these issues. Should robust samples of fish materials be generated from regions adjacent to high-quality sturgeon habitat in the San Pablo Bay and the South Bay in the future, we would anticipate similar patterns to those that we have documented here for the Central Bay. For now, we emphasize that differences in the regional spatial distribution of high-return prey can result in distinctive patterns of variation within the broader trends of declining abundances.

The evidence for sturgeon depression presented here adds to a growing database on the causes and consequences of prehistoric subsistence change in the San Francisco Bay area (e.g., Bartelink 2006, 2009; Beasley et al. 2013; Broughton 1999; Schweikhardt et al. 2011; Simons 1992; Simons and Carpenter 2005; Wake 2012). Apart from the patterns documented at Emeryville, that in some cases appear unique to that locality, evidence for significant, late Holocene depressions have now been documented at a regional scale for black-tailed deer, tule elk, waterfowl, cormorants, and sturgeon (Broughton 1994b; Broughton et al. 2007; Simons et al. 2014). Many of these patterns are consistent with those documented from human bone isotope analyses. Bartelink's (2006, 2009) work with carbon and nitrogen isotope data is especially telling in this context, as it suggests a late Holocene decline in the consumption of high trophic-level marine resources that include estuarine fishes, such as (most notably) sturgeon.

Still, much remains to be learned, and we anticipate a growing contribution from stable isotope and ancient DNA analyses on archaeological vertebrate bone to address issues of resource depression and faunal demographic studies in this setting. Stable isotope analyses allow more direct assessments of potential climate-based population fluctuations, and ancient DNA can be used to reconstruct trends in genetic diversity and effective population size. Securely aligning these and more traditional zooarchaeological data to human skeletal samples and other artifactual records may reveal whether this broad-scale pattern of resource depression and associated decline in foraging efficiency is correlated with other changes in human behavior and biology—including increasing interpersonal violence, increases in morbidity and mortality, and changes in settlement

systems such as the possible late period residential depopulation of the San Francisco Bay shoreline.

Finally, our analysis may have implications for the modern management and conservation of white and green sturgeon, taxa that have, like most sturgeon worldwide, experienced significant historic-period population declines, in addition to the prehistoric depressions we document here. Green sturgeon is listed as threatened under the U.S. Endangered Species Act, and many subpopulations of white sturgeon are listed as critically endangered by the International Council for Conservation in Nature (Duke et al. 2004; St. Pierre and Campbell 2006). However, both commercial and sport fishing still occurs for many white sturgeon populations.

Insofar as sturgeon management strategies continue to allow for human harvesting, aspects of our 3,000-year record of prehistoric human harvesting of these fishes may be instructive. To take one example, recent conservation biology and applied zooarchaeological analyses have considered the importance of protecting large-game “source” areas in regions where hunting occurs but where it is difficult to enforce on-the-ground hunting regulations and bag limits (e.g., Hart 2000; Milner-Gulland et al. 2003; Naranjo and Bodmer 2007; Schollmeyer and Driver 2013). Indeed, recent analyses of prehistoric artiodactyl depression in the Southwest suggest that the long-term resilience of deer is related to the presence of such more-or-less protected source areas in upland settings distant from substantial human settlements (Schollmeyer and Driver 2013; see also Whitaker 2009), and earlier work with San Francisco Bay faunas again suggests a similar phenomenon applied to black-tailed deer in this region.

Our analysis thus generally underscores the importance of these source-sink dynamics in understanding regional patterns of harvest-based prey population declines and perhaps long-term sustainability, but it also reminds us that differences in prey species' spatial structure and natural history, in relationship to the positioning of human foragers, will strongly influence these dynamics. The only point of access to human foragers pursuing sturgeon resources in the San Francisco Bay was the estuary itself, and fish in this context lacked effective source areas that could replenish depressed stocks. For resources that resemble sturgeon in yielding exceptionally high post-encounter return

rates, and that also have slow life-history characteristics and circumscribed spatial distributions (e.g., tule elk), we would clearly anticipate a fate similar to that suffered by the late Holocene sturgeon of San Francisco Bay. For such resources, more restrictive management regulations would seem to be required.

NOTES

¹Following this prey model logic, variation in encounter rates with low-return fishes (outside of the optimal diet) should not affect their inclusion in the diet and the frequency with which they are taken relative to sturgeon (see discussion in Broughton et al. 2011; and complexities introduced by intermediate-ranked prey in Ugan and Bright 2001).

²A considerable use of synonyms and some confusion exists in the osteological nomenclature for Acipenseridae (see for example Jollie 1980). Osteological nomenclature here follows Hilton et al. (2011). Broughton (1999) followed Jollie (1980) and others in referring to the dermopalatine (of Hilton et al. 2011) as the maxilla or maxillary. Broughton (1999) referred to the palatopterygoid (of Hilton et al. 2011) as the “ectopterygoid,” the latter a prominent process on the former.

³Sites CA-CCO-269a and CA-CCO-269b represent separate fish-bone assemblages collected from different excavations at the same site (see Gobalet 1990, 1994).

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