Widening diet breadth, declining foraging efficiency, and prehistoric harvest pressure: ichthyofaunal evidence from the Emeryville Shellmound, California

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The Emeryville Shellmound is a famous but now destroyed midden once located on the east shore of San Francisco Bay. Analyses of the fish remains from the stratified late Holocene deposits indicate that prehistoric peoples had substantial impacts on the sturgeon populations of the Bay. This calls into question the commonly held belief that native peoples lived in harmony with nature and has important implications for the management of modern vertebrate populations.

Introduction

Let us begin by briefly suggesting what North America would have looked like to a late-fifteenth-century European who, through some feat of wizardry, could have soared like an eagle across the continent . . . he would be astonished to see streams thick with salmon and shad, or he might gaze with amazement at a thirty-foot-long sturgeon lying motionless in a deep pool next to a shaded bank . . . He would look with a hunter's eye at the uncountable deer, antelope, elk, bear, and bison, and at the waterfowl that swarmed by the millions . . . This game, and the fish he could easily pull from the lakes and streams, . . . would make up his diet in this pristine new world

SHABECOFF (1993: 3–5)

It is commonly assumed that the distributions and abundances of vertebrate resources recorded during the early historic period in North America reflected a 'pristine' condition. This view follows from the perception that native American population densities and technological capabilities were simply too low to deplete or extirpate vertebrate populations or, alternatively, that native peoples were 'children of nature' and the original conservationists (Redford 1991; Alvard 1994; Kay 1994). In fact, these perceptions underlie modern wildlife management policies and practices. Because pre-Columbian environments are routinely viewed as 'primordial wilderness' (Hewes 1973:150; Shabecoff 1993:3-5), restoring ecosystems to their 'original condition' simply requires the elimination of European influences; this is the principle behind 'hands-off' or 'natural regulation' management (Kay 1994).

This traditional view has, however, been recently challenged on theoretical as well as empirical grounds in several contexts in western North America (e.g. Broughton 1994a; 1994b; Grayson in press; Hildebrandt & Jones 1992; Jones & Hildebrandt 1995; Kay 1994). And since aboriginal human population densities were extremely high in California (e.g. Cook 1976), late Holocene California has been the focus of recent challenges.

In California, recent evidence for human impacts on prehistoric faunas has emerged from analyses of vertebrate remains from late Holocene archaeological sites; these document steadily declining abundances of *large-sized* prey species from environmentally distinct regions throughout the state (see Broughton 1994a; 1994b; Grayson 1991; Hildebrandt & Jones 1992; Jones & Hildebrandt 1995). Most of these analyses have been conducted in the context of evaluating ecologically oriented models of subsistence

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change; all have concluded that the documented declines in the archaeological abundances of large prey is a function of expanding prehistoric forager densities and game depletion.

The ecological models that underlie these analyses suggest that late prehistoric subsistence adaptations in California focused on resources that yielded low caloric returns per unit time of procurement and that significant decreases in overall caloric return rates occurred during the late Holocene (Basgall 1987; Beaton 1991; Bettinger 1991; Broughton 1994a; 1994b; Cohen 1981). As human population densities increased steadily during the late Holocene, it is argued, the per capita and/or absolute abundances of such high-return resources as large-bodied terrestrial herbivores decreased. As a result, diets included higher frequencies of such smaller, lower return resources as molluscs, smaller fishes, and acorns. These hypothetical models suggest the occurrence of *resource intensification*, classically defined as a process by which the total productivity or yield per areal unit of land is increased at the expense of declines in overall caloric return rates or *foraging efficiency* (Boserup 1965; Earle 1980).

The empirical evidence for resource intensification and its specific causes thus has implications not only for the evolution of prehistoric hunter–gatherer subsistence systems but also for the modern management of resources and ecosystems currently threatened by human-caused habitat alteration. Previous analyses of California archaeological vertebrate faunas have documented declining abundances of large-sized vertebrates relative to smaller ones during the late Holocene, supporting resource intensification models; yet taxonomic abundances are only one of several data-sets that might be used to test these models. Since the mean and maximum age and size of exploited vertebrate populations can provide a fairly direct measure of human harvest pressure, these data can provide far stronger tests than those based on taxonomic abundances alone.

In this paper, I incorporate both taxonomic abundances and age/size structure in a test of resource intensification models from the San Francisco Bay region of the central California coast. Specifically, I examine the evidence for declining efficiencies in fish exploitation and human harvest pressure on fish resources from the ichthyofaunal materials of the Emeryville Shellmound, a deep, stratified and well-dated late Holocene residential village site once located on the east shore of the San Francisco Bay estuary.

Archaeological vertebrate measures of foraging efficiency and harvest pressure

Taxonomic composition and foraging efficiency

Resource intensification models proposed for prehistoric California predict declines in overall caloric return rates or foraging efficiencies over time. As a result, measuring foraging efficiency requires consideration of the relative abundances of prey types with distinct differences in energetic returns. The fine-grained prey choice model, drawn from optimal foraging theory, provides a framework for assessing the relative costs and benefits of different resources and how these variables interact with resource abundance and prey choice (Charnov 1976; Pulliam 1974; Pyke *et al.* 1977; Schoener 1971; Stephens & Krebs 1986).

The fine-grained prey choice model, or simply the 'prey model', was designed to predict prey selection by predators foraging within more-or-less homogeneous resource clumps or patches. Initially, the various prey types potentially exploited by a predator are ranked according to their profitability. Prey profitabilities are defined by *post-encounter return rates*, a ratio of the net caloric value gained by acquiring a prey item to the time costs of pursuing and processing the prey once encountered. The model predicts that the most profitable or highest-ranked prey will be taken whenever they are encountered, while prey of lower rank may or may not be selected, depending on the abundance of the highest-ranked prey. As the encounter rates of higher-ranked prey decrease, prey are added to the diet sequentially in order of decreasing rank (see Stephens & Krebs 1986: 17–24 and references therein). It follows that the relative frequency with which high- and low-ranked prey are selected within a given resource patch can provide an index of foraging or predation efficiency. A diet dominated by high-ranked prey indicates a higher caloric return per unit foraging time relative to a diet dominated by low-ranked prey.

For the relative abundances of differently ranked prey in the diet to measure foraging efficiency, the stringent assumptions of the prey

model must be met. Particularly important is the *fine-grained search* assumption, stipulating that all prey types must be sought after simultaneously and randomly encountered within a more-or-less homogenous resource patch. This critical assumption allows search time to be detached from specific prey types and assigned to the set of resources as a whole and, ultimately, the prediction that prey types will be added or dropped from the optimal diet strictly as a function of their post-encounter return rates. Hence, in archaeological applications of the prey model, separate analyses of diet breadth changes should be conducted for prey types that occupied distinct habitat types and/or were likely pursued and captured with different methods and technologies (see Smith 1991: 206).

To the extent that an approximation of fine-grained search is met for prey resources handled with similar methods and taken within the same habitat type directly adjacent to a site locality, the relative abundances of high- and low-ranked prey types selected can measure foraging efficiency: diets dominated by high-ranked prey types would indicate a higher overall energetic return per unit foraging time relative to a diet dominated by low-ranked prey. Prey rank estimates are thus an important first step toward measuring foraging efficiency in archaeological faunas.

Prey ranks can be established empirically through actual measurement of pursuit and processing times and of caloric returns in tests of foraging models among living organisms. When actual return rates cannot be measured, animal ecologists often rely on proxy measures of prey rank, the most common being the *body size* of prey items. Theoretical arguments suggest (Bayham 1979; 1982; Broughton 1994a; 1994b; Griffiths 1975; Schoener 1979) and empirical data from experimental and ethnographic settings demonstrate (e.g. Alvard 1993; Bird 1996; Hill *et al.* 1987; Simms 1987; Smith 1991; Winterhalder 1981), that for singly handled vertebrate prey, post-encounter return rates are closely scaled to prey body mass. At least among the size range of vertebrate species that occurred in late Holocene settings in western North America, the larger the size of the animal, the higher the post-encounter return rates (Broughton 1994b).

Some variation in return rates, however, clearly exists beyond that contained in body weight differences, due to variation in both handling costs and energetic values. Variation in fat content, for example, is especially critical in affecting differences in return rates for similarly sized prey items (see Hill *et al.* 1987; Smith 1991; also Speth & Spielmann 1983 for the nutritional importance of fat).

Technological innovations may also differentially affect the handling costs of different prey types. The adoption of a netting or harpoon technology could reduce handling times associated with the exploitation of aquatic vertebrates and ultimately increase the relative ranks of such resources (see Alvard & Kaplan 1991; Winterhalder 1981).

In sum, while body size is probably the best context-independent measure of prey rank available to archaeologists, this 'rule of thumb' should be viewed with some caution. In any particular setting, factors such as fat content, and/or other peculiarities in the defence mechanisms of particular taxa can be examined and the body size-return rate generalization adjusted accordingly.

Harvest rates and age composition

If increasing human harvest rates caused absolute reductions in the densities of large, high-ranked prey items, the exploited populations as represented archaeologically should exhibit demographic indications of harvest pressure. Specifically, harvest rates on vertebrate populations are systematically reflected in the age composition of individuals in a population. An increase in harvest pressure on vertebrate populations typically reduces the mean and maximum ages of individuals (see Beverton & Holt 1956; King 1995: 177–8; Caughley 1966; 1977). Since age is also correlated with size among species that continue to grow throughout life, such as fishes, increasing harvest rates can be indicated by decreases in mean and maximum size (e.g. Bagenal 1974; Casteel 1976; Jones 1984). Reductions in mean and maximum age and size as a result of increasing harvest rates have been documented empirically in numerous wildlife management settings (e.g. Bannister 1977; Coulson *et al.* 1982; Duncan 1978; Hesselton & Hesselton 1982; Koike & Ohtaishi 1985; 1987; Laws 1962). Hence, harvest pressure on prehistoric fish populations can be measured by changes in the mean and maximum size of individuals within archaeological samples.

Finally, the susceptibility of species to population declines due to harvest pressure should also vary according to their residence times within the predators range. For example, prey species that migrate out of the predator's foraging range seasonally to breed would be less susceptible to depression than resident prey types (see Charnov *et al.* 1976: 251).

The Emeryville Shellmound: stratigraphy and chronology

The Emeryville Shellmound (CA-ALA-309), located on the east shore of San Francisco Bay, was destroyed in the early 20th century (FIGURE 1). The mound itself was huge, minimally 100 x 300 m in area and extending to a depth of over 10 m.

History of excavations

Prior to its destruction, the Emeryville Shellmound was the site of three separate archaeological excavations. The initial excavation was conducted in 1902 by Max Uhle and John C. Merriam of the University of California, Berkeley (Uhle 1907). Uhle and Merriam excavated a lateral section on the west slope of the mound and a tunnel that extended into its centre, excavating over 200 cubic metres of midden and removing the sediments 'stratum by stratum'. In all, 10 distinct strata were encountered and all of the artefacts, including a large sample of vertebrate remains, were collected and provenienced by these strata (Uhle 1907). The vertebrate materials as well as the other artefacts were collected with sieves (Schenck 1926: 167; Uhle 1907: 20), of mesh-size now unknown; the vertebrate faunal collection is consistent with moderate-to-large mesh (e.g. 1/4" (0·64 cm) to 1/3" (0·84 cm)) screening (Broughton 1995).

In the spring of 1906, Nels C. Nelson led the second excavation at Emeryville, stratigraphically excavating a 6' x 6' (1·8 x 1·8 m) unit in the east side of the mound. Nelson, identifying 11 natural strata in this work, collected and provenienced all of the artefacts, including vertebrate remains, by these natural strata (Broughton 1996; Nelson 1906).

The Emeryville Shellmound was levelled to that of the surrounding plain in 1924. Afterwards, W.E. Schenck excavated three 50' x 6' (15·2 x 1·8 m) trenches in the base of the deposit near the very centre of the mound. These trenches, excavated in 1' (0·31 m) arbitrary levels to a depth of nearly 10' (3·1 m), produced a sizable faunal collection (Schenck 1926).

Chronology

Thirteen radiocarbon assays exist for bone and charcoal specimens recovered throughout the Emeryville deposit (TABLE 1). FIGURE 2 shows a profile of the Uhle/Merriam excavation with the radiocarbon determinations indicated in stratigraphic context. They range from 2620±70 b.p. (basal contact between midden and the alluvial clay upon which the mound sits) to 950±50 b.p. for stratum 2. For the Nelson strata, they range from 2370±70 b.p. for stratum 11 to 720±60 b.p. for stratum 3.[1] There are no inconsistencies in the stratigraphic ordering of the dates from either the Uhle/Merriam or Nelson excavations; within each excavation, the oldest dates are from the lowest strata, the youngest from the highest.

A single radiocarbon assay was obtained near the top of one of Schenck's trenches and six for the base of the mound. Together, these bracket the deposition of the Schenck trench sediments between 2600 and 1970 b.p. This time interval incorporates the period of deposition for the basal four strata (stratum 10 through 7) from Uhle's excavation. Accordingly, I aggregated the 1' level samples from Schenck's three trenches into a total of four provenience units.[2]

The ten Uhle strata, the three radiocarbon-dated Nelson strata, and the four Schenck trench levels together yield a total of 17 independent provenience units. Based on stratigraphic relationships and radiocarbon dating, each unit

1 The Nelson excavation yielded a comparatively small sample of vertebrate specimens aside from the basal stratum 11. For this reason and because only two of the upper 10 strata were radiocarbon-dated, I selected only the three dated strata (3, 5 and 11) for the following analyses.

2 For instance, the faunal materials from the 0'–1' and 1'–2' levels from the three trenches were aggregated into a single unit; the 2'–3' and 3'–4' levels were lumped as a single unit for the three trenches, and so on. In the following analyses, I maintain these four Schenck aggregate 2' levels as independent units, but equate them on an ordinal temporal scale with the lower four Uhle strata (see Broughton 1995: 91–3). I emphasize that it is impossible to demonstrate an exact temporal correspondence between the four Schenck levels (excavated by arbitrary levels), and the four basal Uhle strata (excavated by natural strata). However, they should, minimally, represent separate ordinal temporal scales for the period between *c.* 2600 and 1900 b.p. Insofar as the Schenck levels do not correspond precisely to the Uhle natural strata, incorporating them in the following analyses will, at worst, introduce noise into the analysis for this earlier phase of the occupation at Emeryville.

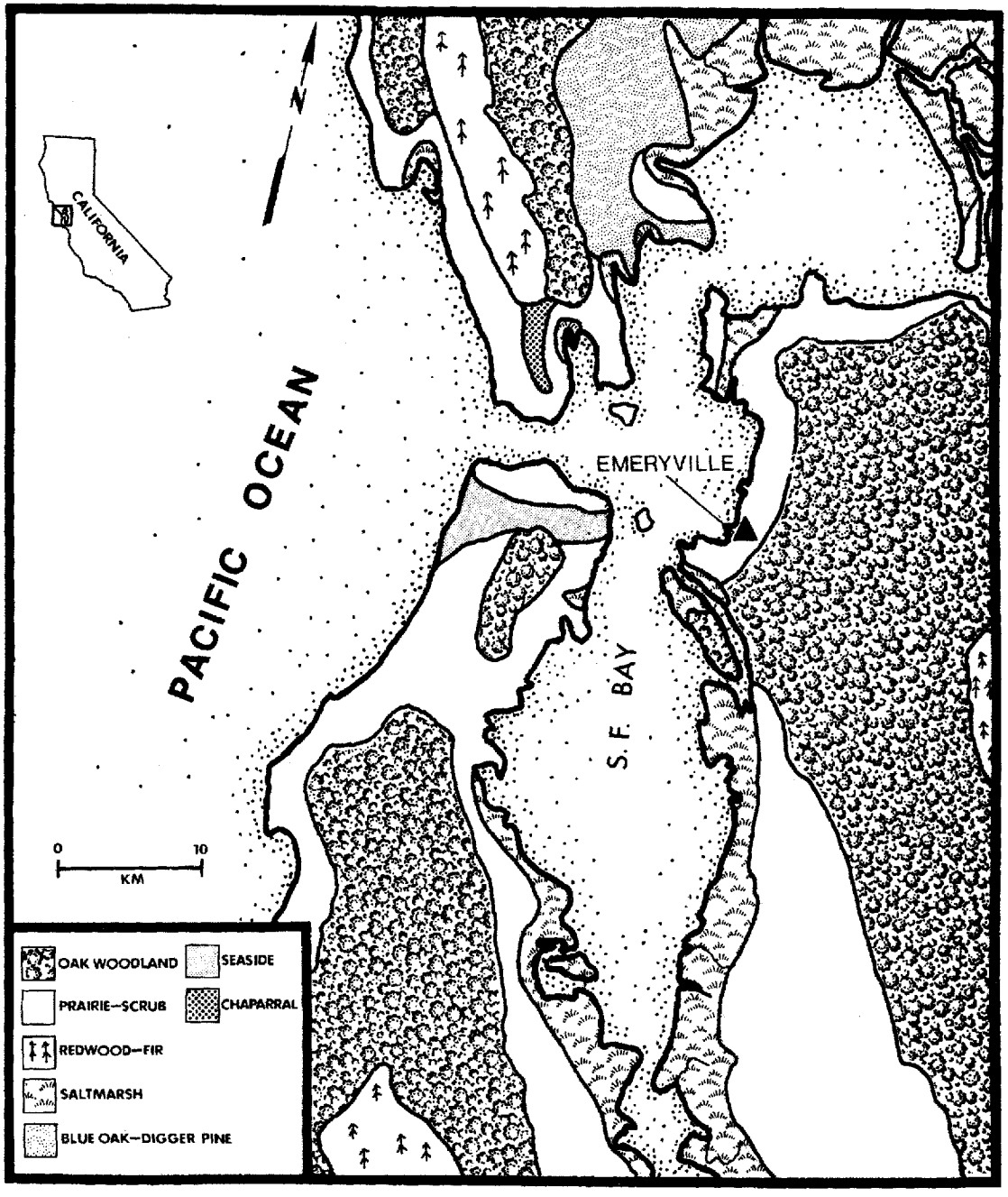


FIGURE 1. *Map of the San Francisco Bay area indicating location of the Emeryville Shellmound (ALA-309) and historic period vegetation (vegetation redrawn from Küchler 1977).*

was assigned to one of 10 'strata' (TABLE 2), which may allow a fine-grained ordinal-scale analysis of change in the efficiency of fish exploitation and evidence for harvest pressure on local fish populations at the Emeryville locality between *c.* 2600 and 700 b.p.

lab. no.	provenience unit	material dated	uncalibrated determinations (b.p.)	calibrated date 2σ, 95% probability
Beta-76866	Nelson, Stratum 3	bone collagen	720±60	AD 1220–1395
Beta-76863	Uhle, Stratum 2	bone collagen	950±50	AD 1000–1215
Beta-76864	Uhle, Stratum 5	bone collagen	1400±50	AD 590–695
Beta-76867	Schenck Trench 1, 1'–2'	bone collagen	1970±50	50 BC–AD 135
Beta-76865	Uhle, Stratum 7	bone collagen	1980±50	60 BC–AD 130
Beta-76862	Uhle, Stratum 8	bone collagen	2070±60	200BC–AD 70
1-9896*	Nelson, Stratum 5	charcoal	1110±70	AD 779–1033
1-9893*	Nelson, Stratum 11	charcoal	2370±70	764–243 BC
1-7964*	Uhle, contact midden/sterile clay	charcoal	2400±70	773–270 BC
1-7963*	Uhle, contact midden/sterile clay	charcoal	1030±60	AD 890–1162
1-7967*	Uhle, contact midden/sterile clay	charcoal	2620±70	903–539 BC
LJ-0199†	base of mound	charcoal	2310±220	898 BC–AD 135
I-7073†	base of mound, southeast corner	charcoal	2530±105	894–391 BC

* Phoebe Hearst Museum Catalog numbers; dates from CAMS Lawrence Livermore National Laboratory.
† From Bickel (1978: 20).

TABLE 1. *Radiocarbon dates from the Emeryville Shellmound.*

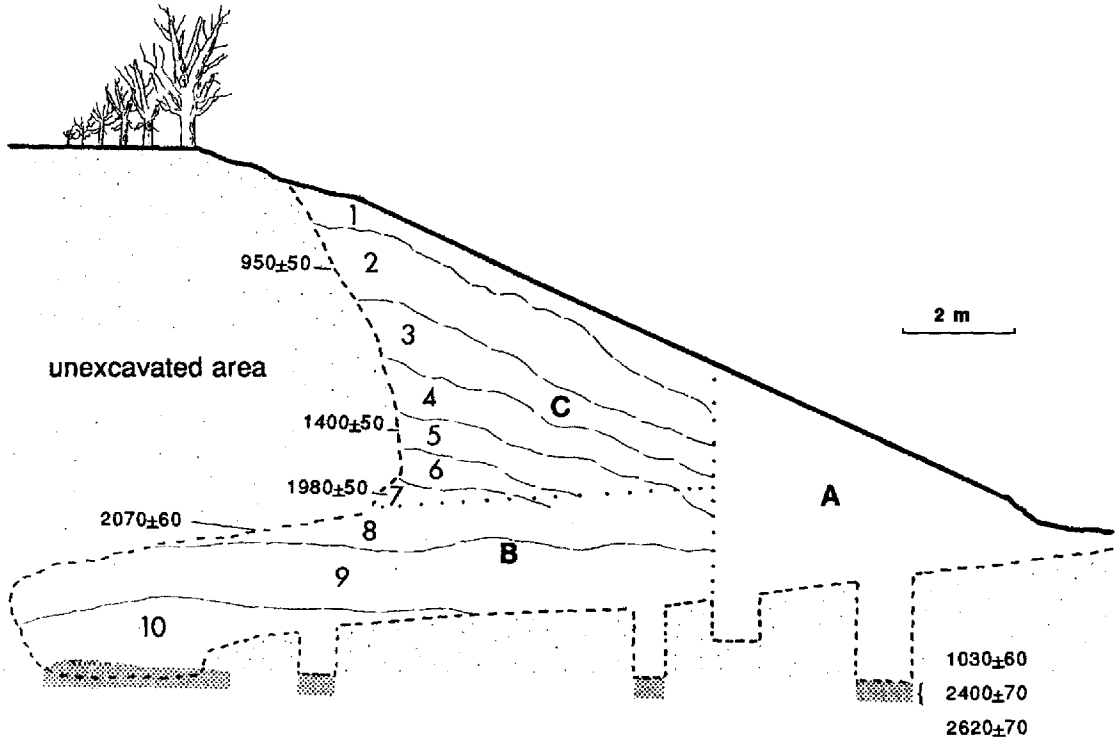


FIGURE 2. *Profile of the Uhle/Merriam excavation showing radiocarbon dates placed in stratigraphic context. 1–10 indicate natural strata. Dashed lines indicate limits of excavation. Hatching indicates sterile alluvial clay (redrawn from Uhle 1907: plate 4).*

The Emeryville Shellmound ichthyofauna

Taxonomic composition

TABLE 3 provides the numbers of identified specimens (NISP) per taxon by stratum for the Emeryville Shellmound ichthyofaunal assemblage. Nine taxa are represented by the 2004

provenience unit	abbreviation	stratum	radiocarbon determinations (b.p.)
Uhle, Stratum 1	U1	1	–
Nelson, Stratum 3	N3	1	720±60
Uhle, Stratum 2	U2	2	950±50
Uhle, Stratum 3	U3	3	–
Nelson, Stratum 5	N5	3	1110±50
Uhle, Stratum 4	U4	4	–
Uhle, Stratum 5	U5	5	1400±50
Uhle, Stratum 6	U6	6	–
Uhle, Stratum 7	U7	7	1980±50
Schenck Trench Level 1: 0'–2'	S1	7	1970±50
Uhle, Stratum 8	U8	8	2070±60
Schenck Trench Level 2: 2'–4'	S2	8	–
Uhle, Stratum 9	U9	9	–
Schenck Trench Level 3: 4'–6'	S3	9	–
Uhle, Stratum 10	U10	10	2620±70, 2400 ±70, 1030±60
Schenck Trench Level 4: 6'–9'	S4	10	–
Nelson, Stratum 11	N11	10	2370±70

TABLE 2. *Emeryville provenience units with associated radiocarbon determinations.*

identified fish specimens.[3] Four taxa comprise over 99% of the identified specimens: requiem sharks (Carcharhinidae), bat ray *(Myliobatis californica)*, salmon (*Oncorhynchus* sp.) and sturgeon (*Acipenser* sp.). All of the identified fishes presently inhabit the open estuary of San Francisco Bay, directly west of the site (FIGURE 1).

Three species of requiem shark commonly occur in San Francisco Bay: the soupfin shark *(Galeorhinus zyopterus)*, the brown smoothhound *(Mustelus henlei)* and the leopard shark *(Triakis semifasciata)*. From the time of the earliest censuses, brown smoothhounds and leopard sharks have represented over 90% of the total smoothhound shark assemblage in San Francisco Bay (deWitt 1975; Herald 1953; Herald & Ripley 1951).[4]

Two species of Pacific salmon were once abundant in San Francisco Bay, coho salmon *(Oncorhynchus kisutch)* and, especially, chinook salmon *(O. tshawytscha)* (Skinner 1962: 66–7); only chinook salmon is securely identified in the Emeryville material.

Two species of sturgeon also occur in the Sacramento–San Joaquin river system, white sturgeon *(Acipenser transmontanus)* and green sturgeon *(A. medirostris)*. While both of these species could be represented in the Emeryville *Acipenser* material,[5] white sturgeon have dominated the sturgeon assemblage in San Francisco Bay throughout historic times (Miller 1972; Moyle 1976; Skinner 1962).

Requiem sharks, bat rays, salmon and sturgeon can each attain substantial sizes; as a group, they dominate all San Francisco Bay shellmounds that have been analysed. Smaller fishes, however, are routinely recovered in ichthyofaunas recovered with fine mesh (1/8" (0·32 cm)) screens (Follett 1957; 1974; 1975a; 1975b; Gobalet 1988; 1990; 1994). The virtual lack of the smaller fishes in the Emeryville ichthyofauna is almost surely a reflection of the coarse-grained recovery methods discussed above. So, while small fishes are probably greatly under-represented in the assemblage as a whole, this systematic recovery bias should be internally consistent throughout the various strata of the deposit.

3 Specimens were identified by comparison with reference materials of the Department of Ichthyology, California Academy of Sciences, San Francisco. All identifiable elements are included in TABLE 3. The osteological criteria I used for those identifications and the element frequencies are provided in Broughton (1995). The Emeryville faunal collection is housed at the Phoebe Hearst Museum of Anthropology, University of California, Berkeley. Taxonomic nomenclature follows Robins *et al.* (1991).

4 Only vertebrae of the requiem sharks were represented in the assemblage. These elements may be identified to species by criteria revealed from radiographs (see Compagno 1988: figure 9.2), analyses not attempted here.

5 Due to both a high degree of osteological similarity between these species and pronounced variation among individuals within a species, it is questionable whether the two sturgeon species can be separated osteologically (Follett 1975b; Gobalet 1994; see also Brinkhuizen 1986); I did not attempt it here (see Broughton 1995).

taxon	stratum (provenience unit) 1 (U1)	1 (N3)	2 (U2)	3 (U3)	3 (N5)	4 (U4)	5 (U5)	6 (U6)	7 (U7)	7 (S1)	8 (U8)	8 (S2)	9 (U9)	9 (S3)	10 (U10)	10 (S4)	10 (N11)	*total*
requiem sharks (Carcharhinidae)	7	–	78	30	–	3	–	–	5	20	34	39	4	24	33	4	–	***281***
bat ray (*Myliobatus californica*)	3	5	55	53	–	49	9	21	13	8	34	20	16	48	39	29	1	***403***
sturgeon (*Acipenser* sp.)	1	–	51	86	–	69	109	57	63	31	236	113	20	87	217	38	15	***1193***
herrings (Clupeidae)	–	–	–	–	–	–	–	–	–	–	–	1	–	6	–	–	–	***7***
salmon (*Oncorhynchus* sp.)	1	–	2	2	–	5	2	4	13	4	22	22	3	26	4	1	2	***113***
chinook salmon (*O. tshawytscha*)	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	***2***
silversides (Atherinidae)	–	–	–	–	–	–	–	–	–	1	–	1	–	–	–	–	–	***2***
white seabass (*Atractoscion nobilis*)	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	–	***2***
surfperches (Embiotocidae)	–	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	***1***
total	***12***	***5***	***186***	***171***	***0***	***126***	***120***	***82***	***95***	***65***	***326***	***197***	***44***	***191***	***293***	***73***	***18***	***2004***

TABLE 3. *Numbers of identified fish specimens per taxon by stratum at the Emeryville Shellmound (see TABLE 2 for provenience unit abbreviations).*

Relative ranks of the Emeryville fishes

To derive a taxonomic index that summarizes the relative contribution of high- and low-ranked fish taxa in the Emeryville strata and test the prediction that the efficiency of fish exploitation declined across the occupational history of this site, estimates of the relative ranks of the fishes represented in the assemblage are required. Data on the seasonal occurrences are also necessary to assess the relative susceptibility of these fishes to human harvest pressure. To this end, data on the body sizes, fat composition and the seasonal occurrence of these fishes in San Francisco Bay are provided in TABLE 4.

White sturgeon are by far the largest species represented in the Emeryville ichthyofauna (TABLE 4). Formerly reaching lengths of up to 6·1 m and weights up to 816 kg, white sturgeon were the largest fish common in North American estuarine habitats. The fat content per gramme of sturgeon flesh is also as high or higher than that of the other fishes.

Sturgeon possess no defence mechanisms that would disproportionately elevate the handling costs of this resource; they are lethargic benthic browsers, easily captured by a variety of methods, even by hand (Kroeber & Barrett 1960: 87; Moyle 1976: 95). Sturgeon almost surely represent the highest-ranked fish taxon available to the Emeryville foragers.

A final issue bearing on the return rates for the Emeryville fishes involves mode of capture. The prey model specifies that prey types are searched for simultaneously, encountered sequentially and handled *one at a time*. This allows the assignment of distinct ranks to different prey types and ultimately the prediction that prey are added to or dropped from the diet as a function of their rank. Yet, if fish are captured in mass, return rates for a given taxon can vary as a function of their densities. Is the assumption of single-prey handling suitable to the set of fishes represented in the Emeryville ichthyofauna?

A wide variety of fishing methods were employed by aboriginal groups of this general region, including netting, seining, angling, harpooning, spearing, snaring and gaffing (Bennyhoff 1950; Follett 1975a; Kroeber & Barrett 1960). Ethnographic reports from northwestern California even indicate that several groups captured large, slow-moving sturgeon by hand (Kroeber & Barrett 1960: 87). Artefacts indica-

taxon	max weight (kg)	mean weight (kg)	fat (%)*	seasonal occurrence S.F. Bay	references	notes
requiem sharks (*M. henlei* and *T. semifasciata*)	32	4·0–4·9†	0·9	spring–autumn	1, 2, 3, 4, 5	fat values for *Mustelus lenticulatus*
bat ray (*M. californica*)	95	3·64–11·45	0·2–2·0	spring–autumn	2, 6, 7, 8, 9	fat values for 'skate' (unspecified species)
chinook salmon (*O. tshawytscha*)	38·6	9–10	2·2–19·0	variable	10, 11, 12, 13, 14	see text for notes on seasonal occurrence
white sturgeon (*A. transmontanus*)	816	18·4	4·04–12.5	year round	3, 10, 13, 14, 15	

* percentage composition for edible portion of raw fish
† values for *T. semifasciata*

References

1 deWitt 1975
2 Herald *et al.* 1960
3 Eschmeyer *et al.* 1983
4 Ferguson & Cailliet 1990: 11
5 Compagno 1984: 433
6 Martin & Cailliet 1988a
7 Martin & Cailliet 1988b
8 Kirk & Sawyer 1991: 506
9 Follett 1975a
10 Moyle 1976
11 Healy 1991
12 Hallock & Fry 1967
13 Exler 1987
14 Nettleton 1985
15 Pycha 1956: table 3

TABLE 4. *Body size, fat content and seasonal occurrence of requiem sharks, bat ray, chinook salmon and white sturgeon in San Francisco Bay.*

tive of fishing methods recovered at Emeryville include net weights, fish hooks and spear points (Uhle 1907; Nelson 1906; Schenck 1926).

Many fish-handling methods used by aboriginal foragers of the region clearly targeted individual fish; these were more commonly used for larger fish than small (Kroeber & Barrett 1960: 73–80). Even with the use of nets, fishes as large as sturgeon, requiem sharks, bat rays and salmon surely required *individual* handling and processing. In sum, for the capture technologies available, and for individual fish as large as the primary four species at Emeryville, the assumption of sequential encounter and single-prey handling is justified.

Artefacts indicative of most of the varied handling techniques — netting included — are represented in the earliest known shellmound deposits in the region; no substantial changes in the basic nature of these technologies are apparent across the late Holocene occupation of the region (see Bennyhoff 1950; Broughton 1994b: 393–4; Wallace & Lathrap 1975). This suggests that technological innovations did not dramatically alter handling efficiencies over the period that Emeryville was occupied.

Harvest pressure and the Emeryville fishes

As TABLE 4 indicates, considerable variation exists in the seasonal distributions of the fishes represented at Emeryville; this allows an assessment of the relative susceptibility of these fishes to human overexploitation.

Requiem sharks and bat rays come into shallow-water estuaries such as San Francisco Bay during spring and summer to bear their young; they move to deeper portions of estuaries and offshore during the fall and winter (TABLE 4). These populations would experience a reprieve from human harvesting by Bay margin foragers for much of the year.

Four distinct races, or 'runs', of chinook salmon move from the Pacific Ocean through the San Francisco Bay to upstream spawning localities in the Sacramento and San Joaquin Rivers: a fall run, a late-fall run, a winter run, and a spring run (TABLE 4). A single run of coho salmon occurs in the fall (Shapovalov & Taft 1954: 33). Individuals from any one salmon run or stock are present in San Francisco Bay only briefly.

The white sturgeon of San Francisco Bay are anadromous, but spend most of their lives in the estuary. White sturgeon move up the Sacramento–San Joaquin river system to spawn

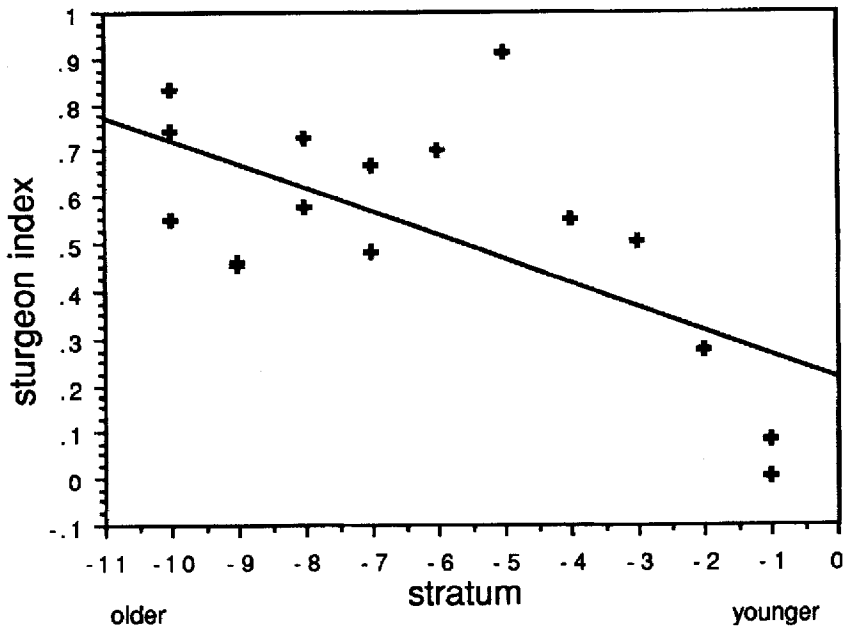


FIGURE 3. *The distribution of the sturgeon index by stratum at the Emeryville Shellmound. (A least-squares regression line indicates the direction of the trend.)*

between mid March and early June. Females do not reach sexual maturity until they are at least 11 or 12 years of age and sexually mature fish only spawn about once every five years (TABLE 4). In any one year, only a small proportion of the population makes the spawning migration (Moyle 1976: 96–7).

In sum, requiem sharks, bat rays and individual salmon stocks spend much less of the year in the Bay than does the more-or-less resident sturgeon population. These other fishes, available for a shorter part of the annual cycle, are less sensitive to pressure from fishing in the Bay.

The sturgeon index

Sturgeon, it seems, is both the highest-ranked fish taxon in the estuarine habitat adjacent to the Emeryville Shellmound and more sensitive to harvest pressure than the other well-represented fishes. Declining overall return rates for the estuarine fishery should be signalled by decreasing abundances of sturgeon relative to the other fishes. A simple quantitative index of the relative abundance of sturgeon, the 'sturgeon index', may be calculated as:

$$\Sigma\text{NISP Sturgeon}/\Sigma\text{NISP (Identified Fishes)}$$

Values of the sturgeon index that approach 1 indicate high frequencies of sturgeon (1·0 = all sturgeon), whereas values closer to 0 indicate few sturgeon remains and more of the other lower-ranked taxa (0·0 = no sturgeon). Temporal patterns in the efficiency of fish exploitation can be revealed by plotting the sturgeon index values across the Emeryville strata.

TABLE 5 presents the sturgeon index values by stratum for the Emeryville Shellmound; the relationship between these variables is depicted graphically in FIGURE 3. A Spearman's rank order correlation coefficient between the sturgeon index and stratum is negative and significant ($r_s = -{\cdot}49$, $P = {\cdot}05$). So, the relative abundance of the largest highest-ranked fish resource declines across the occupational history of the Emeryville Shellmound. Importantly, the sturgeon index is not correlated with the associated sample sizes (total fish NISP) for the various Emeryville strata ($r_s = {\cdot}37$, $P > {\cdot}10$; see Grayson 1984).[6]

6 If all fish elements were destroyed at a constant rate, the remains of smaller specimens would be lost first, followed by larger elements. The increasing ratio of the smaller fish taxa to larger ones through time documented at Emeryville would then be a natural consequence of differential preservation. However, recent research in vertebrate taphonomy shows that mineral bone density is a critical variable influencing bone survivorship and that the density of elements is independent of their absolute size (see Lyman 1984; 1993; Butler 1996; Butler & Chatters 1994; see also Lubinski 1996). For chinook salmon and largescale sucker (*Catostomus macrocheilus*), the only fish species for which bone-density data are available, smaller elements (e.g. vertebrae, articulars, otoliths) have the highest density values. Until density values for the Emeryville fishes, especially sturgeon, are available, it is not possible directly to evaluate the effects of bone density in relation to fish size and differential preservation.

The decrease in the sturgeon index suggests declines in both the encounter rate of sturgeon and the efficiency of fish exploitation. Human harvest pressure and/or changes in the estuarine palaeoenvironment could have caused a decline in the encounter rate with sturgeon.

Changes in the estuarine palaeoenvironment

The distribution and abundance of white sturgeon populations in San Francisco Bay is strongly influenced by fluctuations in estuarine salinity and freshwater inflow into the Bay (Kohlhurst *et al.* 1991). White sturgeon move upstream, out of the central portion of San Francisco Bay — near Emeryville — during years with low freshwater inflow and correspondingly high salinity levels. Recruitment (year-class strength) of white sturgeon is also positively correlated with freshwater inflow into the Bay from the Sacramento and San Joaquin Rivers (Kohlhurst *et al.* 1991).

The isotopic composition of estuarine sediments cored near Oyster Point, *c.* 15 km southwest of Emeryville, provides an empirical record of late Holocene changes in salinity and river inflow (Ingram *et al.* in press). As an index of estuarine salinity, Ingram *et al.* (in press) measured oxygen isotope ($^{18}O/^{16}O$, or $\partial^{18}O$) values from 167 bay mussel *(Mytilus edulis)* shells distributed throughout the radiocarbon-dated Oyster Point core. These data indicate considerable fine-scale oscillations in salinity, yet no directional shifts or trends toward increasing salinity. These data indicate that changes in salinity are unlikely to have caused the significant decline in the relative abundance of sturgeon across the Emeryville strata.

Human harvest pressure

If the decline in sturgeon abundances resulted from human harvest pressure, it should be associated with a lower mean and maximum age/size of sturgeon in the San Francisco Bay population and in the Emeryville ichthyofauna.

Although the precise relationship between the age and size of fish is influenced by environmental factors — water temperature, population densities, food availability and intra- and inter-specific competition — size is a good general index of age for most fish species (Weatherly 1972). Positive relationships between age and length have been documented for many sturgeon species (e.g. Rossiter *et al.* 1995; Keenlyne & Jenkins 1993), including white sturgeon of the San Francisco Bay (Kohlhurst *et al.* 1980; Pycha 1956).

provenience unit	stratum	sturgeon index	total NISP fishes
U1	1	0·083	12
N3	1	0·000	5
U2	2	0·274	186
U3	3	0·503	171
N5	3	–	0
U4	4	0·548	126
U5	5	0·908	120
U6	6	0·695	82
U7	7	0·663	95
S1	7	0·477	65
U8	8	0·724	326
S2	8	0·574	197
U9	9	0·455	44
S3	9	0·456	191
U10	10	0·741	293
S4	10	0·548	73
N11	10	0·830	18
total	**–**	**–**	***2004***

TABLE 5. *Sturgeon index values by stratum at the Emeryville Shellmound.*

For most fish species, the size of individual fish can be tightly predicted from the size of their skeletal elements (see Bagenal 1974; Casteel 1976: 92–124; Summerfelt & Hall 1987). This too has been securely documented for white sturgeon from the San Francisco Bay and Delta (e.g. Brennan & Cailliet 1989; 1991).

I selected the dentary to estimate variation in age and size of the Emeryville *Acipenser* since they were the most abundant, well-preserved element in the assemblage (Broughton 1995). The measurement axis for the dentary is illustrated in FIGURE 4 and summary statistics for dentary widths are presented by stratum in TABLE 6.

FIGURE 5 shows the distribution of sturgeon dentary widths by stratum. Both the mean and maximum dentary widths decline significantly through the strata (mean width by stratum: $r_s = -{\cdot}762$, $P < {\cdot}05$; maximum width by stratum: $r_s = -{\cdot}833$, $P < {\cdot}03$). These data indicate a size decrease in sturgeon dentaries through time. While this pattern is the predicted result of an increase in harvest pressure, it might also reflect variation in the sample sizes of measurable dentaries across these strata. Indeed, the relationship between mean dentary width and dentary sam-

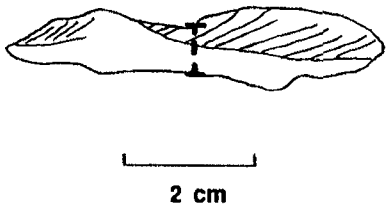


FIGURE 4. *Illustration of a white sturgeon right dentary showing measurement axis. Medial view; anterior is left.*

Stratum*	n	$\bar{X}$	range	s
3	2	8·150	6·65–9·65	2·12
4	3	9·717	8·97–10·45	0·74
5	2	9·240	7·47–11·01	2·50
6	1	7·890	–	–
7	6	9·607	5·84–13·45	2·59
8	8	10·229	7·02–14·42	2·62
9	8	10·588	8·27–13·92	2·87
10	9	11·103	6·34–15·44	2·65

* Strata 1 and 2 contained no sturgeon dentaries

TABLE 6. *Dentary widths (mm) of the Emeryville* Acipenser *by stratum.*

ple sizes by stratum is positive and significant (r_s = ·964, P = ·01): as the size of the measured sample increases, mean dentary width also increases.

Since the correlation between dentary width and dentary sample size is very likely related to the smaller samples of sturgeon material recovered from the upper strata (see FIGURE 5), I recalculated correlation coefficients between mean dentary widths and dentary sample sizes after combining the sample of dentaries from the four upper strata of the mound that contained sturgeon dentaries: strata 6 through 3 (dentary width for combined strata 6–3: $\bar{X}$ = 8·98, n = 8, s = 1·52, range = 6·65–11·01). Using the values from this combined upper strata sample, the relationship between dentary sample sizes and mean width is *insignificant* (r_s = ·70, P = ·18). However, the relationships between both mean and maximum dentary widths and stratum using the aggregated upper strata sample remain negative and significant at ·10 (mean width by stratum: r_s = −1·0, P <·05; maximum width by stratum: r_s = −·90, P = ·07). This analysis suggests that the decline in mean and maximum dentary widths across the Emeryville strata is not a function of variation in sample sizes.

In sum, the reduced abundance of sturgeon is accompanied by a significant decrease in the mean and maximum size of the exploited fish. This is consistent with the hypothesis that the declining abundances of sturgeon was due to increasing fishing pressure on this resource.

Discussion

The relative abundance of sturgeon — the largest, arguably the highest-ranked fish taxon represented in the Emeryville Shellmound ichthyofaunal assemblage — declined significantly through the late Holocene. This decline was not correlated with changes in the salinity of San Francisco Bay, which currently limits the abundance of sturgeon in this setting. The average size/age of the exploited sturgeon also decreased significantly through the period that the mound was occupied. The size/age decrease suggests that the decline in the relative abundance of sturgeon was due to human harvest pressure on that resource.

As I have discussed (Broughton 1995), patterns in the estuarine and terrestrial mammal faunas from Emeryville provide remarkably consistent results. Strong evidence for declining efficiencies in resource extraction occurs among the faunas representing every local habitat examined at this site. Similar trends have been indicated from numerous other San Francisco Bay shellmound sites and for late Holocene archaeological faunas in many other regions of California. Rather than an isolated case, the pattern documented in detail here among the Emeryville fishes now appears to be a very general one.

Mammal faunas from over a dozen San Francisco Bay shellmound sites reveal consistent declines in mammalian foraging efficiency across the occupational histories of particular localities. While large-sized terrestrial mammals, such as tule elk *(Cervus elaphus)* and black-tailed deer *(Odocoileus hemionus)*, dominate the mammalian assemblages during the initial habitations of specific regions, their abundances then steadily decline relative to sea otters *(Enhydra lutris)* (Broughton 1994b; Simons 1993).

Similarly, late Holocene archaeological faunas from sites located along the Sacramento River, one of the two main rivers that feed the San Francisco Bay estuary, document dramatic declines through time in the abundance of me-

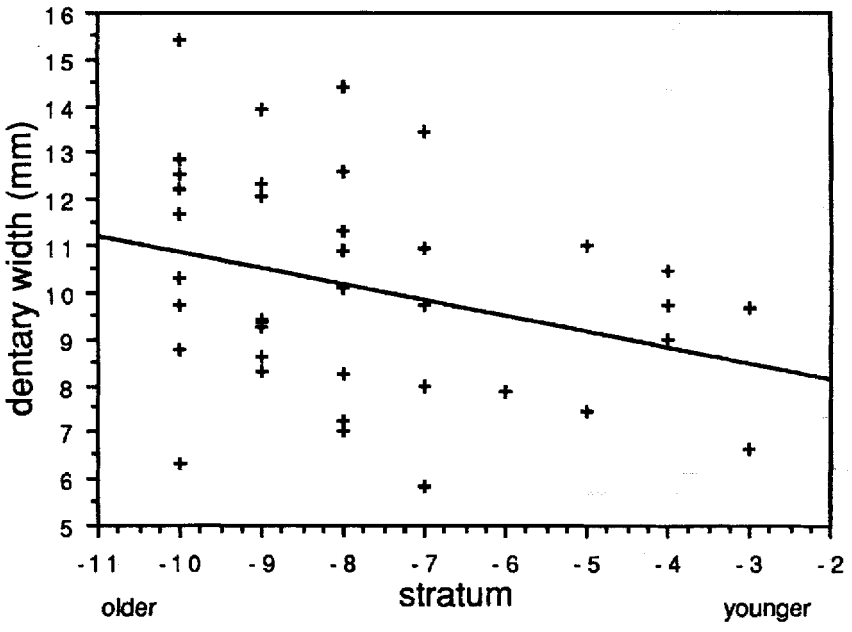


FIGURE 5. *Dentary widths by stratum for the Emeryville Shellmound* Acipenser. *(A least-squares regression line indicates the direction of the trend.)*

dium- and large-sized mammals relative to small resident fishes, such as minnows (Cyprinidae), Sacramento suckers *(Catostomus occidentalis)* and Sacramento perch (*Archoplites interruptus*).[7] When latitudinal and seasonal variation in the expected encounter rates with large, anadromous fishes (sturgeon and salmon) is held constant, significant declines also exist in the abundances of these large fishes, compared to the small resident forms (Broughton 1994a). Thus, declining abundances of sturgeon is documented in both the estuary and the upriver spawning locations of these fish in the Sacramento–San Joaquin river system during the late Holocene.

The archaeological vertebrate faunas from seven sites along terraces above the Pit River, a tributary of the Sacramento in northeastern California, also document changing relative abundances of large- and small-sized vertebrates in the middle and late Holocene (Bayham 1996). The relative abundances of small, resident, freshwater fishes increase compared to large- and medium-sized mammals, especially black-tailed deer, over the last 2000 years. A dramatic reversal in this trend occurs at roughly 250 b.p., when deer rebound once again to dominate the faunal assemblages. This reversal occurs soon after Euro-American contact; it may reflect localized human de-population of the region by introduced infectious diseases (Bayham 1996).

Chatters (1987; 1996) has shown that declining efficiencies of vertebrate use in the Pit River region is accompanied by changes in the intensity of pearl mussel *(Margaritifera margaritifera)* exploitation. From changes in age structure and growth rates, he argues that the pattern of mussel exploitation in this region was 'one of initial, relatively low exploitation intensity, followed by increased intensity and then, sharp decline' (Chatters 1987: 20). The period of 'increased exploitation intensity' occurred between 2000 and 250 b.p, while the 'sharp decline' occurred after Euro-American contact and the collapse of native human populations. Chatters (1987; 1996) argues that fluctuations in mussel use are related to changes in human populations and to the effects such changes have on the exploitation intensity of low-ranked prey. Hence, two independent datasets from the Pit River sites — archaeological vertebrates and freshwater molluscs — provide strikingly consistent results.

Further inland and to the south, Grayson (1991; see also Broughton & Grayson 1993) has also demonstrated dramatic changes through time in the relative abundances of large- and

7 The coarse-grained recovery methods at Emeryville and the virtual lack of small fishes represented in the deposit make such an analysis impossible here.

small-sized mammals from late Holocene high elevation archaeological sites in the White Mountains of eastern California. The abundance of mountain sheep *(Ovis canadensis)* decreases significantly through time relative to yellow-bellied marmots (*Marmota flaviventris*). Grayson (in press) argues 'that the decreasing relative abundances of mountain sheep through time in the White Mountains assemblages reflect the local depletion of those mammals'.

Finally, Hildebrant & Jones (1992; Jones & Hildebrandt 1995) report similar patterns among marine mammal faunas along both the open coasts of California and Oregon. Although certain aspects of the empirical support for their arguments has been questioned (e.g. Lyman 1995), they indicate that large-bodied migratory pinnipeds such as Steller's sea lion *(Eumetopias jubatus)*, California sea lion *(Zalophus californianus)*, and northern fur seal *(Callorhinus ursinus)* decrease over time relative to the much smaller harbour seal *(Phoca vitulina)* and sea otter. Hildebrandt & Jones argue that the populations of larger higher-ranked species were reduced by intensive prehistoric human hunting and over-exploitation and link the depletion of large marine mammals to change in settlement patterns and technology (Jones & Hildebrandt 1995: 94):

> The rise of maritime sedentism, apparent in California only in the Santa Barbara Channel and the northwest coast, was intimately related to the development of sophisticated, labor-intensive watercraft, as a consequence of the overexploitation of migratory breeders and the need to pursue alternative species in more elusive offshore contexts.

Although other causative factors were likely involved (see Arnold 1994; Raab 1996), these arguments underscore how over-harvesting local vertebrate resources may affect changes in other aspects of human behaviour.

While the species involved vary from context to context, disparate archaeofaunal datasets from environmentally distinct regions throughout California document increasing reliance on smaller prey items during the late prehistoric. It is also during this period that substantial increases in human population densities appear to have occurred in California, in a trend likely characterized by considerable spatial and temporal variability (e.g. Beaton 1991; Bouey 1987; Schulz 1981; Lambert & Walker 1991; Kealhofer 1996; Walker *et al.* 1989). Among a matrix of other possible causes involving the emergence of social/political complexity during the late prehistoric, this large-scale pattern of declining efficiency in vertebrate procurement appears linked in part to the depletion of large-bodied, high-ranked species under expanding forager densities. These analyses have far-reaching implications concerning the historic-period distributions and abundances of Pacific Coast vertebrates, as well as for modern ecosystem management policies and practices.

The Emeryville ichthyofaunal data, coupled with late 19th-century records of white sturgeon catches in the San Francisco Bay, are consistent with Hewes' (1947; 1973) largely untested model of the long-term population dynamics of Pacific Coast fisheries. Although he focused on salmon, Hewes suggested that aboriginal exploitation of Pacific Coast fisheries profoundly changed the populations of those resources: intensive aboriginal harvesting maintained fish populations substantially below 'hypothetical pre-human' abundances. When native American populations were decimated by European-introduced infectious diseases, he argued, the fisheries stocks experienced 'a resting period', during which they rebounded to levels higher than had existed for thousands of years. Significantly, Hewes suggested that the increasing catch-per-effort in the late 19th-century commercial fisheries was a function of that increase or rebound of depleted populations. Thus, the dynamics of historic-period harvest yields were intimately linked to aboriginal fishing pressures. Beyond ethnographic evidence that native Americans utilized substantial quantities of Pacific Coast fish resources, Hewes had little empirical evidence to support key aspects of his intriguing model. One of those aspects was that native Americans had pronounced impacts on the populations of Pacific Coast fishes. My analyses of the Emeryville Shellmound ichthyofauna provide strong evidence that, at least for sturgeon, those impacts were indeed substantial.

Models such as Hewes' have had little impact on ecosystem management policy in America, perhaps because they have not been subject to rigorous empirical testing; the perception that native Americans were passive servants of nature has long been a cornerstone

of environmental philosophy (Shabecoff 1993). Many California anthropologists, on the other hand, have argued that native peoples had a substantial influence on local ecosystems in ways that *enhanced* resource productivity; native Californians are thereby positioned as highly effective resource managers (e.g. Blackburn & Anderson 1993a; Lewis 1993; Shipek 1993; Swezey & Heizer 1977; Moratto 1984: 5–6).

Those perceptions have recently culminated in a 'logical alliance' emerging between native cultures and conservation organizations (Alvard 1994: 147; 1995). The government of Colombia has relinquished over 18 million hectares of rain forest to native peoples with the belief that they are best suited to manage that resource in a sustainable fashion (Alvard 1994: 147; Bunyard 1989), and a similar proposal has been issued by the World Bank to conserve Brazilian rain forests (Alvard 1994: 147; Pearce 1992). Finally, Lewis (1993: 398) has advocated that the management of national parks in western North America, such as Banff, Yellowstone, and Yosemite, should be carried out by native peoples using 'indigenous management practices . . . carrying on the day-to-day subsistence activities of harvesting traditional foods, hunting and trapping animals'.

Native American groups clearly have inalienable rights to lands they have occupied for millennia and should have the right to utilize those lands as they see fit. In addition, the vast ecological knowledge such peoples possess can potentially be extremely valuable in addressing particular management issues (Lewis 1993). However, entitling threatened ecosystems or national parks to native peoples because of a perception that they are inherently best suited to carefully manage them is another issue (*cf.* Alvard 1994: 148). The perceived harmony recognized historically may be a function of limited technologies and low population densities (*cf.* Alvard 1994; 1995; Grayson 1993: 299–300; Hill 1995). It is now well-documented that many native American populations were severely decimated by European-introduced infectious diseases during the 16th and 17th centuries, well prior to the detailed documentation of their lifeways (e.g. Dobyns 1983; Ramenofsky 1987; Campbell 1980; Upham 1992; Reff 1991). And although a protohistoric population decline in California has yet to be seriously tested with archaeological data,[8] recent analyses of the *potential* for the spread of infectious diseases into native California during the 16th century suggests that dramatic human losses were highly likely at this time (e.g. Erlandson & Bartoy 1995; Kelsey 1985; Preston 1996; but see also Kealhofer 1996). A substantial protohistoric population decline could easily account for the ethnographically derived impression of native Californians as prudent resource managers. For truly prehistoric times, at least to judge from the California archaeofaunal record, the situation appears to have been very different. With ready access to a market economy, modern medicine and western technologies, there are no compelling reasons to think that native Americans will provide a better stewardship of our threatened habitats than any other peoples. I note that Alvard (1994; 1995) has reached an identical conclusion from his analysis of modern Amazonian foragers.

Informed ecosystem management clearly cannot be accomplished without detailed knowledge of the factors that structured pre-Columbian and historic period environments. Analyses of archaeological vertebrate faunas provide a central avenue for attaining such knowledge and an objective means of evaluating the impacts that native peoples had on prehistoric environments. For many regions of the world, this knowledge resides untapped in museum collections that were derived from archaeological excavations conducted over the last century. The sub-discipline of archaeology is in a unique position to contribute to modern management policies that will ultimately determine the nature of our planet's future environments.

8 Archaeological faunal data may be a source of information for the protohistoric population decline. If such a decline occurred, it should be accompanied by a contraction of the diet breadth and reflected by a protohistoric resurgence in the relative abundances of larger, higher-ranked resources. Bayham (1996) and Chatters (1987; 1996) have provided tantalizing evidence from archaeological vertebrate and mollusc data, respectively, for a late 17th- or 18th-century human population decline in northeastern California.

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