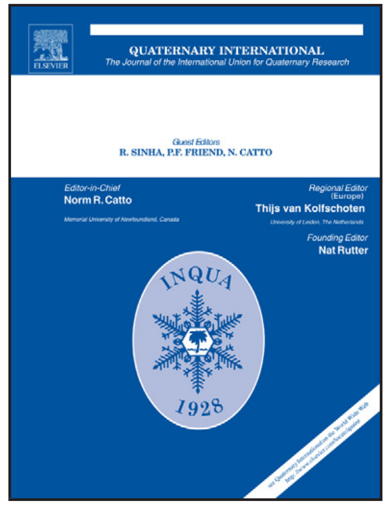


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PII: S1040-6182(08)00004-9
DOI: doi:10.1016/j.quaint.2008.01.002
Reference: JQI 1747

To appear in: *Quaternary International*

Cite this article as: Richard Cooke and Máximo Jiménez, Pre-columbian use of Freshwater fish in the Santa Maria Biogeographical Province, Panama, *Quaternary International* (2008), doi:10.1016/j.quaint.2008.01.002

# Pre-Columbian use of Freshwater Fish in the Santa Maria Biogeographical Province, Panama

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**Abstract**

Freshwater fish faunas on the Isthmus of Panama are less diverse than those of the great South American river basins. Few freshwater species attain a large size (>500 g). The largest species regularly caught today in the lower freshwater sections of many Panamanian rivers are of marine origin. Freshwater fish species diversity and biomass decline rapidly with altitude particularly on the Pacific watershed. Historically, people living inland have compensated for this deficiency by consuming salted and dried marine fish. In four drainages in the Santa María Biogeographical Province that abut onto Parita Bay (central Pacific Panama), archaeologists have recovered well-preserved fish faunas dating from the Late Preceramic period (7000-5000 uncalibrated $^{14}C$ years BP) to Spanish contact in AD 1515-20. Freshwater fish are scarce at most of these sites because they are – or were – located near the coast. Two more inland sites have produced significant samples of freshwater fish bones: a rock-shelter (Aguadulce Shelter, 7000-2500 BP) and a village (Sitio Sierra, 1800-1500 BP). At the Aguadulce Shelter freshwater fish remains represent about 50% of the taxonomically diagnostic teleost bone samples (> 1.5 mm mesh) and at Sitio Sierra, 23% (>3.2 mm mesh). Twelve genera from ten families, probably representing twelve species of primary and secondary freshwater fish, have been recorded. Pre-Columbian communities preferentially consumed tiger-fish (*Hoplias microlepis*), silver catfish (*Rhamdia quelen*) and driftwood catfish (*Trachelyopterus amblops*). Although these are predatory species that readily take hooks, archaeological evidence for hook-and-line fishing is lacking. Since people living in the study area use poison for fishing today (e.g. *Dioscorea* spp.) this method may have been used in pre-Columbian times. Archaeozoological data shed light on the timing of westward migrations of fish species hypothesized to have taken advantage of Pleistocene river anastomosis to cross watersheds during periods of lowered sea level. No archaeofaunas of Pleistocene age are available. However, the presence of the driftwood catfish in Late Preceramic layers at the Aguadulce Shelter indicate that this species had moved into the Santa María drainage of the Santa María Biogeographical Province (SMBP) by 7000-4500 BP. Another South American species, a gar characin (*Ctenolucius beani*), is present in Early Ceramic (4500-2500 BP) deposits at the Aguadulce Shelter and also Monagrillo (4500-3300 BP) in the Parita drainage of the same province.

*Key words: Archaeozoology; prehistoric fishing; freshwater fish; biogeography; Panama.*



## 1. Introduction

Freshwater fish are abundant and diverse in the great river basins of South America east of the Andes. It is to be expected, therefore, that fishing in rivers and flood-plains was not only a primary subsistence activity during pre-Columbian times on this continent, but also an important influence upon settlement location, population density, trade relations, and political control (Erickson, 2000; Heckenberger et al., 1999; Schaan, 2004). In the narrowest parts of the Central American isthmus (southern Nicaragua, Costa

Rica and Panama), the situation is quite different. Most rivers are short and fast-flowing, and have narrow flood-plains. Fish diversity and biomass are considerably lower than in South American rivers except for stretches nearest the sea, which are subject to tidal influence and attract several species of marine origin. The fact that freshwater fish diversity and biomass also decline rapidly with altitude (Hildebrand, 1938) was made apparent to Cooke on a recent visit to Casita de Piedra, a pre-Ceramic site (6800-4300 BP) located four km south of the Continental Divide at 754 m above sea level (Figure 1; Ranere, 1980a, 1980b). The mountain mullet (*Agonostomus monticola*) is the only fish species that local people capture today in the vicinity of this early agricultural site (Dickau et al., 2007). It is a marine species that spends all its adult life in fresh water (Aiken, 1998). Though widely used for food elsewhere in tropical America (Torres-Navarro and Lyons, 1999), it rarely exceeds 250 mm in length. In fast-running streams it is a frenetic swimmer that is difficult to catch in large numbers (Kenny, 1995). It is an adjunct to the diet, rather than a staple. (The English names used for species in this paper are taken from *www.fishbase.org, www.scotcat.com*, and *www.annual.sp2000.org*).

The sediments deposited at Casita de Piedra did not produce a sliver of vertebrate bone (Ranere, 1980b). Nor did middens at several villages occupied after ~2800 BP to the west of this site in the vicinity of the Barú volcano (Figure 1; Linares and Sheets, 1980). Therefore archaeologists cannot prove that mountain mullet were fished in the western highlands of Panama (Chiriquí) in pre-Columbian times even though the modern situation suggests that they were. Nor can archaeozoological data demonstrate that pre-Columbian communities here consumed marine fish dried and salted on the Pacific coast and transported inland on peoples' backs - a practice described in Spanish contact-period chronicles (e.g., Fernández de Oviedo, 1853:140). In the Santa María and Coclé del Sur drainages further east, however, marine fish bones have been recorded at sites between 20 and 60 km inland from the Pacific coast. This suggests that preserved marine fish indeed compensated for the poor returns of freshwater fishing at higher elevations on the Panamanian isthmus (Cooke, 2001; Zohar and Cooke, 1997).

## 2. Pre-Columbian fishing in the Santa María Biogeographical Province

Pre-Columbian middens at archaeological sites located in the Santa María Biogeographical Province (henceforth SMBP) on the central Pacific slopes of Panama contain abundant and well-preserved fish remains that permit accurate taxonomic and anatomical identifications. These sites range in time from the Early Preceramic period (7000-4500 BP) to Spanish contact (AD 1515-20) (Cooke and Jiménez, 2004; Cooke and Ranere, 1999; Jiménez and Cooke, 2001). (All dates are in uncalibrated $^{14}C$ years BP). For summaries of the regional archaeological sequence, see Cooke, 2005; Cooke and Ranere, 1992; and Cooke and Sánchez-Herrera, 2004.

Bones and otoliths of primary or secondary freshwater fish were recorded at nine sites located in four drainages within the SMBP, from east to west: Coclé del Sur, Santa María, Parita, and La Villa (Figures 1 and 2). Primary freshwater fishes are physiologically intolerant of saline conditions and therefore rarely move through marine waters. Secondary freshwater fishes tolerate low or moderate salinity and are believed to be capable of moving from along the coast (Myers, 1966; Smith and Bermingham, 2005). (In Figures 2 and 5, primary freshwater species are identified with ‘1’ and secondary freshwater species with ‘2’). In addition, several marine species recorded in the archaeofaunal samples are considered to frequent fresh water habitats. The most important from a dietary point of view are three sleepers - fat sleeper (*Dormitator latifrons*), spotted sleeper (*Eleotris picta*) and Pacific sleeper (*Gobiomorus maculatus*). These are strongly euryhaline marine species, i.e., they have the ability to tolerate a wide range of salinity conditions (Figure 2).

**3. Recovery Methods and Sampling Bias**

The archaeofaunas under consideration were studied over the period 1969-2006. Recovery techniques were uneven and negatively affect the objectivity of the comparisons and inferences. The fish remains from Natá (Na8) were recovered over a ¼" mesh (6.4 mm). The samples from Cerro Mangote (CM), Monagrillo (He5), Sitio Sierra (Ag3), Vampiros-1 (Ag145), La Mula-Sarigua (LMS), and Cerro Juan Díaz (CJD) were collected over 1/8-inch (3.2 mm) metal mesh screens (samples from above finer meshes are under study). Samples from the Aguadulce Shelter and the Cueva de los Ladrones were hand-picked in the laboratory out of sediments that were washed over 1/16" window screen (1.5 mm). It is to be assumed, therefore, that the largest sample of freshwater fish bones (from Sitio Sierra, N - 3843) over-estimates the importance of larger taxa and larger individuals of freshwater fish vis-à-vis the second largest sample (Aguadulce Shelter, N - 503), which was collected over 1.5 mm meshes. Nineteen of the 46 freshwater species recorded in the SMBP for which we possess biometric data do not exceed 100 mm total length (Figure 3). Further revision of bones recovered beneath 1.5 mm meshes at all sites is required to determine the presence or absence of these very small species. Of course, small size alone does not disqualify a fish species as a human food source. Christopher Columbus' son, Ferdinand, witnessed the capture of very small fish he called "tití" in the Caribbean rivers of Panama (Columbus, 1959). Presumably he was referring to the small goby, *Sicydium*, whose post-larvae migrate seasonally up rivers and are harvested in Panama and world-wide (Bell, 1999). People living in inland communities on the Azuero Peninsula catch tiny pipe-fish (probably *Pseudophallus*) with scoop nets as they congregate seasonally in small rivers and streams (Cooke, personal observation).

**4. Comparative Skeleton Collections**

The fish bone samples were identified using reference collections of fish skeletons housed at the Smithsonian Tropical Research Institute (STRI) archaeology laboratory in Panama City. All skeletons were collected in Panamanian waters. Figure 3 lists the numbers of prepared skeletons available for each species, and the size ranges of specimens (standard and/or total lengths in mm). It also presents length and weight data for primary and secondary freshwater fish recorded in the SMBP (Cooke and Tapia-Rodríguez, 1994; STRI Fish Collection, supervisor: E. Bermingham).

**5. Taxonomy and Nomenclature**

The taxonomy of Neotropical freshwater fish has undergone considerable reorganization since the archaeofaunal samples were recovered. This is due to (1) improved biological survey coverage, and (2) the reconstruction of phylogenies and inter-drainage and inter-regional relationships based on molecular data (e.g., Bermingham and Martin, 1998; Bermingham et al., 1997; Martin and Bermingham, 1998, 2000; Perdices et al., 2002; Smith and Bermingham, 2005; Smith et al., 2004). To avoid confusion, Figure 4 lists alternative names which have been used for some of the recorded freshwater fish taxa in recent biology and archaeozoology publications. The most extreme revision concerns the ubiquitous spiny armored catfish, which has been transferred from genus *Hypostomus* to genus *Hemiancistrus* (Isbrücker, 2001).

Assignation of bone elements to species assumes that the species present in the four study drainages between 7000 and 500 BP are the same ones that are present there today. Ten of the twelve genera identified appear to be represented by a single species even though the precise taxonomic status and genetic affiliations of some of these are not necessarily established or accepted. This is true for the regional tiger-fish species, which is currently assumed to be *H. microlepis*, but may represent a genetically distinct population or populations (differentiated by drainage). *Astyanax* and *Rhamdia* contain more than one species in the SMBP. *R. quelen* is the only *Rhamdia* species that Bermingham and his colleagues collected in the Santa María drainage. All the skeletons prepared from *Rhamdia* specimens obtained in the SMBP, originally identified as *R. guatemalensis,* are assumed to be referable to *R. quelen. R. laticauda* has been collected in other SMBP drainages, but only in fast-flowing mountain streams. We do not have access to a skeleton of this species. However, it was probably not present within the foraging catchments of the studied sites. Consequently, silver catfish elements are referred to *Rhamdia cf. quelen*.

The false sculptured sea-catfish (*Notarius cookei*) – a marine species that frequents fresh water - was recognized osteologically as a distinct species several years ago (Cooke, 1993, 1998), but it was not described until 2002 (Acero and Betancur, 2002) as "*Arius cookei*" (see Betancur et al., 2007, for an updated revision of New World sea catfish [Ariidae]).

**6. Freshwater fish and fishing around Parita Bay**

Primary and secondary freshwater fish are minimally represented at four of the sampled pre-Columbian sites: Cerro Mangote (7000-5000 BP), Monagrillo (He-5) (4500-3300 BP), Vampiros-1 (Ag-145) (~2200 BP), and La Mula-Sarigua (2200-1800 BP) (Figure 2). At these sites they represent <1% of taxonomically diagnostic teleost bones (identified to family and below). This very low frequency is predictable given the fact that all these sites were located on or very near the active marine shore when they were viable pre-Spanish communities. The presence of a few freshwater fish in these archaeofaunas may not have resulted from occasional and intentional fishing in fresh water, but rather from the natural flushing of freshwater species towards a river's marine outlet during periods of strong sediment discharge. Spiny armored catfish (*Hemiancistrus aspidolepis),* silver catfish (*Rhamdia cf quelen*), driftwood catfish (*Trachelyopterus amblops*) and glass knife-fish (*Sternopygus macrurus*) were captured in the lower tidal and oligo- to mesohaline sections of the River Santa Maria during a survey of marine fish diadromy (Cooke and Tapia-Rodríguez, 1994).

On the other hand, freshwater fish were an important food resource at two sites located in the narrow coastal plain adjacent to Parita Bay: Aguadulce Shelter and Sitio Sierra. These two sites are only seven kilometers apart, but are chronologically and functionally dissimilar. The aquatic habitats closest to each one are different. The Aguadulce Shelter is located alongside a perennial stream (the "River" Membrillar). It was presumably occupied by small groups (perhaps single families) during its long occupation (7000-2500 BP). Sitio Sierra was a large nucleated village with pole-and-thatch houses (contiguous cultural materials cover 45 hectares). It was occupied, probably continually, from 2200 BP to Spanish contact. It is adjacent to a freshwater section of the longest river in the SMBP (the Santa María) (Cooke, 1979, 1984; Isaza-Aizuprúa, 1993).

At the Aguadulce Shelter, 503 freshwater fish bones were recovered representing 52% of the taxonomically diagnostic teleost bone sample. Although this small overhang is now about 18 km inland from the active coastline, a model for sedimentation rates in the Santa María river delta, in whose catchment this site lies, suggests that salt-water habitats were closer than today during the Late Preceramic (7000-4500 BP) and Early Ceramic periods (4500-2500 BP) during which middens accumulated under and in front of the overhang (Clary et al. 1984; Piperno et al., 2000; Ranere and Hansell, 1978). The samples collected by Ranere in 1973 and 1975 have been assigned to either the Late Preceramic or Early Ceramic periods by stratigraphical association supported by $^{14}C$ dates. The sample recovered in 1997 (Piperno et al. 2000) has not yet been compared to site formation processes and therefore cannot be assigned to period (Figure 2).

Three thousand eight hundred and forty-three freshwater fish bones were recorded in a midden at Sitio Sierra (75-B-2) thought to have accumulated between 1800 and 1500 BP on the basis of pottery typology (Cooke and Ranere, 1999; Isaza-Aizuprúa, 1993). These represent 23% of diagnostic teleost fish bones in this sample (Figure 2). Sitio Sierra is now 12.5 km from the Parita Bay coast line, but would have been about ca 1.5 km closer to the sea between 1800 and 1500 BP. The River Santa María runs fresh at this point, but is subject to weak tidal influences (Cooke and Tapia-Rodríguez, 1994).

Ten fish bones representing eight freshwater genera were recovered in a small teleost sample (N-25) recovered in a 0.5 $m^2$ column taken from an Early Ceramic (Monagrillo Phase) midden at Cueva de los Ladrones, now located 25 km from the Parita

Bay coast at the head of a very small, but perennial stream. This sample was deposited between 4500 and 2500 BP (Cooke, 1984, 1995). It is the only one which has reported the ubiquitous and speciose small characid genus, *Astyanax*. Three freshwater fish elements were recovered at Natá (Na8), a village on the River Chico (Coclé del Sur drainage), which was occupied between 1000 BP and Spanish contact (Cooke, 1979). Large (6.4 mm) screens were used. Only silver catfish (*Rhamdia cf quelen*) and swamp eel (*Synbranchus marmoratus*) were reported here.

The much more significant samples from the Aguadulce Shelter and Sitio Sierra invite comparison even though they were recovered in different ways. Each site reported ten genera and therefore (assumed) ten species of primary and secondary freshwater fish (Figure 5). Two species that were not shared by both sites are present in minimal numbers (<1% NISP [number of identified specimens]): royal twig catfish (*Sturisoma panamense*) at the Aguadulce Shelter, and Siebold's mojarra (*Tomocichla sieboldii*) at Sitio Sierra. Predictably, in view of the use of finer screens at the Aguadulce Shelter, two small species with fragile bones, the carp headstander (*Cyphocharax magdalenae*) and "chogorro" (*Aequidens coeruleopunctantus*), are more frequent at this site than at Sitio Sierra. Sagittal otoliths, vertebrae and cranial bones of small individuals of these species were identified (body mass estimated by comparison with modern skeletons between 5 and 25 g, total length [TL]=50-125 mm) (Figure 6 a,b).

Nonetheless, the two samples allude to similar cultural choices in other aspects of fishing. Three species are dominant at both sites: tiger-fish (*Hoplias sp*.), silver catfish (*Rhamdia cf quelen*), and driftwood catfish (*Trachelyopterus amblops*). These three species represent 69% freshwater fish NISP at Aguadulce and 90% at Sitio Sierra. Since tiger-fish and silver catfish grow to larger sizes than any other SMBP freshwater species (except the spiny armored catfish), selective fishing for them is to be expected. Allometric predictions calculated with the basioccipital and third vertebra suggest that over half the estimated 49 tiger-fish individuals at Sitio Sierra had body masses between 150 g and 400 g and total lengths of 125-295 mm; four individuals are estimated to have weighed between 500 g and 1000 g (total length: 310-360 mm). Silver catfish do not grow as large in isthmian rivers as tiger-fish. However, four specimens out of an estimated MNI (minimum number of individuals) of 23 at Sitio Sierra have body masses of 300-400 g and TL of ca. 340-380 mm, based on visual comparison of bones with specimens in the comparative skeleton collection.

MNIs were first calculated on the basis of the most frequent element, taking paired elements into consideration. This estimate was subsequently revised by arranging the entire bone sample from each taxon into size groups by the comparative method. Additional individuals were added to the first calculation if their estimated sizes were observed to be meaningfully different from those inferred by the most frequent elements. The larger the sample of bones, and the smaller the size ranges of individual taxa, the more difficult it is to apply this procedure.

On the other hand, the driftwood catfish is a much smaller fish (TL < 200 mm, BM < 80 g). In the Sitio Sierra sample, this species exhibits an MNI-NISP relationship that is strikingly different from the relationship observed for the other frequent freshwater species. The proportion of bones per individual is considerably lower (Figure 7). For the driftwood catfish there is an estimated seven bones per individual; for the ghost knife-eel 18 bones; silver catfish, 20 bones; and tiger-fish, 44 bones. Vertebrae constitute 66% of the tiger-fish sample, and 0.2% of the driftwood catfish sample. The smaller size of the driftwood catfish compared to that of the tiger-fish should influence the numbers of vertebrae taken over a 3.2 mm mesh. Even so the lateral processes of driftwood catfish vertebrae are very long in proportion to the width of the centrum. Therefore one would expect a minimum number of 123 individuals to leave many more than 2 vertebrae over screens of this size. The most frequent body parts of the driftwood catfish are cleithra (28%), pectoral spines (20%) and coracoids (12%) (Figure 8 j, m). Thirty-five percent of the bones were found burnt or charred as opposed to 51% in the tiger-fish sample. Probably both species were cooked over open wood fires. One can envisage barbecued driftwood cats being broken behind the fused vertebral complex, the heads and spines discarded, and the bodies consumed whole, vertebrae and all. As fewer vertebrae from larger fish were ingested, more would be present in refuse accumulations.

## 7. Fish behavior and Fishing Techniques

In spite of the large numbers of fish bones recovered at the studied pre-Columbian sites, very few artifacts that can be interpreted as fishing tackle have been recovered in excavations. At Cerro Juan Díaz, Mayo (2004) reported a few drilled stones lined up in a refuse dump, which she interpreted as net weights. Documents written at Spanish contact describe fishing with hook-and-line, e.g., Fernando Columbus's (1959) description of turtle shell fish-hooks on the central Caribbean coast. However, archaeologists have not reported indisputable fish hooks, which were presumably made out of materials that do not usually survive in tropical archaeological sites, such as thorns and wood. We are left with making analogies with modern fishing practices, and fish behavior and ecology to infer fishing techniques (Cooke and Ranere, 1999; Cooke and Jiménez, 2004).

Modern subsistence fishing practices as well as collection records from a middle-range study of fish amphidromy in the lower Santa María valley (Cooke and Tapia-Rodríguez, 1994) indicate that all the freshwater fish species reported in the studied archaeofaunas will take baited hooks, except the two armored (loricariid) catfish and the carp headstander which swims in small shoals (hence its local name of "sardina manada" [shoal sardine]). Today spiny armored catfish and headstanders are caught with throw- and gill-nets or are speared using masks. At Cooke's farm, located 25 km up the River Chico in the Coclé del Sur drainage, local fisherfolk catch large numbers of the royal twig catfish (*Sturisoma panamense*) and spiny armored catfish (*Hemiancistrus aspidolepis*) in gill-nets placed at right angles to the river banks (Cooke, personal observation). Cooke and Tapia-Rodríguez (1994: Table 1) captured 20 spiny armored catfish in gill-nets in the River Santa María. Therefore it is curious that this species was represented by only three bones (0.1%) at Sitio Sierra (Ag3), which is very close to the two freshwater fishing stations where Cooke and Tapia caught most of the spiny armored catfish. This catfish's low archaeological representation at Sitio Sierra vis-à-vis its present-day abundance in the River Santa María may be related to some unknown cultural or biological factor, such as rejection for food or a natural resistance to barbasco-like fish poisons.

On the other hand, the three preferred freshwater species throughout the time-periods covered by the study samples (tiger-fish, driftwood catfish and silver catfish) are voracious takers of baited hooks. So is the ghost knife-fish, which grows to a large size in the Santa María drainage (at least 680 mm TL) (Figure 3). This species, whose remains represented 5% freshwater fish bones at the Aguadulce Shelter and 4% at Sitio Sierra (Figure 2), is most active at night, a behavior it shares with the marbled swamp eel (*Synbranchus marmoratus*). Local fisherfolk catch the marbled swamp eel either with hook and line or by flushing it from its burrows.

Cooke has caught driftwood catfish in throw-nets on many occasions. It is very difficult to take them out of the nets because their large and robust pectoral and dorsal spines, not only inflict nasty wounds, but also damage equipment. Forty-two pectoral spines (24%) of this species were found intact at Sitio Sierra. This suggests that driftwood catfish were not netted, but rather caught with a technique that obviated breaking their spines, i.e., on hooks or with poison. A fish poison extracted from the roots of a native yam species (*Dioscorea mexicana*) (formerly *D. macrostachia*) - called locally “cabeza negra” (“black head”) - is still used to poison fish in this part of Panama (Escobar, 1972:92).

**8. Marine fish in freshwater sections of Parita Bay rivers**

Freshwater sections of Neotropical rivers are home to several species of fish of marine origin. The mountain mullet, mentioned earlier, spends most of its adult life in fast-flowing water. Likewise the purplemouth grunt (*Pomadasys bayanus*) spends sufficient time a long way from the sea to be considered a component of the freshwater fish fauna irrespective of its genetic origin. It has been recorded at elevations >600 m above sea level (McKay and Schneider, 1995). It is fished regularly in the four SMBP drainages today reaching a total length of more than 500 mm (>1.5 kg) (STRI reference collection: 03501). *P. bayanus* bones were recovered at Sitio Sierra and Cerro Juan Díaz (Cooke and Ranere, 1999; Jiménez and Cooke, 2001).

Three species of euryhaline sleepers (Eleotridae) are widespread in the study region. It is likely that they spawn in brackish water moving into fresh water as they grow. The Pacific sleeper (*Gobioromus maculatus*) and spotted sleeper (*Eleotris picta*) are recorded at elevations of 100-130 m; the fat sleeper (*Dormitator latifrons*) to 30 m above sea level (*www.fishbase.org*). Around Parita Bay, juvenile fat sleepers congregate in tidal channels and pools in the high tidal flats where they can be easily captured with nets and scoops (Cooke and Ranere, 1999). At Late Preceramic (7000-5000 BP) Cerro Mangote, this species is the second most abundant marine fish. All the bones were estimated by comparison with specimens in the comparative collection to belong to individuals with sizes between 50-200 g and 100-200 mm total length (TL). This suggests that the inhabitants of this coastal settlement acquired fat sleepers in these marine littoral habitats rather than in freshwater sections of the River Santa María where large specimens appear to congregate. The largest fat sleeper specimen in the STRI skeleton collection (32x-1-1-2) was a gravid female collected in an ancient endorrheic meander of the River Santa María, just north of the Sitio Sierra site. It measured 280 mm TL and weighed 930 g (Cooke and Ranere, 1999).



The largest spotted sleeper in the STRI collection was collected in the main channel of the River Santa María: it weighed 1930 g (32x-2-1-07; it was not measured). Local fisher-folk say that even larger spotted sleepers can be caught in the deepest sections of the rivers that empty into Parita Bay. Locally, this species is known as the "river toadfish" ("pejesapo de río").

Other marine species are diadromous, moving upstream opportunistically or seasonally to feed. For example, in the tropical eastern Pacific, bull shark (*Carcharhinus leucas*), snook (*Centropomus nigrescens* and *C. viridis*), and sawfish (*Pristis spp*.), which reach very large sizes, travel considerable distances inland, and can be found impounded in human-made lakes (Vásquez and Thorson, 1982).

Cooke and Tapia-Rodríguez (1994) recorded seven species of diadromous or purportedly diadromous marine fish in freshwater sections of the lower River Santa María, at collection stations located 12 and 20 km (straight line distance) from the present river mouth: sawfish (*Pristis spp*.), false sculptured sea-catfish (*Notarius cookei*), river sea-catfish (*Cathorops tuyra*), Pacific dog snapper (*Lutjanus novemfasciatus*), white snook (*Centropomus viridis*), black snook (*Centropomus nigrescens*), and white mullet (*Mugil curema*). White and black snook captured during this project returned live weights of 1.1-1.5 kg (Cooke and Tapia-Rodríguez, 1994: Table 1). A small white snook (standard length [SL]-220 mm) was collected at San Juan on the River Gatú, 60 km from the mouth and 300 m above sea level (Figure 1; Cooke and Tapia-Rodríguez 1994:104).

The false sculptured sea-catfish (*N. cookei*) and river sea-catfish (*C. tuyra*) are frequently captured today in freshwater sections of the River Santa María. An example of the former species taken with a gill-net in fresh water in the River Santa María measured 405 mm (SL) and weighed 3855 g. Whether these species spend their entire adult lives in fresh water (moving into brackish water to spawn), is not currently known, but seems likely. All the above species were recorded in the archaeofaunal samples from Sitio Sierra (Cooke and Ranere, 1999).

Two small gobies (*Awaous transandeanus* and *Sicydium salvini*) are also widespread in SMBP freshwater basins including fast-flowing sectors with clear water currents. They have not been identified in the archaeofaunal samples.

In the absence of biochemical studies, and referring to comments on the fat sleeper at Cerro Mangote, it is not possible to prove that bones of freshwater-tolerant marine fish found in the Parita Bay middens were actually captured in fresh water in pre-Columbian times. It is clear, however, that several marine species frequently or regularly enter the drainages of the SMBP at considerable distances from the sea. The ubiquity, ease-of-capture, and large size of many of them enhance the value of river-fishing in the lower stretches of SMBP rivers.

**9. Zoogeography**

The Central American land-bridge has acted as a conduit for the dispersal of fish and other vertebrates between South and North America at different points in its complex and protracted physical transformation towards an isthmian state, and under variable paleogeographic and paleoclimatic conditions. Land-bridge freshwater fish faunas contain species that are of both northern and southern origin. Miller (1966) argued that salt-water tolerant cichlids and poeciliids made a south-north sea crossing between the islands of a late Tertiary isthmian archipelago. This hypothesis has been confirmed and fine-tuned by more recent molecular studies, which suggest that cichlids, poeciliids and also *Rivulus* arrived on the land-bridge approximately 15-18 Ma, perhaps aided by a dramatically reduced sea level (Murphy and Collier, 1996; Smith and Bermingham, 2005). Subsequently a radiation of these families occurred in north-western lower and nuclear Middle America. This was followed by the southwards re-infiltration of Costa

Rican and Panamanian basins by these taxa after isthmian closure. Cichlid and poeciliid species richness is greatest at the western margin of the land-bridge (Lake Nicaragua) (Smith and Bermingham, 2005). On the other hand, only two native cichlid species have been recorded in the River Santa María drainage: "chogorro" (*Aequidens coeruleopunctatus*) and Siebold's mojarra (*Tomocichla sieboldi*). Several non-American *Tilapia* species and the Central American jaguar guapote (*Parachromis managuensis*), now present in this basin (Cooke and Tapia-Rodríguez, 1994), are recent human-induced introductions.

The final closure of the Central American land-bridge between about 3.5 and 3.1 Ma also permitted the northward dispersal of other primary freshwater species that originated in the great river basins of South America. This movement is epitomized by primary freshwater catfish (Auchenipteridae, Loricariidae, and Heptapteridae), knife-eels (Gymnotiformes), and Characiformes (Characidae, Ctenoluciidae, Erythrinidae, and Curimatidae). Their diversity is highest in the easternmost river basins (i.e., the Tuira), a fact that reflects both proximity to southern American drainages and regional diversification. These orders and families provide nine of the twelve freshwater fish species that were utilized by the pre-Columbian populations resident in the SMBP.

Zoogeographers have been aware for some time that the SMBP exhibits closest similarities with the Tuira Biological Province. This fact is attributed by Smith and Bermingham (2005: 1849) to "the gradual decline of the continental shelf in the Bay of Panama combined with periods of reduced sea level, which during glacial maxima would have greatly facilitated fish dispersal through anastomizing lowland streams and swamps extending from the River Tuira to the streams of the Azuero Peninsula". Two species, which are shared by Santa María and Tuira drainages, but have not yet been recorded in rivers of the Chiriquí Biographical Province directly to the west, are the driftwood catfish (*Trachelyopterus amblops*) and gar characin (*Ctenolucius beani*). The driftwood catfish is the second most abundant freshwater fish species in the Santa María drainage archaeofaunal samples by NISP (Figure 2), and the most abundant by MNI (Cooke and Ranere, 1999). Loftin (1965) did not collect this species in the SMBP in1961-62; at that time it had been recorded only from Darién and eastern Panama province (i.e., in the Tuira Biological Province). Believing that this species was not a natural component of the Santa Maria basin fish, Cooke failed to identify the large sample of bones belonging to *T. amblops* at Sitio Sierra (recovered 1970-75) until he collected live specimens near this site in the 1980s.

Loftin's collection of the gar characin (*Ctenolucius beani*) in the Santa María river drainage prompted him to propose that this species had a disjunct distribution, being present in the Tuira, Santa María and perhaps Coclé del Sur and La Villa drainages, but absent from rivers between these basins. He attributed this situation to river anastomosis in glacial periods. Three other important freshwater food fish in the archaeofaunal samples - tiger-fish (*Hoplias sp*.), ghost knifefish (*Sternopygus macrurus*) and carp headstander (*Cyphocharax magdalenae*) - have penetrated the Pacific slopes of the land-bridge as far as Costa Rica (Bussing and López, 1987).

Although Smith and Bermingham (2005) warn that some local absences of fish species on the isthmus can be attributed to insufficient sampling effort in particular drainages, they believe that the absence of the driftwood catfish and gar characin west of the Santa María drainage of the SMBP is a strong hypothesis. The recovery of 25 driftwood catfish (*T. amblops*) bones in Late Preceramic deposits at the Aguadulce Shelter suggests that this species was present in the Santa María drainage at least by 7000-4500 BP. Three elements referred to *T. amblops* at the Cueva de los Ladrones and one element from Monagrillo indicate its presence in the River Grande valley of the Coclé del Sur drainage and in the Parita valley of the Parita drainage by the Early Ceramic period (4500-2500 BP) (Figure 1). Five gar characin (*C. beani*) bones recovered in the Aguadulce Shelter during the 1997 excavations confirm this species' presence in the Santa María drainage some time between 7000 and 2500 BP (Figure 2).

**10. Conclusion**

The many rivers and streams of the isthmus of Panama have relatively low numbers of freshwater fish species, and very few that grow to sizes large enough to be able to sustain the intensive fisheries that conferred considerable economic advantages on the pre-Columbian inhabitants of the great South American river basins. Freshwater fish diversity declines rapidly upstream, especially on the Pacific side. This means that communities living in the highlands, where large human populations were concentrated in pre-Columbian times, developed the custom of acquiring marine fish dried and salted on the coast. This practice has continued to the present-day (Zohar and Cooke, 1997). Ethnohistoric accounts describe the inland movement of salted marine fish, even across the central cordillera, while archaeologists have identified pre-Columbian sites (e.g., Vampiros 1 and 2) which, they propose, were used specifically to prepare fish for inland consumption (Carvajal et al., in press; Cooke et al. 2008).

Archaeozoological data demonstrate, however, that several primary freshwater fish species were regularly captured in the lower freshwater reaches of rivers and streams belonging to the Santa María Biogeographical Province on the central Pacific watershed of Panama. The preferred freshwater species were two that grow to quite large sizes (>500 g) – the tiger-fish (*Hoplias sp*.) and silver catfish (*Rhamdia cf quelen*) – and another, considerably smaller (<200 g) species, the driftwood catfish (*Trachylopterus amblops*). The ghost knife-fish (*Sternopygus macrurus*), marbled swamp-eel (*Synbranchus marmoratus*), carp headstander (*Cyphocharax magdalenae*), and a small cichlid ("chogorro") (*Aequidens coerulepunctatus*) were also taken regularly to judge from data obtained at two sites of different ages: the Aguadulce Shelter (7000-2500 BP) and Sitio Sierra (1800-1500 BP). The fact that marine fish species were consumed equally or more frequently at these sites, however, demonstrates not only the importance of the inland transport of fish obtained in marine habitats, but also the fact that several sizable species of marine origin (e.g., sawfish [*Pristis spp*.], euryhaline sleepers [Eleotridae spp.], sea-catfish [*Cathorops spp., Notarius spp.*], snook [*Centropomus spp.*], and purplemouth grunt [*Pomadasys bayanus*]) spend considerable periods of time in freshwater sections of larger rivers, and thus, from an ecological point of view, can be considered components of the regional freshwater ichthyofaunas.

The extreme rarity of artifacts interpreted as fishing-gear at the studied sites means that fishing techniques can only be inferred from fish ecology and behavior, and by making analogies with present-day capture methods in an area where (by way of caveat) Spanish conquest caused cultural discontinuities among pre- and post-Columbian communities. Hooks, and sisal and cotton nets are described in colonial documents, and were surely employed in Pacific-side rivers. Most of the recorded freshwater species take baited hooks, and were probably sometimes caught in this way in the past. Presumably, if bone and shell fish-hooks are not found in the study area, these artifacts were made of materials that do not survive, such as thorns or wood. Even so, the fact that about a quarter of the sample of driftwood catfish pectoral spines found at Sitio Sierra had remained intact suggests that these fish were not necessarily captured with nets because extricating them without breaking the spines them would inflict wounds and damage equipment. Body part proportions suggest that these small fish were barbecued over wood fires and their bodies consumed whole after head and spine removal. The rarity of the sizable spiny armored catfish (*Hemiancistrus semispinosus*) at Sitio Sierra is inconsistent with its present-day abundance and ease-of-capture in nets and suggest that this inconsistency may be due to cultural factors (such as rejection for food) or behavioral ones, such as resistance to barbasco-like fish poison derived from wild American yams (*Dioscorea*), which are still used today in the study region. It would be illuminating to conduct experimental studies in order to evaluate this poison's species-specific effectiveness.

The taxonomy of the isthmian freshwater fish faunas is currently being scrutinized on-going molecular studies, which are leading to revisions of both taxonomic status and the relationships among species and separate populations of species. It is assumed that the species of ten freshwater genera that are apparently monotypic in the archaeofaunal samples are the same ones that are present in the four study drainages today. Most of these species represent South American lineages that are hypothesized to have migrated westwards along the land-bridge after final closure between 3.1 and 3.5 Ma. The anastomosis of rivers during periods of lowered sea level during the Pleistocene is offered as one reason for the westward expansion of some of these lineages (Smith and

Bermingham, 2005). Two species present in the samples have not expanded westwards beyond the Santa María Biogeographical Province: the driftwood catfish (*Trachyleopterus amblops*) and the gar characin (*Ctenolucius beani*). Although it is likely that their presence in the SMBP dates back to the Pleistocene, there are no archaeofaunal samples of this antiquity. However, the driftwood catfish was present in the Santa María drainage by the period 7000-4500 BP, and in the Coclé del Sur and Parita drainages by 4500-2500 BP. The gar characin was present in the Santa Maria drainage by 7000-4500 BP. In addition to providing information about prehistoric diet, and food procurement and preparation methods, archaeozoological records are relevant to the study of fish distributions in the past.

*Acknowledgments*

The studied archaeofaunas were provided by excavations conducted by RGC and colleagues (A.J. Ranere, P. Hansell, O.F. Linares, and D.R. Piperno) with research grants obtained from various sources: National Science Foundation (BNS-811-2475, BNS-811-2475 and BNS-831-8381), Smithsonian Institution (Scholarly Studies Fund, Collections-Based Research Fund, International Activities Directorate and Walcott Foundation), and National Geographic Society (for research at Cerro Juan Díaz). Máximo Jiménez's participation has been possible due to grants from the Smithsonian Tropical Research Institute (student fellowship programs) and Smithsonian Institution (Scholarly Studies Fund, Collections-Based Research Fund, and Walcott Foundation). We gratefully acknowledge assistance with the preparation and identification of fish bone samples provided by Conrado Tapia-Rodríguez and Aureliano Valencia. The two anonymous reviewer's comments were an excellent combination of criticism and assistance, and are sincerely acknowledged. We also owe our gratitude to Eldredge Bermingham, Ruth Reina, and Oris Sanjur (Genetics Laboratory, Smithsonian Tropical Research Institute) for assistance with information about fish taxonomy and distribution. We take full responsibility, however, for any mistakes that have resulted from with our presentation and interpretation of these data.

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*Figure Captions*

**Figure 1**

A: Map of Panama showing the location of pre-Columbian archaeological sites where freshwater fish bones have been found, the four drainages in which they are situated, and the River Gatú, an inland basin where snook (*Centropomus viridis*) have been reported..

B: The freshwater biogeographical provinces of Panama and neighboring areas of Costa Rica (after Smith and Bermingham, 2005)

**Figure 2**

Numbers of bones of primary and secondary freshwater fish, and euryhaline sleepers (Eleotridae) found in pre-Columbian middens at nine archaeological sites in the Santa Maria Biogeographical Province, Panama. On zoogeographical grounds, it is likely that all genera except *Astyanax* and *Rhamdia* are represented by a single species (see Figure 3). [1] : numbers refer to diagnostic teleost bones, i.e., those that were identified to family or below. ST: degree of saltwater tolerance, 1 = primary species, 2 = secondary species (after Smith and Bermingham, 2005).

<u>Drainages</u>: SM – Santa María, CS – Coclé del Sur, PA – Parita, LV – La Villa. Site and context abbreviations with estimated ages (uncalibrated radiocarbon years BP): <u>CM</u> – Cerro Mangote; RZ – red zone, 7000-6000 BP, BZ – brown zone, 6000-5000 BP. <u>Ag13</u> – Aguadulce Shelter; PC – preceramic (1973/5 excavations), 7000-4500 BP, CER – early

ceramic (1973/5 excavations, 4500-2500 BP), 97 – preceramic and early ceramic levels combined, 1997 excavations. Ladrones - Cueva de los Ladrones, early ceramic levels (4500-2500 BP). He-5 – Monagrillo (4500-3000 BP). Ag3 – Sitio Sierra, context 75-B-2 (1800-1500 BP). Ag145 – Vampiros-1 (~2200 BP). LMS – La Mula-Sarigua (2200-1800 BP). CJD - Cerro Juan Díaz; CJD-1: 1800-1500 BP, CJD-2: 1500-1300 BP, CJD-3: 1000-700 BP. Na8 – Natá (1000-500 BP).

**Figure 3:** *Distribution of freshwater fish in four river drainages in the Santa Maria Biogeographical Province of Panama.*

Primary and secondary freshwater species are listed, giving their presence in each drainage, as determined by surveys conducted by E. Bermingham and colleagues and capture records for specimens in the Smithsonian Tropical Research Institute (STRI) skeleton reference collection. Fish with **boldened** names were recorded in pre-Columbian archaeofaunas. The numbers of skeletons used for this study are given. Total length (TL), standard length (SL), and body mass estimates have been taken from www.fishbase.org or (if different) from STRI collection records (square brackets indicate that the length or weight of specimens in the STRI skeleton collection exceed those given in www.fishbase.org).

**Figure 4:**

Alternative names used (not necessarily correctly) by biologists and archaeozoologists for the freshwater species recorded in archaeological sites around Parita Bay, Panama with a partial listing of prior references to these species.

**Figure 5**

Relative abundance of primary and secondary freshwater fish at Aguadulce Shelter and Sitio Sierra, Parita Bay, Panama, expressed as the percentage of specimens in samples of freshwater fish bones that allowed identification to family or below (see Figure 2). The figures for Aguadulce combine bones from Late Preceramic (7000-4500 BP) and Early Ceramic (4500-2500 BP) layers. The Sitio Sierra sample was recovered in context 75-B-2 (Isaza, 1993). Ho – *Hoplias sp*, Rh – *Rhamdia cf quelen*, Tr – *Trachelyopterus amblops*, Cy – *Cyphocharax magdalenae*, Sy – *Synbranchus marmoratus*, Ae – *Aequidens coeruleopunctatus*, St – *Sternopygus macrurus*, He- *Hemiancistrus aspidolepis*, Ct – *Ctenolucius beani*, Sa – *Sturisoma panamense. Tomocichla sieboldii* - recorded by only one element at Sitio Sierra - is not included. 1 = primary freshwater species, 2 = secondary freshwater species.

**Figure 6**

Otoliths and bones of freshwater fish found at Aguadulce Shelter (A, B) (estimated age: 4500-2500 BP), and Sitio Sierra (C, D, E, F, G and H) (estimated age: 1800-1500 BP).

A: *Cyphocharax magdalenae*, right sagittal otolith; B: *Aequidens coeruleopunctatus*, left sagittal otolith; C: *Aequidens coeruleopunctatus*, left hyomandible; D: *Aequidens coeruleopunctatus*, right dentary; E: *Cyphocharax magdalenae*, left frontal, compared with E': *Cyphocharax magdalenae,* left frontal, modern specimen, STRI cat: 19x-3-6-5; TL – 190 mm, fresh weight: 120 g, F: *Cyphocharax magdalenae,* left hyomandible, G: *Ctenolucius beani*, left premaxilla, burnt black; H: *Ctenolucius beani*, right opercular, burnt black.

**Figure 7**

Log scale relationship between number of identified specimens (NISP) and estimated minimum number of individuals (MNI) among ten freshwater fish genera from Sitio Sierra (context 75-B-2; Isaza, 1993). Numbers above the line represent NISP, numbers below the line, MNI. Ae – *Aequidens coeruleopunctatus*, Ct – *Ctenolucius beani*, Cy – *Cyphocharax magdalenae*, He- *Hemiancistrus aspidolepis*, Ho – *Hoplias sp*., Rh – *Rhamdia cf quelen*, To – *Tomocichla sieboldii*, Tr – *Trachelyopterus amblops*, Sa – *Sturisoma panamense*, Sy – *Synbranchus marmoratus*, St – *Sternopygus macrurus*.

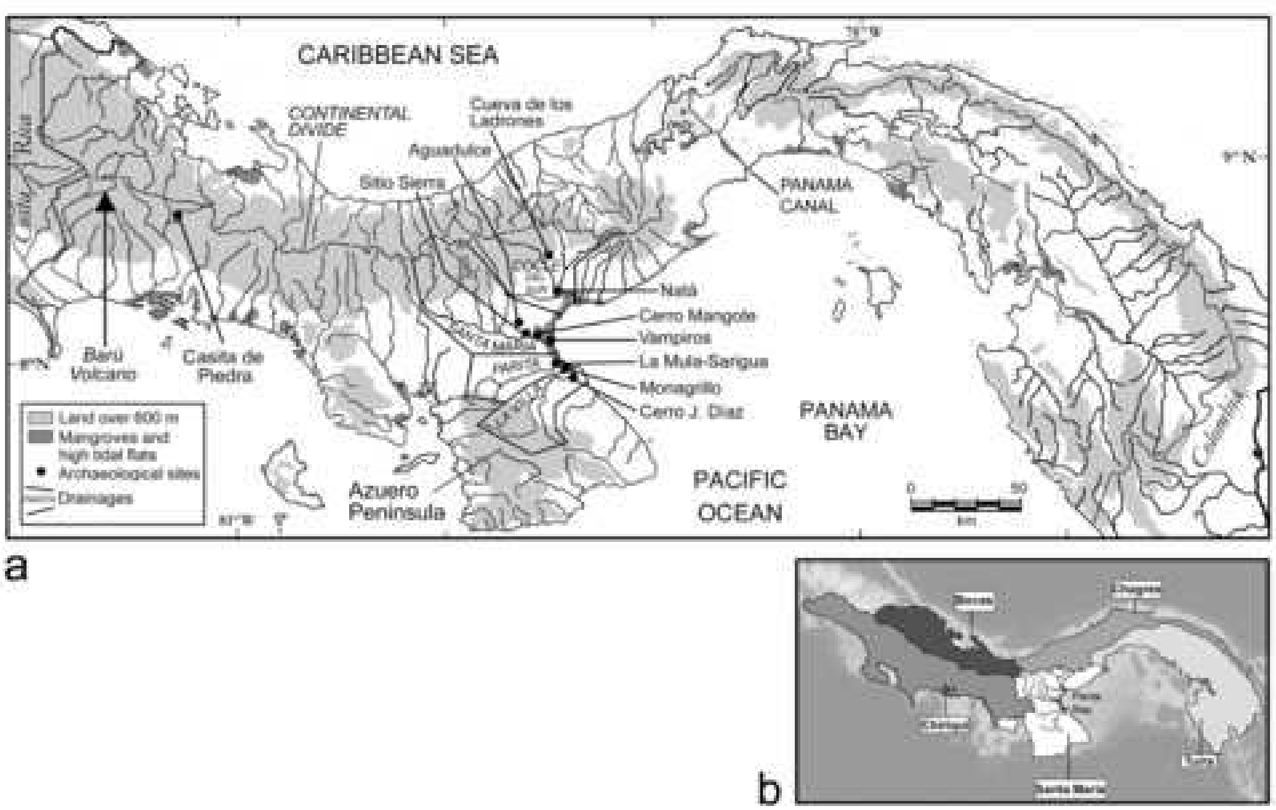
Figure 8: Bones of freshwater fish found at Sitio Sierra, Coclé, Panama (context 75-B-2, estimated age: 1800-1500 BP).

A: *Hoplias sp.,* left cleithron; B: *Hoplias sp*., left premaxilla; C: *Hoplias sp*., left dentary; D: *Sternopygus macrurus*, right keratohyal; E: *Sternopygus macrurus*, vertebra 3; F: *Sternopygus macrurus*, right articular; G: *Synbranchus marmoratus*, right dentary; H: *Synbranchus marmoratus*, right keratohyal; I: *Trachelyopterus amblops*, supracoccipital; J: *Trachylopterus amblops*, right pectoral spine, burnt black; K: *Rhamdia cf quelen,* left prefrontal; L: *Rhamdia cf quelen,* right frontal; M: *Trachelyopterus amblops*, left cleithron, internal view, compared with M': *Trachelyopterus amblops*, left cleithron, modern specimen in STRI collection (cat. No. 6x-3-1-6, TL – 180 mm, fresh weight – 60.7 g, male).

Figure 1






CARIBBEAN SEA
CONTINENTAL DIVIDE
Cueva de los Ladrones
Aguadulce
Sitio Sierra
PANAMA CANAL
Barú Volcano
Casita de Piedra
Natá
Cerro Mangote
Vampiros
La Mula-Sarigua
Monagrillo
Cerro J. Díaz
PANAMA BAY
PACIFIC OCEAN
Azuero Peninsula
Land over 600 m
Mangroves and high tidal flats
Archaeological sites
Drainages
0
50
km
a
b

| | S.T. | CM-RZ | CM-BZ | Ag13-PC | Ag13-C | Ag13-97 | *Ag13-Total* | Ladrones | He5 | Ag3 | Ag145 | LMS | CJD-1 | CJD-2 | CJD-3 | *CJD-Total* | Na8 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Drainage: | | SM | | SM | | | | CS | PA | SM | SM | PA | LV | | | | CS |
| Mesh size (mm): | | 3.2 | 3.2 | 1.5 | 1.5 | 1.5 | 1.5 | 1.5 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 3.2 | 6.4 |
| OSTEICHTHYES [1] | | 236 | 2390 | 315 | 280 | 378 | *973* | 14 | 9083 | 16983 | 4125 | 2850 | 3487 | 10201 | 5322 | *19010* | 74 |
| FRESHWATER FISH: | | | | | | | | | | | | | | | | | |
| *Astyanax* | 1 | | | | | | | 1 | 1 | | | | | | | | |
| *Tomocichla* | 2 | | | | | | | | | 1 | | | | | | | |
| *Aequidens* | 2 | | | 7 | 8 | 16 | *31* | 1 | | 28 | | | | | | | |
| *Ctenolucius* | 1 | | | | | 5 | *5* | | | 18 | | | | | | | |
| *Cyphocharax* | 1 | | | 6 | 5 | 30 | *41* | 1 | | 33 | | | | | 1 | *1* | |
| *Hoplias* | 1 | | | 70 | 60 | 98 | *228* | 1 | | 2137 | | | | | 28 | *28* | |
| *Hemiancistrus* | 1 | | | 5 | 1 | | *6* | | | 3 | | | | | 1 | *1* | |
| *Sturisoma* | 1 | | | 1 | 1 | 2 | *4* | 1 | | | | | | | | | |
| *Trachelyopterus* | 1 | | | 25 | 25 | 3 | *53* | 3 | 1 | 864 | | 1 | | | | | |
| *Rhamdia* | 1 | 1 | | 22 | 21 | 25 | *68* | 1 | | 474 | | | | | | | 1 |
| *Sternopygus* | 1 | | | 7 | 8 | 12 | *27* | | | 166 | 1 | | | 6 | 3 | *9* | |
| *Synbranchus* | 2 | | | 16 | 10 | 14 | *40* | 1 | 1 | 119 | | | | 2 | 7 | *9* | 2 |
| TOTAL: | | 1 | | 159 | 139 | 205 | *503* | 10 | 3 | 3843 | 1 | 1 | | 8 | 40 | *48* | 3 |
| % contribution to fish NISP | | 0.4 | 0 | 50 | 49 | 54 | *52* | 71 | 0.03 | 23 | 0.02 | 0.03 | 0 | 0.08 | 0.8 | *0.3* | 4 |
| EURYHALINE MARINE SLEEPERS: | | | | | | | | | | | | | | | | | |
| *Dormitator* | 2 | 37 | 388 | 6 | 7 | 7 | *20* | | 1 | 242 | | | 3 | 6 | 39 | *48* | |
| *Eleotris* | 2 | | 3 | 3 | 3 | 3 | *9* | | | 17 | | | 1 | 3 | 37 | *41* | |
| *Gobiomorus* | 2 | 1 | 3 | 8 | 6 | 4 | *18* | | | 3 | | | 1 | 3 | 4 | *8* | |
| TOTAL: | | 38 | 394 | 17 | 16 | 14 | *47* | | 1 | 262 | | | 5 | 12 | 80 | *97* | |
| % contribution to fish NISP | | 16 | 17 | 5 | 6 | 4 | *5* | 0 | 0.01 | 2 | 0 | 0 | 0.1 | 0.1 | 1.5 | *0.5* | 0 |

Figure 2

| FAMILY | Genus | species | Authority | Maximum recorded TL (mm) | Maximum recorded body mass (g) | Skeleton collection: No. skeletons at STRI | Skeleton collection: Length range | Drainage: recorded presence and absence: Coclé del Sur | Santa Maria | Parita | La Villa |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Auchenipteridae** | ***Trachelyopterus*** | ***amblops*** | Meek & Hildebrand, 1913 | ***190*** | | 6 | | | x | | |
| Characidae | *Astyanax* | *aeneus* | Gunther, 1860 | *120* | | | | x | x | | x |
| **Characidae** | ***Astyanax***[1] | *ruberrimus* | Eigenmann, 1913 | | | 5 | 75-85 (TL) | | | | |
| Characidae | *Brycon*[2] | *behreae* | Hildebrand, 1938 | *265* | *2273* | 3 | 140-355 (SL) | | | | |
| Characidae | *Brycon* | *obscurus* | Hildebrand, 1938 | *96* | | | | x | | | |
| Characidae | *Bryconamericus* | *emperador* | Eigenmann and Ogle, 1907 | *104* | | | | | | | |
| Characidae | *Bryconamericus* | *zeteki* | Regan, 1908 | | | | | | | | |
| Characidae | *Odontostilbe* | *dialeptura* | Fink and Weitzman, 1974 | *30* | | | | x | x | x | x |
| Characidae | *Compsura* | *gorgonae* | Evermann & Goldsborough, 1908 | *30* | | 1 | 60 (TL) | | x | | |
| Characidae | *Gephyrocharax* | *intermedius* | Meek & Hildebrand, 1916 | *44* | | | | | | | |
| Characidae | *Hemibrycon* | *dariensis* | Meek & Hildebrand, 1916 | *65* | | | | x | x | | x |
| Characidae | *Pseudocheirodon* | *arnoldi* | Boulenger, 1909 | *43* | | | | x | x | | x |
| Characidae | *Roeboides*[3] | *occidentalis* | Meek & Hildebrand, 1916 | *130* | | 4 | 90-105 (SL) | x | x | | x |
| **Cichlidae** | ***Aequidens*** | ***coeruleopunctatus*** | Kner, 1863 | ***145*** | | 6 | 56-125 (TL) | x | x | | x |
| **Cichlidae** | ***Tomocichla*** | ***sieboldii*** | Kner, 1863 | ***250*** | | 3 | 65-188 (TL) | | x | | |
| **Ctenoluciidae** | ***Ctenolucius*** | ***beani*** | Fowler, 1907 | ***286*** | | 12 | 170-265 (TL) | | x | | |
| **Curimatidae** | ***Cyphocharax*** | ***magdalenae*** | Steindachner, 1878 | ***[260]*** | | 14 | 72-260 (TL) | x | x | | x |
| **Erythrinidae** | ***Hoplias***[4] | ***microlepis*** | Gunther, 1864 | ***360*** | | 17 | 135-410 (TL) | x | x | | x |
| Loricariidae | *Ancistrus* | *spinosus* | Meek & Hildebrand, 1916 | *176* | | | | | x | | |
| **Loricariidae** | ***Hemiancistrus*** | ***aspidolepis*** | Gunther 1867 | ***280*** | | 9 | 150-280 (TL) | | x | | |
| Loricariidae | *Leptoancistrus* | *canensis* | Meek & Hildebrand, 1913 | *76* | | | | x | | | |
| Loricariidae | *Rineloricaria* | *uracantha* | Isbricker, 1980 | *165* | | 2 | 230-330 (TL) | | | | |
| **Loricariidae** | ***Sturisoma*** | ***panamense*** | Eigenmann & Eigenmann, 1889 | ***260*** | | 1 | 240 (SL) | x | x | | x |
| Heptapteridae | *Imparales* | *panamensis* | Bussing, 1970 | *72* | | | | | x | | |
| Heptapteridae | *Pimelodella* | *chagresi* | Steindachner, 1877 | *100* | | 3 | 75-90 (TL) | x | x | | x |
| Heptapteridae | *Pimelodella* | sp. nov. | | | | | | x | x | | |
| Heptapteridae | *Rhamdia* | *laticauda* | Kner, 1858 | *225* | | | | | | | |
| **Heptapteridae** | ***Rhamdia***[5] | ***quelen*** | Quoy & Gaimard, 1824 | ***[360]*** | ***4020*** | 11 | 100-360 (TL) | x | x | | |
| Hypopomidae | *Brachyhypopomus* | *occidentalis* | Regan, 1914 | *175* | | | | x | x | | |
| **Sternopygidae** | ***Sternopygus*** | ***macrurus*** | Bloch & Schneider, 1801 | ***[680]*** | | 4 | 380-680 (TL) | x | x | | |
| Trichomycteridae | *Trichomycterus* | *striatus* | Meek & Hildebrand, 1939 | *84* | | 3 | 21-115 (TL) | x | x | | |
| Anablepidae | *Oxyzgonectes* | *dovii* | Gunther, 1866 | | | | | | | | |
| Rivulidae | *Rivulus*[6] | *frommi* | Berkenkamp & Etzel, 1993 | *60* | | 1 | 45 (SL) | | | | |
| Rivulidae | *Rivulus* | *hildebrandi* | Myers, 1927 | *90* | | | | | x | | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Rivulidae | *Rivulus* | *monikae* | Berkenkamp & Etzel, 1993 | *80* | | | x | | | |
| Poeciliidae | *Brachyrhaphis* | *roseni* | Bussing, 1988 | *60* | | | x | | | |
| Poeciliidae | *Brachyrhaphis* | *roswithae* | Meyer & Etezel, 1998 | *26* | | | x | | | |
| Poeciliidae | *Brachyrhaphis* | *terrabensis* | Regan, 1907 | *60* | | | | | | |
| Poeciliidae | *Neoheterandria* | *tridentiger* | Garman, 1895 | *25* | | | x | x | | |
| Poeciliidae | *Poecilia* | *gillii* | Kner, 1863 | *60* | | | | x | | |
| Poeciliidae | *Poeciliopsis* | *elongata*' | Gunther, 1866 | *130* | 4 | 85-118 (TL) | | | | |
| Poeciliidae | *Poeciliopsis* | sp. nov. | | | | | x | x | | |
| Poeciliidae | *Poeciliopsis* | *turrubarensis* | Meek, 1912 | *40* | | | | | | x |
| Poeciliidae | *Priapichthys* | *darienensis* | Meek & Hildebrand, 1913 | *40* | | | x | x | | |
| Poeciliidae | *Xiphophorus* | *hellerii* | Heckel, 1848 | *140* | | | | | | |
| **Synbranchidae** | ***Synbranchus*** | ***marmoratus*** | Bloch, 1795 | ***[560]*** | 2 | 430-560 (TL) | x | | | |

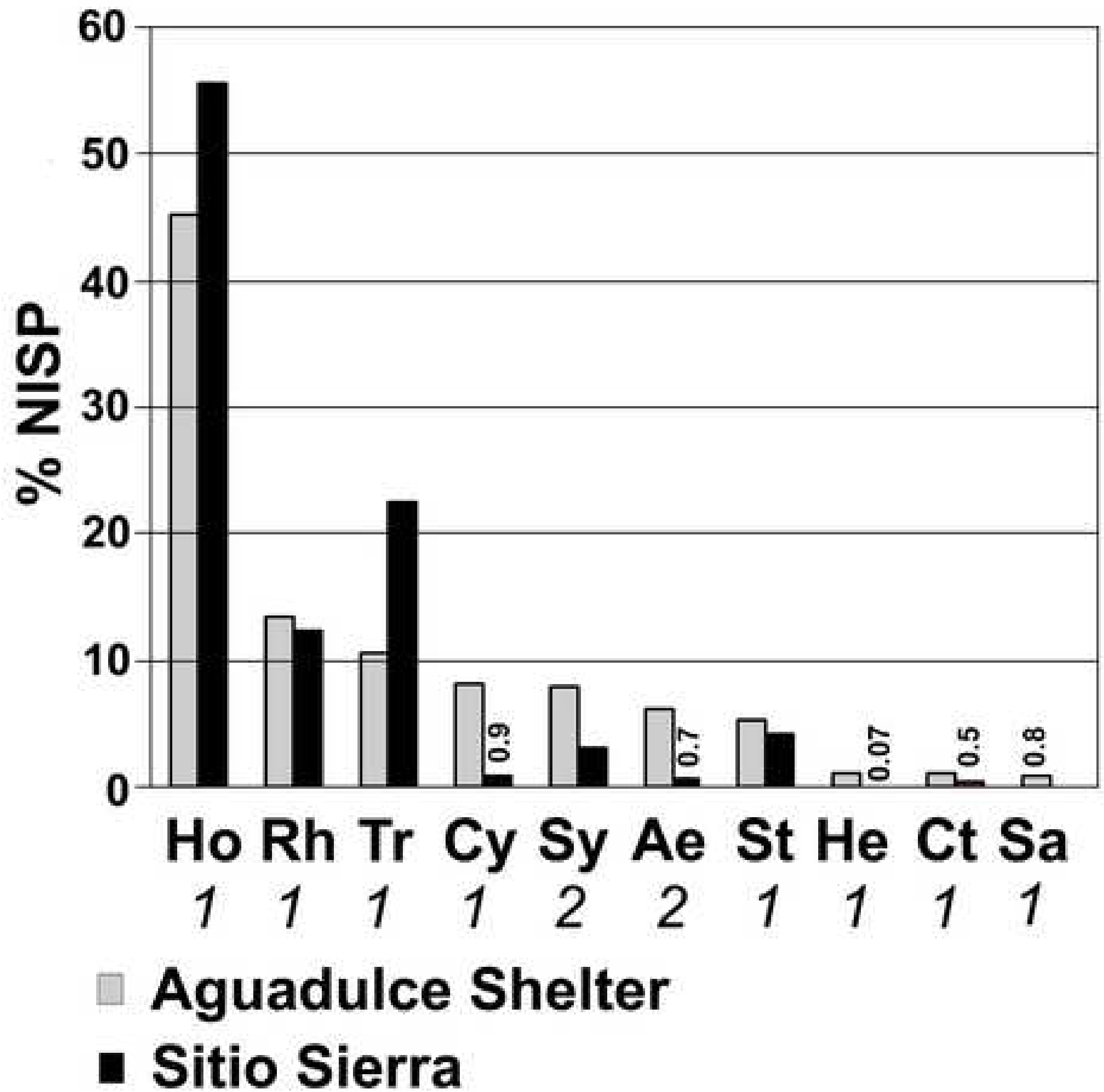
Figure 3

| Current nomenclature | | | References for current status | Names formerly used in publications that discuss the SMBP freshwater fish fauna | | |
|---|---|---|---|---|---|---|
| FAMILY | Genus | species | | FAMILY | Genus | species |
| Auchenipteridae | *Trachelyopterus* | *amblops* | Burgess, 1989 | Doradidae | *Trachycorystes* | *amblops* |
| | | | Ferraris, 2003 | | *Parauchenipterus* | *amblops* |
| Ctenoluciidae | *Ctenolucius* | *beani* | Vari, 1995 | Characidae | *Ctenolucius* | *hujeta* |
| Curimatidae | *Cyphocharax* | *magdalenae* | | Characidae | *Curimata* | *magdalenae* |
| Loricariidae | *Hemiancistrus* | *aspidolepis* | Isbrucker, 2001 | | *Hypostomus* | *panamensis* |
| | | | | | *Plecostomus* | *plecostomus* |
| Heptapteridae | *Rhamdia* | *quelen* | | Pimelodidae | *Rhamdia* | *wagneri* |
| | | | | Pimelodidae | *Rhamdia* | *guatemalensis* |
| Sternopygidae | *Sternopygus* | *macrurus* | Hulen et al., 2005 | | *Sternopygus* | *dariensis* |
| | | | Ortega and Vari, 1986 | | | |
| Cichlidae | *Tomocichla* | *sieboldii* | Burgess, 2000 | | *Cichlasoma* | *sieboldi* |
| | | | Reis et al., 2003 | | | |
| Ariidae | *Notarius* | *cookei* | Acero and Betancur, 2002 | | *"Arius"* | *species A* |
| | | | | | *Arius* | *species B* |

| Regional biological and archaeological references |
| --- |
| |
| Loftin, 1965 |
| Cooke and Tapia-Rodríguez, 1994 |
| Loftin, 1965, Cooke and Ranere, 1999 |
| Bussing, 1987; Loftin, 1965, Cooke and Ranere, 1999 |
| Cooke and Tapia, 1994, Cooke and Ranere, 1999 |
| Loftin, 1965 |
| Loftin, 1965 |
| Cooke and Tapia, 1994, Cooke and Ranere, 1999 |
| Cooke and Tapia, 1994, Cooke and Ranere, 1999 |
| |
| Bussing, 1987; Loftin, 1965, Cooke and Ranere, 1999 |
| |
| Cooke, 1993, 1998; Cooke and Tapia, 1994; Cooke and Ranere, 1999 |
| Bussing and López, 1993; Kailola and Bussing, 1995 |

Figure 5

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60
50
40
30
20
10
0
0.9
0.7
0.07
0.5
0.8
Ho Rh Tr Cy Sy Ae St He Ct Sa
1 1 1 1 2 2 1 1 1 1
Aguadulce Shelter
Sitio Sierra

Figure 6



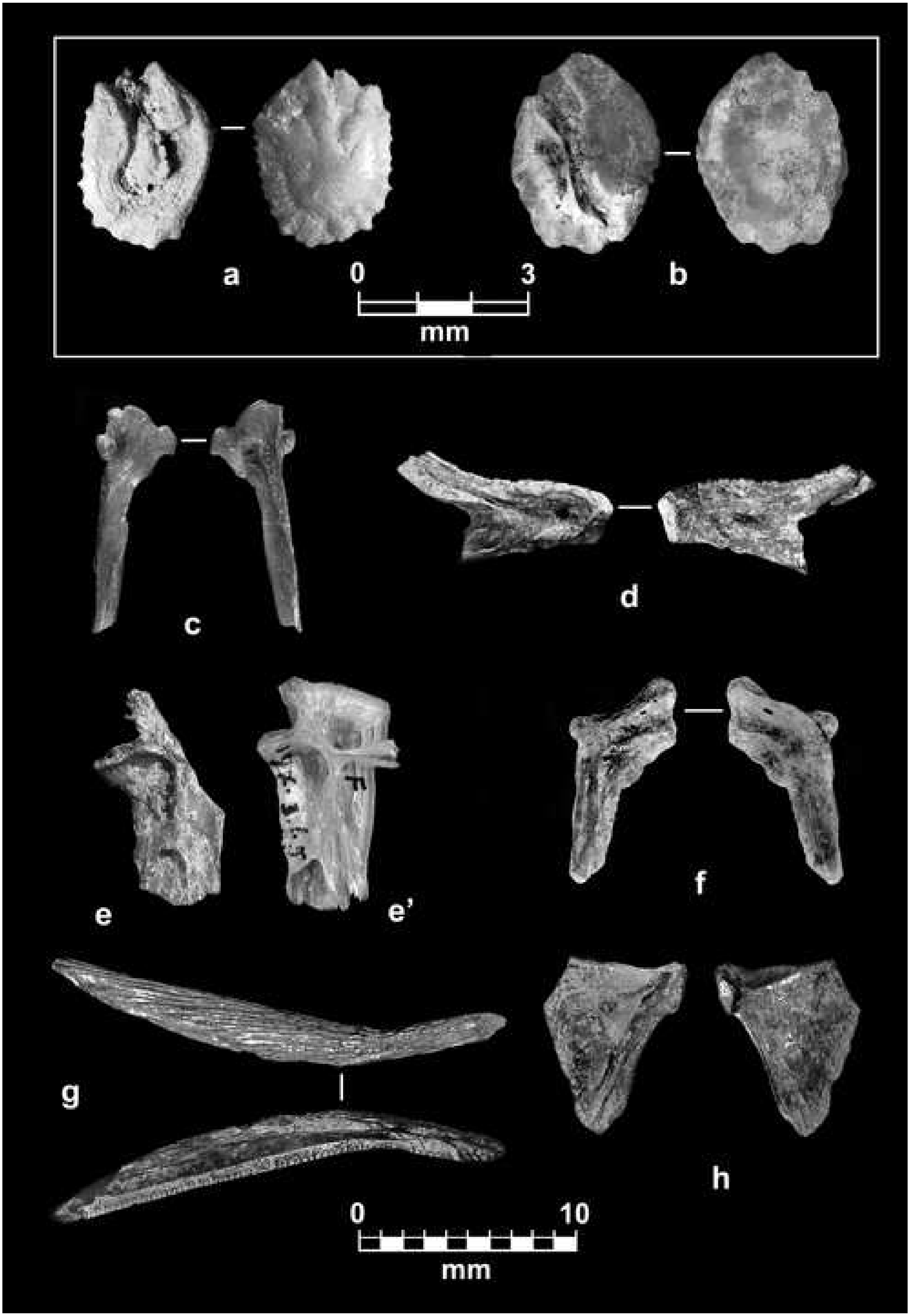
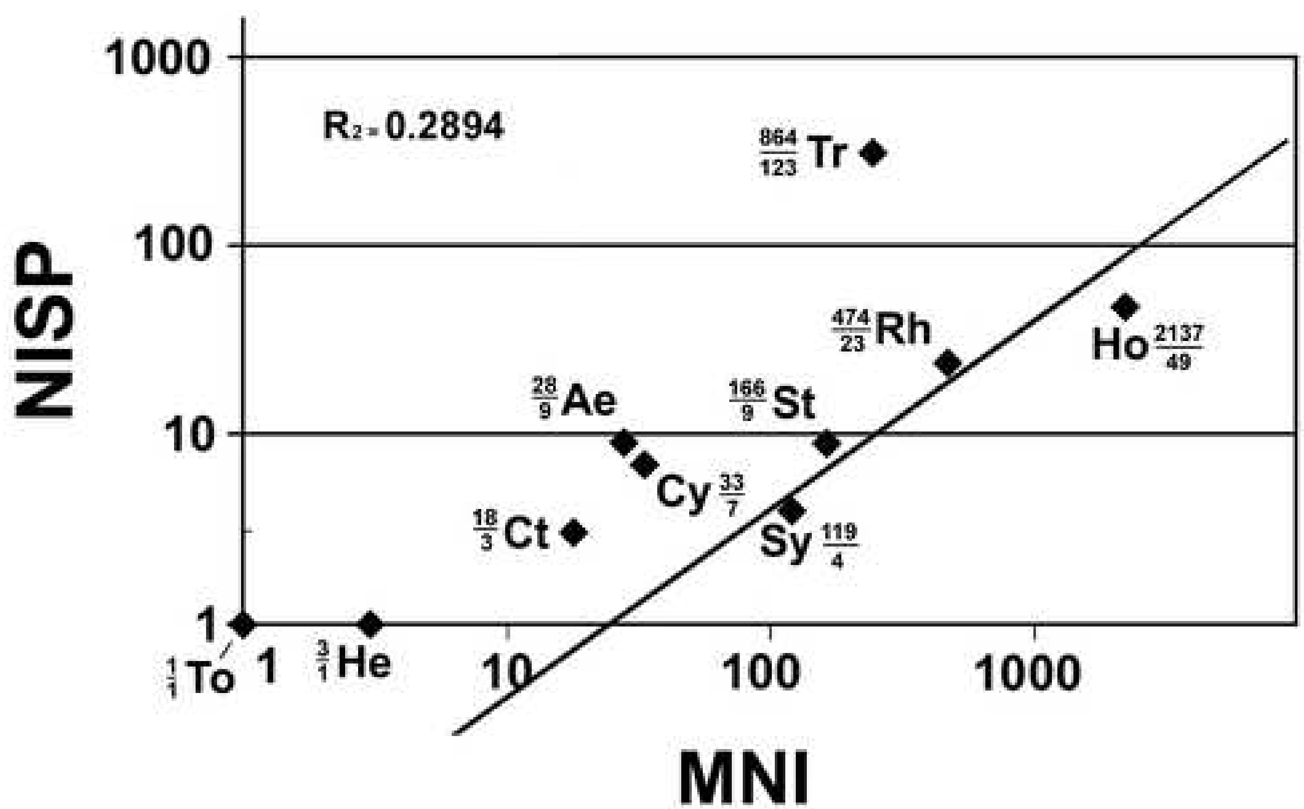


Figure 7







1000
100
10
1
NISP
R2 = 0.2894
864/123 Tr
474/23 Rh
Ho 2137/49
28/9 Ae
166/9 St
Cy 33/7
18/3 Ct
Sy 119/4
1/1 To
3/1 He
1
10
100
1000
MNI

Figure 8