



# Evaluating the Economic Significance of Sharks, Skates, and Rays (Elasmobranchs) in Prehistoric Economies

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Establishing the significance of elasmobranchs in ancient economies is complicated by a variety of biological and taphonomic problems that hinder NISP, MNI, and weight measures and comparisons with other fish or faunal classes. To help address these problems, we present length and live weight estimates for 53 elasmobranch specimens, along with bone weight to edible meat weight ratios for 38 specimens. We argue that quantification is best accomplished using NISP and MNI measures in conjunction with meat weight estimates obtained from modern specimens. These data illustrate the importance of using multiple quantitative measures (i.e., NISP, MNI, weight, etc.) when evaluating the economic significance of various taxa within faunal assemblages.

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## Introduction

During the last 20 years, there has been considerable interest in the development of maritime societies and the role marine resources played in fostering high coastal population densities, sedentism, and cultural complexity (e.g., Moseley, 1975; Perlman, 1980; Yesner, 1980, 1987; Quilter & Stocker, 1983; Glassow & Wilcoxon, 1988; Jones, 1991; Arnold, 1992; Erlandson, 1994). A key issue in understanding such developments is determining the role that fishing played in the evolution of maritime and other aquatic societies, especially the relatively intensive fishing of many Holocene cultures (Walters, 1989; Glassow, 1993; Gobalet & Jones, 1995; Matson & Coupland, 1995; Moss & Erlandson, 1995; Plew, 1996). Crucial to understanding the significance of fishing, of course, is estimation of the economic importance of various types of faunal remains found in archaeological sites (Casteel, 1976; Leach, 1986; Wheeler & Jones, 1989; Colley, 1990; Butler, 1993; Reitz & Wing, 1999).

In coastal regions around the world, a variety of measures including NISP (Number of Identified Specimens), MNI (Minimum Number of Individuals), raw

weight, and meat yield estimates are used to evaluate the abundance of fish, shellfish, birds, mammals, and other faunal classes to human societies. As a number of researchers have pointed out, evaluating the dietary significance of various taxa requires conversion of raw counts, weights, or other zooarchaeological measures to more meaningful nutritional currencies such as calories or edible meat yields. Often faunal data are not directly comparable within or between sites because of variation in the way faunal materials have been quantified. Estimating the significance of fish is often difficult because the remains of many fish preserve relatively poorly, are recovered only by using fine-mesh screens and other labour intensive methods, and are differentially affected by human processing techniques. Sharks, skates, and rays, collectively known as elasmobranchs, are especially problematic because their skeletons are composed primarily of cartilage, which rarely preserves in archaeological sites. Although elasmobranch vertebral centra, teeth, spines, and dermal denticles may be preserved under certain conditions (e.g., in shell middens), quantifying such remains has been difficult due to biological differences between elasmobranchs and bony fishes (Johnson, 1980; Salls,

1988; Masse, 1989; Rick & Glassow, 1999; Rick & Erlandson, 2000). These differences, discussed in detail below, may result in underestimating the economic significance of sharks, skates, and rays.

Despite such problems, it is clear that elasmobranchs were utilized by numerous coastal societies of North America (see Kozuch & Fitzgerald, 1989; Bernstein, 1993; Kozuch, 1993; Erlandson, 1994; Handley, 1996; Broughton, 1997; Rick & Glassow, 1999; Rick & Erlandson, 2000), the Caribbean (Wing & Reitz, 1968), Mesoamerica (DeBorhegyi, 1961), the Pacific Islands (Masse, 1986, 1989; Kirch, 1990), Scandinavia (Rosenlund, 1986), and other regions around the world. Even though elasmobranchs have been identified in coastal archaeological sites throughout the world, reports specifically on elasmobranchs are rare (see Kozuch & Fitzgerald, 1989 & Kozuch, 1993 for significant exceptions). Publications focused on the methods of reconstructing the economic significance of elasmobranchs, moreover, are virtually non-existent. In this paper, we assess current zooarchaeological methods of determining the relative importance of elasmobranchs, presenting live weight estimates, meat yields, and bone-to-meat ratios for some common Pacific and Atlantic Coast elasmobranchs. The practical application of bone-to-meat conversions is demonstrated on two fish assemblages from the southern California Coast.

### A Brief History of Quantifying Coastal Faunal Resources

In the 1970s and 1980s, a number of pivotal publications on quantifying archaeological faunal remains gained widespread attention (Casteel, 1976; Grayson, 1979, 1984; Binford, 1981; Lyman, 1982; Klein & Cruz-Uribe, 1984). These works defined three basic numerical comparative measures, raw weight of remains, NISP, and MNI, which remain the most widely used measures today. Each unit has strengths and weaknesses (see Grayson, 1984; Klein & Cruz-Uribe, 1984; Lyman, 1994; Reitz & Wing, 1999) and its utility may vary depending on the nature of the faunal assemblage studied or the particular research questions investigated (Glassow, 2000). In virtually every case, however, evaluating the economic significance of various faunal taxa using such techniques is complicated by problems associated with differential utilization, preservation, and recovery of archaeological faunal remains. The exclusive use of one technique or another by researchers has sometimes led to difficulties in comparing faunal assemblages within a region or between regions (Mason *et al.*, 1998). In our recent research we have found that an integrated approach to the analysis of faunal collections, in which all three measures (weight, NISP, and MNI) are utilized together, allows for more effective economic evaluations and regional comparisons.

California archaeologists pioneered early attempts to quantify various constituents of coastal shell middens, including the shell and bone refuse from a variety of faunal classes. For decades, such quantification has often relied solely or primarily on comparison of the raw weights of shell and bone (Uhle, 1907; Gifford, 1916; Cook & Treganza, 1950). Simply comparing raw bone and shell weights is highly problematic, however, because various faunal classes (as well as many taxa within classes) have dramatically different ratios of skeletal to edible flesh weights (Tartaglia, 1976; Glassow & Wilcoxon, 1988; Erlandson, 1994).

For better measures of dietary significance, shell- and bone-to-meat weight ratios derived from butchering experiments have been used by many Pacific Coast archaeologists to convert raw bone or shell weights into edible meat yield estimates for comparative analysis of various faunal classes. This method differs from another method championed by White (1953), which relies on average meat yields calculated using MNI. For many coastal California sites, the bone-to-meat method makes maximum use of fragmented faunal remains that are not identifiable to family, genus, or species, bone fragments that often comprise a large proportion of assemblages. Of course, there are numerous problems when comparing numbers from different taxonomic levels (e.g., family versus species; see Driver, 1992). For the "weight method," a multiplier based on the average ratio of dry skeletal weight versus edible meat weight is obtained from modern specimens and is used to convert bone or shell weights into nutritional currencies (see Erlandson, 1994: 57–58). Cook (1946) first used such conversions on shellfish assemblages in California, but the method was being used at roughly the same time in Europe (see Casteel, 1978). Later California archaeologists also used this method (Cook & Treganza, 1950; Meighan, 1959; Koloseike, 1969; Tartaglia, 1976), but these early studies often employed a generic multiplier for whole classes of fauna such as shellfish (see Koloseike, 1969).

Recognizing the crude nature of such economic evaluations, a number of researchers sought to collect more specific data to improve estimates of meat yields from skeletal weights (Koloseike, 1969; Tartaglia, 1976; Ham, 1982; Erlandson, 1988; Glassow & Wilcoxon, 1988; Moss, 1989). Multipliers for numerous shellfish species are now available, but relatively few specific multipliers are available for vertebrate taxa. To improve this method of approximating edible meat yields, better numbers for specific fish, mammals, and birds are needed (Erlandson, 1994: 57–58). The elasmobranch multipliers presented in this paper are one step in this direction. Recognizing that animals of differing size, age, and sex have differential amounts of biomass, meat yield estimates which rely on the principle of allometry have also become popular in recent years (see Schmidt-Nielsen, 1984; Reitz *et al.*, 1987; Barrett, 1993). The allometric technique, like other methods, is best used when sample sizes are large and

multiple individuals of the same species are available for analysis.

Similar to other zooarchaeological methods, results obtained by the weight method should only be used as general approximations of the dietary significance of faunal remains recovered from a site. Such estimates are subject to a variety of sources of error (Casteel, 1978; Lyman, 1982: 359–363; Klein & Cruz-Uribe, 1984: 26–29; Moss, 1989; Brewer, 1992; Barrett, 1993; Erlandson, 1994: 57–58; Mason, Peterson & Tiffany, 1998; Reitz & Wing, 1999). For example, differential bone density within and between taxa affects both the preservation and identifiability of specimens. In other words, different skeletal elements of individual animals, and different quantities (counts and weights) of remains of different taxa have different probabilities of being preserved and identified. Bone leaching, mineralization, and other taphonomic problems also potentially bias estimates produced using the weight method, but these problems also plague other zooarchaeological measures. Despite such problems, numerous Pacific Coast researchers have used the weight method, making it useful for comparative analysis (Clarke & Clarke, 1980; Ham, 1982; Erlandson, 1984, 1991, 1997; Peterson, 1984; Dietz, Hildebrandt & Jones, 1988; Glassow & Wilcoxon, 1988; Moss 1989; Glassow, 1992, 1993; Colten, 1993, 1995; Vellanoweth & Erlandson, 1999; Vellanoweth, Rick & Erlandson, 2000; Tveskov, 2000). It has been used successfully to identify spatial and temporal variation in general subsistence patterns within a region (see Glassow & Wilcoxon, 1988; Erlandson 1994) and may help elucidate other archaeological problems as well (e.g., site disturbances and settlement patterns; see Glassow, 2000). Specifically, it is one of the few methods available to produce integrated estimates of the relative dietary significance of various faunal classes (shellfish, mammal, fish, etc.). Used cautiously in conjunction with other zooarchaeological measures, the weight method can be a valuable comparative method for faunal analysis, especially when a set of sites from a specific region are investigated together (see Moss, 1989; Colten, 1993; Erlandson, 1994; Glassow, 1996).

### Elasmobranch Natural History and Ethnobiology

Because of the unique nature of their mostly cartilaginous skeletons, elasmobranchs pose special problems in interpreting NISP and MNI, but are relatively well suited to bone-to-meat weight conversions. Largely eschewed by North American palates until relatively recently, elasmobranchs have become an increasingly important commercial fishery. There are over 900 known species of Chondrichthyes or cartilaginous fishes (sharks, skates, rays, and ratfish) living in the oceans and freshwater systems of the world (Wourms & Demski, 1993; Last & Stevens, 1994). The elasmobranchs include sharks, skates, and rays, with over 375 species of sharks assigned to at least eight orders, and more than 494 species of skates and rays assigned to five orders (Compagno, 1984a, 1984b, 1988; Wourms & Demski, 1993: 8). Most cartilaginous fishes (55%) are marine, ranging from the intertidal zone to a depth of 200 m and deeper (Wourms & Demski, 1993: 8). Elasmobranchs are found in all of the world's oceans, but are most diverse in tropical and warm-temperate continental marine habitats. A few species are also found in freshwater and hyper-saline habitats. Compared to most bony fishes, sharks grow relatively slowly, have few young, mature late, and do not reproduce every year (Camhi *et al.*, 1998).

The elasmobranch skeleton is almost entirely cartilaginous and lacks true bones (Daniel, 1922; Castro, 1983; Last & Stevens, 1994). However, parts of elasmobranch skeletons—including the skull, spines, and vertebrae—are often strengthened by the deposition of calcium and salts. When this deposition is sufficient, these elements become calcified and resemble bone (Castro, 1983). Cartilage decays relatively rapidly and rarely preserves in palaeontological or archaeological contexts. Consequently, the fossil and archaeological record of elasmobranchs consists almost entirely of spines, dermal denticles, teeth, and vertebral centra. The absence of complete fossil skeletons makes it difficult to trace the evolutionary history of these animals. The oldest evidence for ancient relatives of sharks and rays comes from the Late Silurian-Early Devonian-Carboniferous boundary about 400 million years ago or earlier (Lineaweaver & Backus, 1970; Springer & Gold, 1989: 30; Wourms & Demski, 1993; Stevens, 1999; Grogan & Lund, 2000). They are among the oldest surviving groups of jawed vertebrates and are exceptionally resilient, having survived a number of global extinctions (Wourms & Demski, 1993: 7).

The prevalence of elasmobranchs in the marine environment has made them an attractive and intriguing resource for numerous maritime societies. Elasmobranchs have been identified in coastal archaeological sites around the world and are rich in protein, vitamin A, and oil (Olsen, 1999). On the Pacific Islands, special hooks termed shark hooks were designed to catch these fish (Gudger, 1926). Shark products were also used for a variety of utilitarian purposes. Shark teeth, for example, were important raw materials for producing cutting tools, weapons, and ornaments (see Kozuch, 1993). Shark skin was used for sandpaper and some skins were even tanned. Fossil shark teeth collected from palaeontological deposits, apparently as heirlooms, are also found in archaeological sites. In southern California, elasmobranch centra were used to make beads that are sometimes found in funerary contexts (King, 1990). Handley (1996) maintains that sharks may have held a spiritual role in the northeastern United States, and numerous Hawaiian myths and rituals also involve sharks (Malo, 1951: 82; Westervelt, 1987). Along the Northwest Coast of North America, a

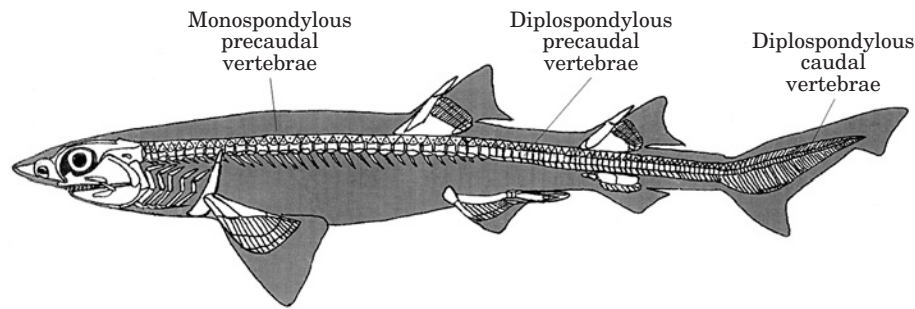


Figure 1. The location of caudal and precaudal vertebrae in sharks (adapted from Compagno, 1999).

variety of skates and sharks were caught for food, but also played an important role in myths and a generic “shark” and dogfish were crests among the Tlingit (Laguna, 1972: 53–54).

### Problems of Quantifying Elasmobranchs

Elasmobranchs, which comprise less than 5% of modern fish species, are differentiated from the bony fishes (Osteichthyes) by their cartilaginous skeleton, the presence of dermal denticles (small tooth-like scales), a skull without sutures, mouths and nostrils that are usually on the underside of the head, and teeth that are continuously replaced or grow with the animal in fused plates (Wheeler & Jones, 1989; Last & Stevens, 1994). The primarily cartilaginous skeleton of elasmobranchs makes them especially problematic for certain types of zooarchaeological analysis. One problem in quantifying elasmobranchs is the low number of ossified and identifiable elements present in their skeletons. Only six types of elements—centra, teeth, dermal denticles, fin ray spines, tail spines, and rostral cartilage—are found in archaeological sites, and some of these are either too small to recover or are not present in all species of elasmobranch. In contrast, Colley (1990: 213) refers to 26 elements from bony fish commonly encountered in archaeological sites that are identifiable to specific taxa. Since most sharks, skates, and rays have far fewer bones than teleosts normally do, comparing NISP values of these two types of fish can be highly misleading.

Other than teeth, cartilaginous fish remains also tend to have few distinct morphological features, which hinders specific identification (Kozuch & Fitzgerald, 1989; Colley, 1990: 215). X-rays of elasmobranch centra may aid in their identification (Wheeler & Jones, 1989; Colley, 1990), but this can be expensive and impractical for many researchers.

Because of the limited number of identifiable elasmobranch elements, it is also more difficult to calculate MNI than for most bony fishes. Elasmobranch teeth, for example, are continually replaced throughout the lifecycle, making them problematic for determining MNI (Kemp, 1999). Some sharks produce as many as 34,000 teeth in a lifetime and may have as many as 280

teeth at any one time (Reitz & Wing, 1999: 47–48). Among the smaller elasmobranchs (shovelnose guitarfish, thornback, smoothhounds, etc.) whose remains are found in Pacific Coast archaeological sites, moreover, the teeth are generally quite small and rarely recovered (Rick & Glassow, 1999). In contrast to teeth and vertebrae, fin ray spines, tail spines, and calcified rostral cartilage occur in known numbers for a limited number of species, and may be used to determine MNI (Kozuch, 1993).

Although vertebrae may also be used in calculating MNI, the number of centra in elasmobranch spinal columns is highly variable (Ridewood, 1921; Daniel, 1922; Clothier, 1950), with centra counts ranging from 60 to over 475 among various species (Springer & Garrick, 1964; Compagno, 1999: 83). The range within a single species varies, but on average is relatively low (see Springer & Garrick, 1964). Elasmobranch centra are cylindrical and biconcave in shape and are generally divided into only two primary types, precaudal and caudal. The number of vertebrae a given individual contains is set during embryonic development when calcification also begins, with precaudal vertebrae generally forming before caudal vertebrae (Figures 1 & 2). The process of calcification is also highly variable, with some species (especially deep-sea and primitive forms) having little calcification while in others the entire spinal column is calcified (Compagno, 1999).

In addition to having relatively high numbers of vertebral centra, the size of centra often varies dramatically down the spinal column (see Cailliet *et al.*, 1983; Cailliet *et al.*, 1985; Natanson & Cailliet, 1990: 1137; Yudin & Cailliet, 1990: 193; and others). In general, precaudal vertebrae are larger, while caudal vertebrae are smaller (Kozuch & Fitzgerald, 1989). Elasmobranch centra also appear to grow throughout the life span of an individual, or at least until an individual reaches maturity (approximately 10–20 years), resulting in a wide range of centra sizes in an individual. Martin & Cailliet (1988: 765), for example, presented diameters for bat ray centra that ranged in size from less than 2 mm to almost 12 mm. The dramatic differences in the size of centra in many elasmobranchs, along with the limited morphological variability found along the spinal column, make it difficult to estimate

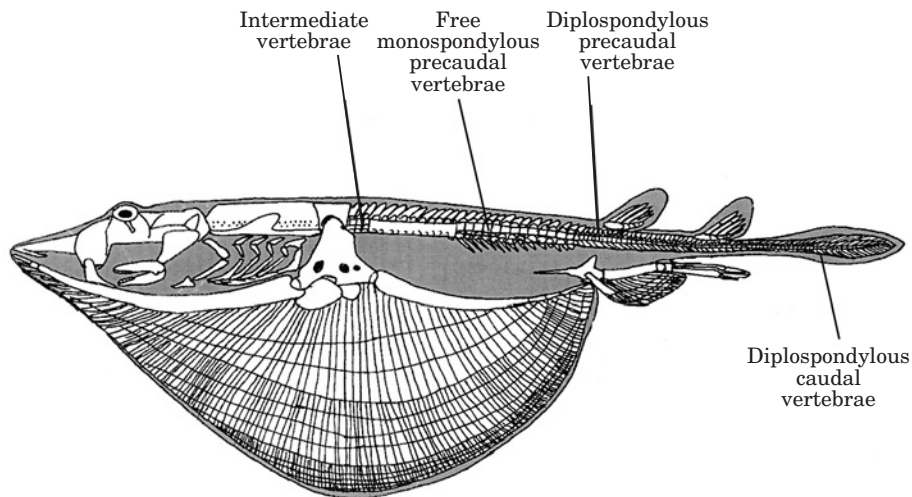


Figure 2. The location of caudal and precaudal vertebrae in rays (adapted from Compagno, 1999).

MNI, body size, or other attributes important to assessing population structure and economic significance. X-ray analyses may help determine elasmobranch age and other attributes, but require highly specialized training, and are often impractical, especially when collections are comprised of fragmentary or weathered specimens (see Cailliet *et al.* 1986).

## Methods

To help circumvent such problems, we use bone-to-meat weight conversions as one method to assess the significance of elasmobranchs within fish and other faunal assemblages. By accounting for the relatively large meat yields for most elasmobranchs, this method helps correct for the general under-representation of elasmobranchs in NISP values. Without correcting for the generally high ratio of edible meat to bone, however, meat weight conversion will also underestimate the significance of most elasmobranchs.

To illustrate the nature of this problem, 22 elasmobranchs caught along the California and Oregon coasts by commercial fisherman, state fish and wildlife staff, and recreational fisherman were obtained and dissected (Table 1). We also present total weights and meat yields for 31 Atlantic Coast elasmobranch specimens, which were obtained and processed by individuals at the Florida Museum of Natural History and the University of Florida (Table 2). The skeletal remains for the Pacific Coast specimens are now housed at the Departments of Anthropology at the University of Oregon and the University of California, Santa Barbara. Because edible meat weights were not recorded for all the elasmobranchs, it was possible to obtain edible meat weights for 38 of the 53 animals. The fish were measured and weighed, and then either processed immediately or frozen for later processing. Except for the California angel shark, all animals were

weighed whole and then butchered. The head of the angel shark was removed by California Department of Fish and Game representatives before measurements were obtained. Although we were unable to obtain the teeth from this animal, it is similar in size to another specimen from the UCSB collection and we used the weight of teeth from this animal to estimate the total bone weight.

The seven Pacific Coast specimens used for meat weight conversions (bat ray, thornback, shovelnose guitarfish, spiny dogfish, angel shark, and brown smoothhound) were processed at the University of Oregon using identical butchering techniques, skeletal preparation, and treatment. The remains were weighed whole to obtain their total weight, then measured, eviscerated, weighed again, and recorded. Each animal was butchered to separate all edible meat from skin, cartilage, and other non-edible body parts. The edible meat weights were recorded, with the type of meat considered edible limited to high-grade pieces of meat devoid of cartilage. Since other body portions (organs, fins, etc.) can also be eaten or used for oil, our estimated edible meat yield conversions are conservative. It should also be noted that shark parts, such as teeth and skin, have important economic uses other than as food and were not accounted for in our study.

Once the animals were measured, butchered, and weighed, the centra, teeth, spines, and dermal denticles were removed and placed in a container for maceration (see Casteel, 1976; Wheeler & Jones, 1989; Colley, 1990). The centra and teeth were soaked in tap water for several weeks until all flesh had been removed from the calcified elements. The remnants were then water-screened over 1.0 mm mesh. Although some teeth and dermal denticles may have been too small to be recovered, these do not represent a significant bias since such tiny elements weigh very little and are unlikely to be recovered by archaeologists. The recovered skeletal elements were thoroughly dried and weighed, then

Table 1. Length (cm), total weight (g), meat weight (g), and conversion ratios for Pacific Coast elasmobranchs

Taxa	Common name	Total length	Total wt.	Eviscerated wt.	Edible meat wt.	Bone wt.	Bone-to-meat multiplier	Total wt./bone ratio
Alopiidae								
<i>Alopias vulpinus</i>	Thresher shark	149	9000	—	—	26.5	—	340:1
Heterodontidae								
<i>Heterodontus francisci</i>	Horn shark	88	5768	—	—	44.3	—	130:1
Myliobatidae								
<i>Myliobatis californica</i>	Bat ray A	120	8629	7301.0	1951.3	9.6	203	899:1
	Bat ray B	120	11,000	—	—	15.3	—	719:1
Platyrrhinidae								
<i>Platyrrhinoidis triseriata</i>	Thornback A	51	631	501.7	169.1	4.5	38	140:1
	Thornback B	61	1800	—	—	7.4	—	243:1
Rajidae								
<i>Raja inornata</i>	California skate	48	780	—	—	2.8	—	279:1
Rhinobatidae								
<i>Rhinobatos productus</i>	Shovelnose guitarfish A	57	720	641.0	151.8	3.1	49	232:1
	Shovelnose guitarfish B	80	2300	—	—	9.1	—	253:1
	Shovelnose guitarfish C	87	—	1669.0	—	9.9	—	—
Scyliorhinidae								
<i>Cephaloscyllium ventriosum</i>	Swell shark	70	2130	—	—	7.8	—	273:1
Squalidae								
<i>Squalus acanthias</i>	Spiny dogfish A	56	396	335.9	144.0	0.9	160	440:1
	Spiny dogfish B	66	1235	1040.7	541.3	—	—	—
	Spiny dogfish C	82	1404	—	—	8.8	—	160:1
Squatinae								
<i>Squatina californica</i>	Angel shark A	91	—	5628.4	2706.4	98.5	28	—
	Angel shark B	109	—	10,600.0	—	134.6	—	—
Triakidae								
<i>Mustelus californicus</i>	Gray smoothhound A	73	—	810.0	—	6.2	—	—
	Gray smoothhound B	72	790	—	—	6.7	—	118:1
<i>Mustelus henlei</i>	Brown smoothhound A	68	1418	870.2	503.1	4.1	123	346:1
	Brown smoothhound B	61	1063	862.6	466.3	3.5	133	304:1
	Brown smoothhound C	82	—	1495	—	9.0	—	—
<i>Triakis semifasciata</i>	Leopard shark	81	1950	—	—	14.2	—	137:1

bone-to-meat yield conversion factors were calculated from the ratio of edible meat weight to skeletal weight for each animal.

## Results

All the elasmobranchs we studied have very high ratios of total weight and edible meat weight to the weight of their bones and teeth. For the 16 Pacific Coast specimens for which total and bone weights were available, skeletal weight averages about 0.3% (1:313) of the total weight, with values ranging from approximately 0.1% (1:899) to 0.8% (1:118). Except for two highly variable spiny dogfish specimens, the calculated total weight to bone weight ratios varied more between taxa than between individuals of the same species. Although the number of specimens remains low, and multiple specimens were available for only five taxa, this suggests (as should be expected) that there is a correlation between bone weight, total weight, and edible meat weights for individuals of the same species.

Though a limited number of Pacific Coast specimens ( $N=7$ ) were processed so meat weight conversions could be calculated, a number of interesting patterns are present. The ratios of edible meat to bone weight

range from 28:1 for angel shark to 203:1 for bat ray, with an average of 105:1. The validity of these results is supported by the similar multipliers obtained from the species for which we had multiple specimens. Dissection of two brown smoothhounds, for instance, which were roughly the same size, produced ratios of 123:1 and 133:1.

The 31 Atlantic Coast elasmobranch specimens also demonstrate that elasmobranchs have unusually high bone-to-meat ratios, with ratios of total weight to bone weight ranging from 41:1 for an Atlantic stingray to 319:1 for a bonnethead shark, and an average ratio of 116:1 for all 31 specimens. The meat multipliers are also high, with an average of 100.2 for all 31 specimens a value that is again much higher than multipliers for fish and other animals traditionally used by zooarchaeologists. There is also consistency in the ratio of edible meat to bone weight between individuals of the same species. The ratios for three silky sharks, for example, are 63:1, 63:1, and 69:1. Similarly, for three bull sharks the ratios are 139:1, 140:1, and 152:1. Ratios for several clearnose skates, Atlantic stingrays, and dusky smoothhounds also demonstrate consistency in the ratio of bone-to-meat weight. These taxa, however, demonstrate some variability between individual

Table 2. Length (cm), total weight (g), meat weight (g), and conversion ratios for Atlantic Coast elasmobranchs

Taxa	FLMNH cat #	Common name	Total length	Total wt.	Edible meat wt.	Bone wt.	Bone-to-meat multiplier	Total wt./bone ratio
<b>Carcharhinidae</b>								
<i>Carcharhinus acronotus</i>	2540	Blacknose shark	60	2910	2540.5	24.5	104	119:1
<i>Carcharhinus acronotus</i>	2547	Blacknose shark	61	2740	2363.7	26.3	90	104:1
<i>Carcharhinus falciformis</i>	2410	Silky shark	85	3090	2693.9	42.6	63	73:1
<i>Carcharhinus falciformis</i>	3087	Silky shark	92	4218	3736.0	54.0	69	78:1
<i>Carcharhinus falciformis</i>	3088	Silky shark	89	3920	3479.2	55.6	63	71:1
<i>Carcharhinus isodon</i>	2718	Finetooth shark	78	2240	1906.0	19.4	98	115:1
<i>Carcharhinus isodon</i>	2719	Finetooth shark	77	2233	1909.9	21.9	87	102:1
<i>Carcharhinus isodon</i>	2720	Finetooth shark	76	1975	1738.0	13.9	125	142:1
<i>Carcharhinus leucas</i>	5425	Bull shark	80	2200	1750.0	12.6	139	175:1
<i>Carcharhinus leucas</i>	5426	Bull shark	79	2200	1740.0	12.4	140	177:1
<i>Carcharhinus leucas</i>	5427	Bull shark	80	2370	1848.0	12.2	152	194:1
<i>Carcharhinus limbatus</i>	3498	Blacktip shark	38	221	195.2	3.0	65	74:1
<i>Carcharhinus limbatus</i>	3500	Blacktip shark	40	257	231.3	3.9	59	66:1
<b>Dasyatidae</b>								
<i>Dasyatis sabina</i>	1604	Atlantic stingray	70	680	606.1	13.9	44	49:1
<i>Dasyatis sabina</i>	2777	Atlantic stingray	70	660	651.0	9.2	71	72:1
<i>Dasyatis sabina</i>	1665	Atlantic stingray	53	520	460.5	12.6	37	41:1
<i>Dasyatis sabina</i>	2865	Atlantic stingray	36	300	245.0	4.2	58	71:1
<i>Dasyatis sabina</i>	3248	Atlantic stingray	43	321	274.5	1.5	183	214:1
<b>Triakidae</b>								
<i>Mustelus canis</i>	1654B	Dusky smoothhound	62	730	641.3	5.7	113	128:1
<i>Mustelus canis</i>	1654A	Dusky smoothhound	66	770	678.8	9.2	74	84:1
<i>Mustelus canis</i>	3501	Dusky smoothhound	28	39	34.1	0.4	85	98:1
<i>Mustelus canis</i>	3502	Dusky smoothhound	28	41	36.5	0.3	122	137:1
<b>Rajidae</b>								
<i>Raja eglanteria</i>	3702	Clearnose skate	50	910	774.1	7.2	108	126:1
<i>Raja eglanteria</i>	3821	Clearnose skate	41	215	201.6	1.1	183	195:1
<i>Raja eglanteria</i>	3822	Clearnose skate	71	1330	1107.0	10.6	104	125:1
<i>Raja eglanteria</i>	3824	Clearnose skate	57	803	741.9	9.1	82	88:1
<i>Raja eglanteria</i>	3825	Clearnose skate	69	1020	870.5	7.5	116	136:1
<b>Sphyrnidae</b>								
<i>Sphyrna tiburo</i>	1653A	Bonnethead shark	66	1020	916.8	3.2	287	319:1
<i>Sphyrna tiburo</i>	1653C	Bonnethead shark	60	700	626.5	8.5	74	82:1
<i>Sphyrna tiburo</i>	1653B	Bonnethead shark	62	750	670.8	9.2	73	82:1
<i>Sphyrna tiburo</i>	2546	Bonnethead shark	69	2990	2472.5	67.5	37	44:1

\*All specimens obtained from Florida Museum of Natural History/University of Florida web catalog located at [http://www.flmnh.ufl.edu/db/zooFshy\\_pub.htm](http://www.flmnh.ufl.edu/db/zooFshy_pub.htm). All specimens were collected from Florida, Georgia, or the Caribbean, but many have worldwide distributions.

ratios, a factor that may be related to the size, age, or sex of an individual. These results nonetheless illustrate the high meat yields of elasmobranchs in relation to the overall weight of their calcified skeletons and demonstrate consistency between individuals of the same species.

Most of our elasmobranch ratios are also significantly higher than those reported for Pacific Coast Osteichthyes (Table 3, Figure 3). Tartaglia (1976: 165, 170) reported four ratios of 24.1:1 (black perch), 25.5:1 (turbot), 28:1 (white croaker), and 30.6:1 (California halibut), averaging 27.7:1. This average value, comparable only to the angel shark, is the most common multiplier used by California archaeologists to estimate the meat yield of archaeological fish bone using the weight method (see Glassow & Wilcoxon, 1988; Colten, 1993; Erlandson, 1994). Moss (1989) also reported edible meat-to-bone ratios for two Pacific Coast bony fishes, salmon (38.8:1) and herring (46.2:1). These ratios are higher than those suggested by

Table 3. Calculated ratio of edible meat to bone weight for Pacific Coast specimens (N=16) discussed in text and Figure 3

#	Taxa	Edible meat wt.: bone wt.	Log edible meat
1	Bat ray	203:1	2.31
2	Spiny dogfish	160:1	2.20
3	Brown smoothhound	133:1	2.12
4	Brown smoothhound	123:1	2.09
5	Shovelnose guitarfish	49:1	1.69
6	Herring	46:1	1.66
7	Salmon	39:1	1.59
8	Thornback	38:1	1.58
9	California halibut	30:1	1.48
10	Angel shark	28:1	1.45
11	White croaker	28:1	1.45
12	Turbot	26:1	1.41
13	Black perch	24:1	1.38
14	Sole	19:1	1.28
15	Pacific sanddab	10:1	1.00
16	Greenstriped rockfish	4:1	0.60

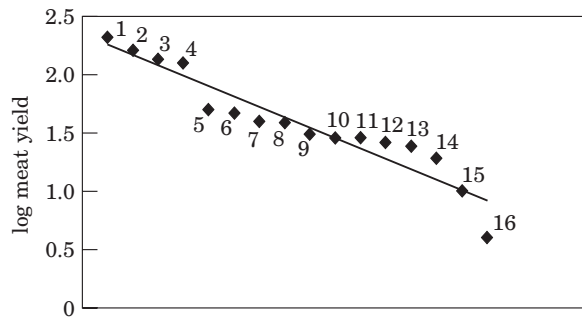


Figure 3. The relationship between edible meat and bone weight of elasmobranchs and teleosts. See Table 3 for key.

Tartaglia (1976), but still represent only 37% and 44% of our average elasmobranch value. As part of this study, Rick calculated edible meat-to-bone ratios for three Pacific Coast teleosts using the same procedures as the elasmobranchs. The first, a Dover sole (*Microstomus pacificus*) from the Oregon Coast, produced a ratio of 18.8:1. The second, a Pacific sanddab (*Citharichthys sordidus*) from southern California, produced a ratio of 10.1:1. The third, a greenstriped rockfish (*Sebastes elongatus*) from Oregon waters, produced an unusually low meat-to-bone ratio of 4.4:1.

Together, these elasmobranch and teleost data suggest that edible meat-to-bone ratios for fishes vary dramatically between species and that elasmobranchs generally have much higher ratios than teleosts. They also suggest, however, that archaeologists using generic conversion factors to estimate the nutritional yield of archaeological fish bone would be wise to evaluate the specific nature of their fish bone assemblages and adjust their calculations accordingly. Similar to NISP measures, weight method evaluations of the economic significance of fish using generic teleost multipliers will significantly underestimate the importance of elasmobranchs.

Our results also illustrate that elasmobranchs generally have higher ratios of edible meat to NISP than most common bony fishes. Our data also demonstrate that brown smoothhounds and California thornbacks have ratios of edible meat to NISP of 3.8:1 and 1:1.1 respectively, compared to 1:2 for a greenstriped rockfish and 1:2.4 for Dover sole. This suggests that comparisons of the abundance of teleost versus elasmobranch fish by NISP, and therefore MNI, are heavily biased towards teleost fish. This does not mean that a limited number of elasmobranch bones necessarily indicates that they were more important than teleosts—in most cases in California they probably were not. It does suggest, however, that large amounts of edible meat found on elasmobranchs should be factored into economic interpretations. A thorough analysis would look at all measures, NISP, MNI, raw weight, and meat yields collectively to deduce the most accurate conclusions.

## Discussion

The significance of these results can be illustrated with two brief archaeological examples from the California Coast. During the Early and Middle Holocene, many large estuaries existed along the southern California Coast. Where present, these estuaries were a focal point of settlement and subsistence, producing numerous shell middens rich in estuarine fish and shellfish (Erlandson, 1994). The protected sandy bottom environments of bays and estuaries are ideal environments for a number of small to medium-sized elasmobranchs, including shovelnose guitarfish, rays, and smoothhounds (Eschmeyer, Herald & Hammann, 1983).

CA-SBA-2057 is an 8200 year old shell midden from the western Santa Barbara Coast located near a small palaeoestuary. Rick & Erlandson (2000) analysed 3080 fish bones from the site, of which just 32 (about 1%) were from elasmobranchs. Fifteen identifiable elasmobranch elements are from at least six distinct taxa, and 1025 identifiable specimens represent at least 9 teleosts. Bony fish, therefore, make up roughly 99% of both the identifiable and total NISP for fish. With MNI values of 29 teleost fish and just six elasmobranchs, teleosts comprise roughly 83% of the MNI for all fish recovered from CA-SBA-2057.

Using Tartaglia's average bone-to-meat ratio for several southern California fish species, Erlandson (1994: 154, 158) estimated that fish provided roughly 13% of the edible meat represented in the faunal sample recovered, with elasmobranchs providing roughly 2% of the fish total. Recognizing the high meat yields of elasmobranchs, and using a larger sample of fish remains from the site, we estimated the meat yields for the teleosts and elasmobranchs using multipliers presented in Table 4. The results suggest that elasmobranchs supplied roughly 35% of the total fish meat yield, roughly 3-4 times more than the use of Tartaglia's generic multiplier suggested. Increases in the estimated nutritional contribution of stingray (5.5 times) and bat ray (5 times) were even more dramatic.

The NISP, MNI, and weight methods produced three different values. As expected, elasmobranchs represent less than one percent of the total NISP. This is not surprising, since many bony fishes have several hundred individual bones (see Wheeler & Jones, 1989), while some of the elasmobranchs have only 60 centra (Springer & Garrick, 1964). The MNI and weight method results, however, are more similar, with elasmobranchs accounting for roughly 17% of the MNI, and 35% of the edible meat. Since most of the teleost MNI consisted of relatively small clupeid fish (sardines, etc.) that are significantly smaller than the elasmobranchs represented, we suspect that the higher values derived from our bone-to-meat weight conversions better estimate the economic significance of sharks and rays. By using all three methods, Rick &

Table 4. Dietary significance of fish from CA-SBA-2057\*

Taxon	Multiplier	Bone wt.	Meat wt.	%Meat
Osteichthyes**	27.7	25.14	696.4	64.6
Elasmobranch sp.	114.6	0.39	44.7	4.1
Bat ray	203.0	0.38	77.1	7.2
California thornback	38.0	0.03	1.1	0.1
Shovelnose guitarfish	49.0	0.04	2.0	0.2
Spiny dogfish	160.0	<0.01	1.6	0.2
Smoothhound family	123.0	1.97	242.3	22.5
Stingray	203.0	0.06	12.2	1.1
Elasmobranch subtotal		2.88	381.0	35.4
Total		28.02	1077.4	

\*All weights in grams, for unit 1, bulk sample 1 and 2 (Rick & Erlandson, 2000).

\*\*The Osteichthyes multiplier was obtained from Tartaglia (1976). The multiplier for the elasmobranch species is an average of all five multipliers. The smoothhound multiplier is from brown smoothhound, and the stingray multiplier is from bat ray.

Table 5. Dietary significance of fish from CA-SBA-53\*

	Multiplier**	Unit 1		Unit 2		Unit 3		Total	
		Wt.	Meat yield	Wt.	Meat yield	Wt.	Meat yield	Wt.	% Meat
Osteichthyes	27.7	46.9	1299.13	35.2	975.0	65.5	1814.35	4088.48	60.0
Elasmobranch	80.5	10.1	813.05	8.2	660.1	15.5	1247.75	2720.9	40.0
Total		57.0	2112.18	43.4	1635.1	81.0	3062.1	6809.38	100

\*All weights in grams for each unit, levels 0–90 cm (Rick & Glassow, 1999).

\*\*The Osteichthyes multiplier was obtained from Tartaglia (1976). The elasmobranch multiplier is an average of brown smoothhound and California thornback.

Erlandson (2000) illustrated that elasmobranchs were an important component of an Early Holocene fishing industry at CA-SBA-2057, despite the very small number of elements recovered.

For the 5000 year old site of CA-SBA-53, Rick & Glassow (1999) analysed over 5000 fish bones representing 18 teleost taxa and five elasmobranchs. Of these, 991 identifiable bones were from teleosts (73%) and 372 from elasmobranchs (27%). Bony fish comprise roughly 81% of the fish bone weight totals, while elasmobranchs provide about 19%. At least 68 individuals, including 53 (78%) teleosts and 15 (22%) elasmobranchs were identified in the assemblage. Using an elasmobranch multiplier that averaged values from brown smoothhound and thornback, however, Rick & Glassow (1999) estimated that teleosts provided roughly 60% of the edible fish meat and elasmobranchs approximately 40% (Table 5).

At CA-SBA-53, the NISP and MNI calculations are roughly comparable, but the estimated meat yield of elasmobranchs is nearly twice the value of the other measures. Due to the methods used, the MNI are probably substantially lower than the number of fish actually deposited. All the fish remains analysed by Rick & Glassow (1999) are from three units dug in 20 cm arbitrary levels to a depth of 90 cm. Because of

stratigraphic mixing from bioturbation, the NISP of each individual taxon was added together for the entire unit to calculate the MNI. In all three units, vertebral counts from shovelnose guitarfish and stingray ranged between 33 and 52 per unit. It seems improbable that all these remains are from one individual scattered throughout a 1 m × 1 m unit. Due to variation in the centra sizes of individual elasmobranchs (see Kozuch & Fitzgerald, 1989: 148), however, it was not possible to precisely distinguish between individuals on criteria other than counts. Assuming the MNI values are underestimated, the percentage may actually be higher. By using all three measures, however, we were able to get around some of the limitations or biases in each of the data sets, and estimate that elasmobranchs probably provided between about 25% and 40% of the edible fish flesh represented in this faunal sample.

## Summary and Conclusions

Elasmobranchs are a unique group of animals encountered in archaeological deposits. Their mostly cartilaginous skeletons leave them underrepresented in measures such as bone weight, NISP, and MNI. Total weight estimates are problematic due to difficulties in

differentiating between discrete elements and estimating the size of individuals represented. Vertebral centra, teeth, spines, and dermal denticles are the most conspicuous shark parts that preserve in archaeological deposits. In contrast to the limited number of bony elements, elasmobranchs contain large quantities of edible meat, vitamin A, oil, and various other useable materials (Olsen, 1999). Consequently, elasmobranchs have played a significant role in many coastal fisheries around the world.

Quantifying the remains of elasmobranchs found in archaeological sites, however, has long been difficult. Because of the small number of bones and identifiable elements most elasmobranchs contain, they tend to be under-represented by traditional quantitative measures such as NISP, MNI, and bone weight. Our studies of Pacific and Atlantic Coast fish, although limited to a relatively small number of individuals and taxa, demonstrate that many elasmobranchs have unusually high ratios of edible flesh to skeletal weights. Consequently, the generic bone-to-meat conversions for Pacific Coast fish used by archaeologists tend to underestimate the economic significance of sharks, skates, and rays, and may underestimate the overall significance of fish in assemblages where elasmobranchs are abundant.

In coastal shell middens, bone-to-meat weight measures derived from dissection of modern elasmobranch specimens can be valuable aids in the zooarchaeological analysis of fish assemblages. This is particularly true when weight method assessments are used to complement NISP and MNI measures, as they produce values that account for the unusually high meat yield of elasmobranchs. Nonetheless, further research should focus on obtaining weight and meat yield information from a wider variety of vertebrates. By expanding the sample of elasmobranchs to include a wider range of individuals of differing age, sex, and size, effective allometric formulas may also be calculated and might add yet another technique to evaluate the economic significance of elasmobranchs.

The complexity of quantifying elasmobranchs is an important cautionary tale for faunal analysts. Similar problems may affect fish assemblages where sturgeon, lamprey “eels,” or other primarily cartilaginous fishes were a significant food source. In addition, zooarchaeologists have long recognized that faunal remains are subject to a variety of agents—diagenesis, bioturbation, butchering practices, decalcification, etc.—that often hinder comparative analyses of different faunal classes (i.e., birds, fish, mammals, etc.). After acknowledging these problems, many faunal analysts often draw conclusions based primarily on NISP and MNI, with minimal emphasis on the problems associated with these methods. As we have demonstrated, bone-to-meat weight measures reveal one more aspect of faunal assemblages. We argue that multiple quantitative measures should be used to deduce a more complete evaluation of the economic importance of various taxa.

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