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Teasing Out the Species in Diverse Archaeofaunas: Is It Worth the Effort? An Example from the Tropical Eastern Pacific

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ABSTRACT: The species remains the basic unit of biological classification. However, since archaeofaunal analysis is time-consuming and costly (especially when fish are the dominant class), it is important to ask whether making species-level identifications is worthwhile in view of the fact that even anciently diverged species can be difficult to differentiate osteologically with fragmented material. This is why many experienced archaeozoologists prefer to analyze their archaeological ichthyofaunas at the family or genus level. But in biologically diverse environments, such as the tropical eastern Pacific, it is advantageous for archaeologists to be able to distinguish among fish species. The most important food fish families here are speciose: the marine catfish (Ariidae), croakers (Sciaenidae), and grunts (Haemulidae). Although most of their component species live inshore, their habitat preferences, trophic ecology, and age-group behavior vary considerably. Therefore, separating them osteologically enhances interpretations of ancient fishing preferences and techniques. The distribution and abundance of marine catfish (Ariidae), croaker (*Cynoscion*), and grunt (*Pomadasys*) species at 10 archaeological sites located around Parita Bay on the central Pacific coast of Panamá, in the Panamic region of the tropical eastern Pacific, provide particularly useful information about the littoral habitats that were exploited by pre-Columbian fisherfolk at different stages in the geological and cultural evolution of this small Neotropical estuarine system. In some cases, they point towards specific fishing practices and techniques.

KEYWORDS: PRE-COLUMBIAN FISHING, PANAMÁ, MARINE CATFISH, GRUNTS, CROAKERS

RESUMEN: La unidad principal de clasificación biológica continúa siendo la especie. Aún así, dado que el análisis de faunas arqueológicas es, tanto lento, como costoso (especialmente si los peces son el grupo dominante), cabe preguntarse si vale la pena llevar las identificaciones hasta nivel de especie, toda vez que para especies que divergieron hace tiempo, pueden ser difíciles de distinguir osteológicamente máxime cuándo los materiales están muy fragmentados. Por ello, muchos arqueozoólogos experimentados prefieren limitar el análisis de las ictiofaunas arqueológicas a nivel de familia o género. En regiones biológicamente ricas, sin embargo, el poder identificar los peces a nivel de especie resulta ventajoso para el arqueólogo. Tal es el caso del Pacífico tropical americano en donde las familias de peces más relevantes de cara a la dieta humana contienen numerosas especies. Este sería el caso, por ejemplo, de los bagres marinos (Ariidae), las corvinas (Sciaenidae) y los roncadores (Haemulidae). Si bien es cierto que la mayor parte de estas especies frecuentan zonas costeras, también lo es que muchas dentro de una misma familia varían mucho en lo que se refiere a su hábitat, ecología trófica o el comportamiento de las diferentes cohortes de edad. Por consiguiente, el poder identificarlas osteológicamente hace más sólidas las interpretaciones que estudian los modos en que las sociedades seleccionaban tales especies y los modos en que las capturaban. La distribución y abundancia de las especies de bagres marinos (Ariidae), corvinas (*Cynoscion*) y roncadores (*Pomadasys*) en diez sitios arqueológicos localizados en la costa central del Pacífico panameño evidencian ser útiles herramientas para inferir los ambientes litorales aprovechados por los pescadores precolombinos durante distintas etapas de la evolución geológico-cultural de este estuario neotropical, así como para inferir el uso de determinadas prácticas y técnicas pesqueras.

PALABRAS CLAVE: PESCA PRECOLOMBINA, PANAMÁ, BAGRE MARINO, RONCADOR, CORVINA

INTRODUCTION

The species remains the basic unit of biological classification even though the addition of molecular techniques to the description and analysis of external characteristics, osteology, and behavior has often enhanced the way biologists perceive the phylogenetic relatedness of specific breeding populations within the same genus (e.g., Bermingham & Martin, 1998). Although our mandate as archaeozoologists is to identify each bone specimen with the maximum possible taxonomic and anatomical rigor, our efforts are circumscribed by (a) the fragmentary nature of bone samples from kitchen middens, (b) the geographical, taxonomic, and ontogenetic completeness of the comparative collections we use to identify them, and (c) time and funds in the light of the research questions that the archaeologists responsible for the bone samples deem to be most relevant.

The more diverse the hypothetical life assemblage (Klein & Cruz-Uribe, 1984) from which archaeofaunas derive, the more time-consuming the analysis; so much so, in fact, that it is worth reflecting, first, whether teasing out species is, intellectually, viable, and, if it is, whether the results justify the effort and money. Although many archaeozoologists with specialized knowledge in fish remains are justifiably circumspect about the reliability of species-level identifications (e.g., Leach 1986; Desse & Desse-Berst, 1996; Van Neer & Lentacker, 1996; Van Neer & Ervynck, 1998), we argue that this procedure can be both objective and worthwhile judging from the inferences about inshore fishing practices that we have been able to draw from bone remains representing three widespread families (Ariidae, Haemulidae, and Sciaenidae) recovered at pre-Columbian sites on the central Pacific coast of Panamá.

GEOGRAPHIC AND TEMPORAL FOCUS

Since the 1970s a small group of archaeologists has endeavored to reconstruct settlement patterns, social organization, funerary customs, subsistence, and exchange in an area of central Panamá that was occupied continuously by pre-Columbian people from the late glacial (Clovis technological horizon) to the mid-16th century AD (Cooke & Ranere, 1992 a, b; Cooke & Sánchez, 2003; Cooke, in press). The focus of this project's archaeozoological component is Parita Bay, a small mangrove-fringed estuarine system, which is itself the northwesterly arm of Panamá Bay in the Panamic region of the tropical eastern Pacific (TEP). The studied archaeofaunas come from 10 sites, whose location is presented in Figure 1. Table 1 gives the approximate ^{14}C ages of the samples in addition to a record of the fish species that we have identified either tentatively ("cf") or, in our opinion, objectively at each site. All these sites are currently located within 25 Km of the present-day coastline of Parita Bay. Their relationship to littoral landforms, the active coastline, and river, stream, and marine channels, however, has changed since the time periods during which they were occupied. Sediment studies undertaken in the 1970s and 1980s and aerial photographic interpretation have indicated that, since the deceleration of sea level rise about 7,000 radiocarbon years BP, the Parita Bay coastline has prograded seawards – at a faster rate (about 1 Km every 1,000 years) at its center (where the River Santa María discharges) than at the southern edge (about 0.5 Km every 1,000 years) (Clary *et al*., 1984; Cooke & Ranere, 1999). Therefore, the distribution of fish species in each archaeofaunal sample reflects not only human cultural factors (such as dietary preference and fishing gear), but also topographies and water conditions that were different from those of today – markedly so in the case of the oldest sites and samples. Cerro Mangote, for example, which is now 8 Km from the active coastline, is likely to have been only 1.5 Km inland when first occupied 7000 BP. Whereas several freshwater fish taxa can be fished in front of the site today, only one bone of a freshwater taxon was recovered in the archaeofauna (Cooke & Ranere, 1999).

The following questions have guided our study of pre-Columbian fishing around Parita Bay: (1) When did people begin to fish? (2) How did they fish? (3) Did fishing technology change through time? (4) How far did people travel from their settlements to obtain fish? (5) Did they acquire fish themselves, get someone else to fish for them, or exchange other products for fish caught elsewhere? (6) How far was fish transported and in which state (i.e., fresh, salted, or dried; whole, eviscerated, or butchered)? (7) How selective was fishing in terms of the available life assemblage of species (i.e., which species were consumed or rejected as food)? (8) How did people perceive fish, not just as food, but also in ritual or semiotic contexts (Cooke, 2004)?

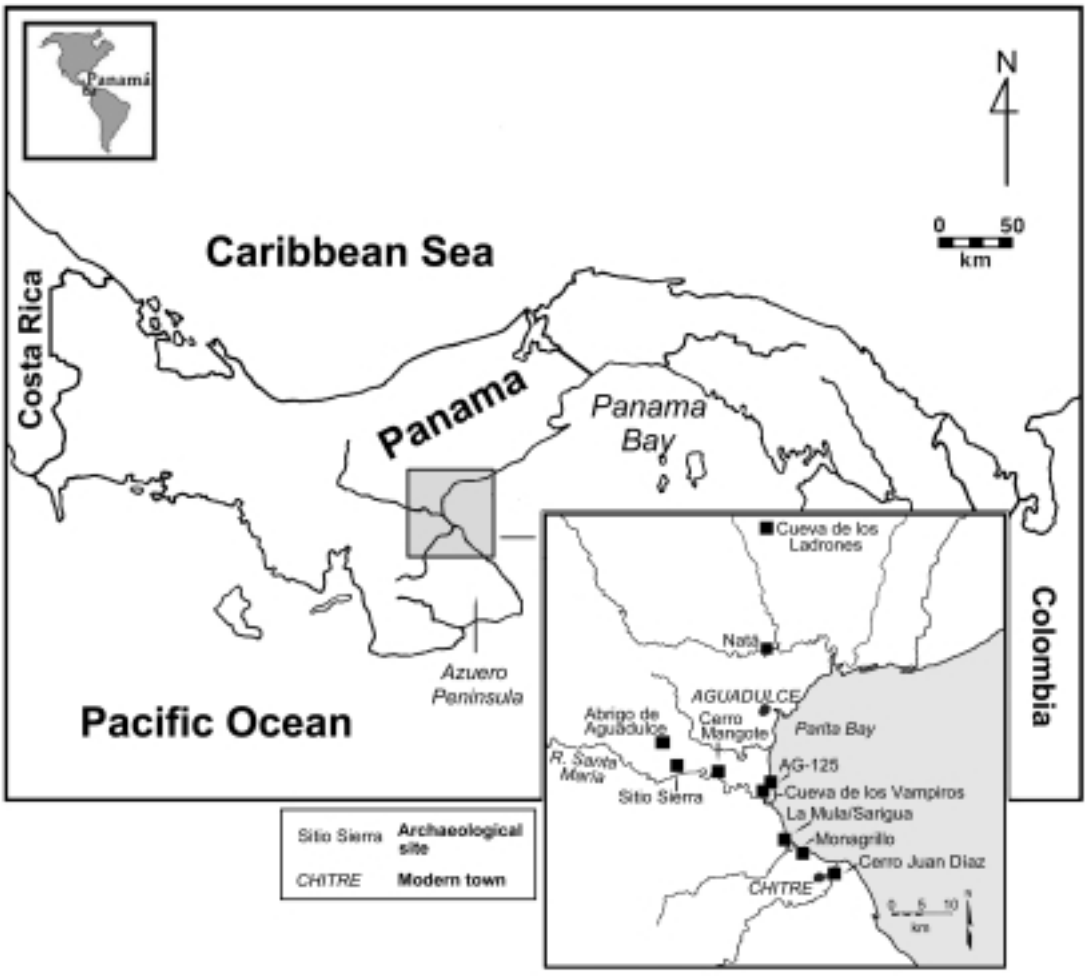

FIGURE 1

Map of Panamá, showing (inset) the location of the 10 pre-Columbian archaeological sites whose archaeoichthyofaunas are summarized

COMPARATIVE SKELETON COLLECTIONS VIS-À-VIS ZOOGEOGRAPHY AND TAXONOMY

A prerequisite of accurate and meaningful species-level identifications is the completeness of the consulted comparative skeleton collection, from the taxonomic, zoogeographic, and ontogenetic points of view. Although pre-European human-induced extinctions of Holocene-age terrestrial faunas have been documented, particularly on islands (e.g., Martin & Steadman, 1999; Steadman *et al.*, 2002), it seems reasonable to assume *a priori* that pre-Columbian peoples who lacked ocean-going watercraft during the mid- to late Holocene are unlikely to have focused on fish species that are no longer present within easy reach of their settlements. (It cannot be assumed, however, that the *abundance* of individual fish species within particular coastal systems has remained immutable, as we comment later). There is no evidence that the pre-Columbian peoples who fished around Parita Bay developed vessels more sophisticated than single-hull dugout canoes (Cooke & Sánchez, 2001).

The macro-geographic marine region to which the Parita Bay sites belong is the tropical eastern Pacific (TEP), whose inshore marine fish fauna is taxonomically very diverse (Robertson & Allen, 2002). Three families, which provided most of the fish that pre-Columbian people exploited across

				Site:	Cerro Mangote	Aguadulce Shelter	Ladrones	Vampiros	Monagrillo	La Mula-Sarigua	Sitio Sierra	Cerro Juan Diaz	AG-125	Natá
	Genus		Species											
Carcharhinidae	Carcharhinus								x		x			
reef sharks	Carcharhinus	cf	altimus		x					x				
	Carcharhinus		altimus									x		
	Carcharhinus		leucas		x	x			x	x	x	x		
	Carcharhinus		limbatus							x	x	x	x	
	Carcharhinus	cf	porosus									x		
	Negaprion		brevirostris							x	x	x		
	Rhizoprionodon		longurio *			x		x	x	x	x	x		
Ginglymostomidae	Ginglymosotoma		cirratum *									x		
Sphymidae	Sphyma									x		x		
hammerhead	Sphyma	cf	lewini								x		x	
sharks	Sphyma		lewini						x	x		x		
	Sphyma	cf	tiburo									x		
Dasyatidae	Dasyatis				x				x	x	x			
sting-rays	Dasyatis	cf	longus							x				
	Dasyatis		longus						x		x	x	x	
Myliobatidae	Aeteobatus		narinari *								x	x		
devil rays	Rhinoptera		steindachneri *						x		x			
Narcinidae	Narcine		entemedor						x		x			
Pristidae	Pristis		unclear (1)		x					x	x	x		
Urolophidae	Himantura		pacifica *								x			
sting-rays	Urotrygon				x				x		x	x	x	
Albulidae	Albula	cf	nemoptera									x		
bonefish	Albula		nemoptera										x	
	Albula		neoguinaica		x			x	x	x	x	x		x
Ariidae	Ariopsis		seemanni		x	x		x	x	x	x	x	x	x
marine catfish	Arius				x	x		x	x	x	x	x	x	x
	Arius		cookei		x	x				x		x		x
	Arius	cf	dasycephalus					x						
	Arius		dasycephalus							x	x		x	
	Arius		kessleri		x	x		x	x	x	x	x		x
	Arius		lentiginosus		x									
	Arius		osculus		x	x		x	x		x			
	Arius	cf	planiceps		x			x						
	Arius		planiceps									x		
	(Arius)		platypogon		x			x			x			x
	Arius		troschelii		x	x		x	x	x	x	x		x
	Bagre		panamensis		x			x	x	x	x	x		
	Bagre		pinnimaculatus		x	x		x	x	x	x	x		
	Cathorops				x	x		x	x	x	x	x		
	Cathorops	cf	furthii			x							x	
	Cathorops		furthii		x			x	x	x	x	x		x
	Cathorops		hypophthalmus		x	x		x				x		
	Cathorops	cf	multiradiatus											x
	Cathorops		multiradiatus		x			x	x		x	x	x	
	Cathorops		steindachneri					x		x	x	x		
	Cathorops		tuyra		x	x			x	x	x	x	x	x
	Selenaspis		dowi *		x	x		x	x	x	x	x	x	x
Balistidae	Sufflamen		verres *								x			
Batrachoididae	Batrachoides				x			x		x		x		
toadfish	Batrachoides		boulengeri		x	x		x		x		x		x
	Batrachoides	cf	pacifici						x		x			
	Batrachoides		pacifici					x	x	x		x		x
	Daector										x			
	Daector		dowi									x		
	Daector		reticulata		x			x	x			x		
Belonidae	Strongylura							x			x	x		x
needlefish	Strongylura		exilis							x				

	Strongylura	cf	scapularis	x									
	Strongylura		scapularis				x	x	x	x	x		x
	Tylosurus						x	x	x	x		x	x
	Tyolosurus		acus				x						
	Tylosurus		cocodrilus				x	x	x	x		x	
Bothidae	Citharichthys	cf	gilberti				x	x	x	x		x	x
flounders	Cyclopsetta		quema				x	x	x				
	Paralichthys		woolmani				x	x					
Carangidae	Alectis		ciliaris *				x	x		x			
jacks and allies	Caranx									x	x		
	Caranx		caballus				x	x	x	x	x	x	x
	Caranx		caninus	x			x	x	x	x	x		x
	Caranx		otrynter	x			x			x	x		
	Caranx		vinctus						x		x		
	Chloroscombrus		orqueta *	x	x		x	x	x	x	x	x	x
	Hemicaranx						x		x	x	x		
	Hemicaranx	cf	leucurus				x	x	x				
	Hemicaranx		leucurus								x		
	Hemicaranx	cf	zelotes					x					
	Hemicaranx		zelotes										
	Oligoplites						x		x	x	x		x
	Oligoplites		altus	x			x	x	x	x	x	x	x
	Oligoplites		refulgens				x	x	x	x			x
	Oligoplites	cf	saurus								x		
	Oligoplites		saurus					x		x			
	Selar *		crumenophthalmus				x			x	x		
	Selene						x	x	x	x		x	x
	Selene		brevoorti	x			x		x	x	x		
	Selene	cf	oerstedii				x						
	Selene		oerstedii						x	x	x		
	Selene		peruviana	x			x	x	x	x	x	x	x
	Trachinotus		kennedyi				x				x		
	Trachinotus		paitensis				x						
Centropomidae	Centropomus				x		x	x	x	x	x	x	x
snook	Centropomus		armatus	x	x		x	x	x		x	x	x
	Centropomus	cf	medius				x						
	Centropomus		medius	x				x	x	x	x		x
	Centropomus	cf	nigrescens		x								
	Centropomus		nigrescens	x					x	x	x		x
	Centropomus	cf	robalito						x			x	
	Centropomus		robalito	x			x			x	x		x
	Centropomus	cf	unionensis	x	x								
	Centropomus		unionensis				x				x		x
	Centropomus	cf	viridis				x						
	Centropomus		viridis	x	x					x	x		
Cichildae	*Aequidens*		*coeruleopunctatus*							x			
	Vieja		*sieboldi*							x			
Clupeidae	Opisthonema	cf	libertate	x	x	x	x	x	x	x	x	x	x
Congridae	Cynoponticus		coniceps *								x		x
Ctenoluciidae	*Ctenolucius*		*species(2)*		x					x			
Curimatidae	*Cyphocharax*		*magdalenae*		x					x	x		x
Cynoglossidae	Symphurus	cf	chabanaudi								x		
Elopidae	Elops		affinis *	x					x		x		x
Eleotrididae	Dormitator		latifrons *	x	x			x		x	x		x
sleepers	Eleotris		picta	x	x					x	x		x
	Gobiomorus		maculatus	x	x					x	x	x	x
Engraulidae	Anchoa			x									
anchovies	Anchoa		spinifera		x						x		
	Anchovia		macrolepidota *								x		x
	Cetengraulis		mysticetus *	x			x				x		
	Lycengraulis		poeyi *				x	x		x	x		
Ephippidae	Chaetodipterus		zonatus				x		x		x		
	Parapsettus		panamensis *				x	x	x	x			x
Erythrynidae	*Hoplias*		*species (2)*		x					x	x		x
Fistulariidae	Fistularia												
cornetfish	Fistularia		corneta				x						
Gerreidae	Diapterus		peruvianus	x	x		x		x	x	x		x
mojarras	Eucinostomus		currani	x								x	
	Eucinostomus		dowii				x		x		x	x	x

	Eugerres									x			
	Eugerres		brevimanus	x									
	Eugerres	cf	lineatus										
	Eugerres		lineatus	x						x			x
	Gerres		cinereus *				x		x				
Gobiidae	Bathygobius									x			
gobies	Bathygobius	cf	andrei	x						x			x
	Gobioides		peruanus	x						x			x
Haemulidae	Anisotremus			x				x			x		
grunts	Anisotremus		dovii	x				x		x	x		
	Anisotremus		pacifici					x	x		x		
	Haemulon												
	Haemulon	cf	flaviguttatum								x		
	Haemulon		flaviguttatum	x									
	Haemulopsis								x	x	x		x
	Haemulopsis	cf	elongatus	x				x					
	Haemulopsis		elongatus				x			x	x	x	
	Haemulopsis	cf	leuciscus					x					
	Haemulopsis		leuciscus	x			x			x	x	x	x
	Haemulopsis		nitidus	x			x			x	x	x	
	Orthopristis		chalceus	x			x	x	x	x	x	x	x
	Pomadasys										x		
	Pomadasys		bayanus				x	x	x	x	x		x
	Pomadasys		macracanthus	x				x		x	x		x
	Pomadasys		panamensis				x			x	x	x	x
	Xenichthys		xanti								x		
Hemiramphidae	Hyporhamphus										x		
halfbeaks	Hyporhamphus	cf	unifasciatus										
Lobotidae	Lobotes		surinamensis	x			x	x	x	x	x		
Lutjanidae	Lutjanus				x					x			
snappers	Lutjanus	cf	aratus					x					
	Lutjanus		aratus								x		
	Lutjanus		argentiventris	x	x		x	x					
	Lutjanus	cf	colorado							x			
	Lutjanus		colorado	x									
	Lutjanus		guttatus	x							x		
	Lutjanus		novemfasciatus	x									
Loricariidae	*Hypostomus*		*Species*		x				x	x	x		x
	Sturisoma		*panamense*		x	x							
Mugilidae	Agonostomus		monticola *								x		
mullet	Chaenomugil		probodiscens *				x		x		x		x
	Mugil	cf	curema	x			x	x	x	x	x		x
Ophicthidae	Echiophis		brunneus						x			x	
snake eels	Myrichthys		tigrinus					x					
Parauchenipteridae	*Parauchenipterus*		*amblops*		x			x	x				
Pimelodidae	*Rhamdia*		*species (2)*		x	x			x				
Polynemidae	Polydactylus									x			
threadfins	Polydactylus		approximans	x			x	x	x	x	x	x	x
	Polydactylus		opercularis	x			x	x	x	x	x	x	x
Pristigasteridae	Ilisha		furthii	x			x	x	x	x	x	x	x
long-fin herrings	Odontognathus				x								
	Opisthopterus										x		
	Opisthopterus		dovii					x			x	x	x
	Opisthopterus		equatorialis								x		
Sciaenidae	Bairdiella			x						x	x		
croakers and	Bairdiella		armata	x			x	x	x		x	x	x
corvinas	Bairdiella	cf	ensifera									x	
	Bairdiella		ensifera	x			x	x			x		
	Cynoscion						x	x	x	x	x	x	x
	Cynoscion		albus	x	x		x	x	x	x	x	x	x
	Cynoscion		phoxocephalus	x			x				x		
	Cynoscion		praedatorius	x			x	x	x	x	x	x	x
	Cynoscion		squamipinnis				x	x		x	x		
	Cynoscion		stolzmanni	x			x		x	x	x	x	x
	Ellatarchus		archidium *				x						
	Isopisthus		remifer *					x			x		
	Larimus			x			x		x				
	Larimus		acclivis				x	x	x		x	x	x
	Larimus		argenteus								x		

	Larimus		pacificus								x		
	Macrodon		mordax *								x		
	Menticirrhus						x				x		
	Menticirrhus		elongatus				x				x		
	Menticirrhus	cf	panamensis						x	x			
	Menticirrhus		panamensis				x	x			x	x	x
	Micropogonias		altipinnis	x			x	x	x	x			x
	Nebris		occidentalis *								x		
	Ophiscion								x	x	x		
	Ophioscion		scierus	x			x	x	x	x	x	x	x
	Ophioscion		typicus	x	x			x	x	x	x	x	x
	Ophioscion		vermicularis	x				x			x		
	Paralonchurus		dumerilii	x			x			x	x		
	Stellifer										x		
	Stellifer		chrysoleuca				x		x		x	x	x
	Stellifer	cf	furthii								x		
	Stellifer		oscitans	x				x			x	x	x
Scombridae	Euthynnus		lineatus *							x	x		
thunnies	Scomberomorus		sierra					x	x	x	x	x	x
Serranidae	Epinephelus						x						
groupers	Epinephelus		analogus	x			x		x				
	Epinephelus	cf	labriformis				x						
Sphyraenidae	Sphyraena	cf	ensis				x		x	x	x	x	x
Sternopygidae	*Sternopygus*		*species (2)*		x		x			x	x		
Stromateidae	Peprilus							x	x		x		
	Peprilus		medius								x	x	x
	Peprilus		snyderi				x	x		x	x	x	x
Synbranchidae	*Synbranchus*		*marmoratus*		x			x		x			
Tetraodontidae	Arothron											x	x
pufferfish	Arothron		hispidus								x		
	Guentheridia		formosa *	x			x	x	x	x	x	x	x
	Sphoeroides											x	x
	Sphoeroides		annulatus	x			x	x	x	x	x	x	x
	Sphoeroides		rosenblatti										
Approximate dates				7000-5000 BP	7000-3000 BP	5000-3000 BP	2300-1800 BP	3500 BP	2300-1800 BP	1900-1500 BP	2300-1500 BP	1000 BP	700-500 BP
Nos. of fish bones analyzed, 1/8" mesh				3553	871	27	6800	14.365	4508	19.482	37.050	2731	124

Notes:
* = monotypic genus in tropical eastern Pacific
(2) - genera under taxonomic revision. It is assumed that each genera has but one species in this area
Taxa in italics are freshwater

TABLE 1

Presence of fish genera and species at 10 pre-Columbian sites around Parita Bay, Panamá, including tentative identifications ("cf").

*: Monotypic in the TEP or in Central America (in the case of freshwater taxa). (1): The specimens in the STRI comparative collection were keyed out as this species before we were aware that *C. obscurus* is found inshore in the Panamic region. This identification requires verification. (2): It is unclear whether there are one or two species of *Pristis* in the TEP. (3): It is likely that the skeletons listed under *A. osculus* in the STRI comparative collection represent two species, one of which is undescribed (R. Betancur, personal communication). (4): According to R. Betancur, the TEP species assigned to *Arius* are likely to represent three genera. (5): Although is likely that all the *Opisthonema* remains refer to this species, which is very abundant today in inshore waters in Parita Bay, we lack specimens of *O. bulleri* and *O. medirastre*, which occur in Panamic waters. (6): The status of the species of these freshwater genera in Panamá is under revision.

this region (Cooke, 1992), epitomize this diversity: the marine catfish (Ariidae, whose New World taxonomy is under revision), comprising 20 described species and some undescribed ones (Betancur *et al.*, in preparation); the grunts (Haemulidae), at least 10 genera and 35 species; and the croakers and corvinas (Sciaenidae), at least 25 genera and 78 species (Robertson & Allen, 2002). Some of these species occur only at the northern and southern edges of the TEP or on offshore islands. Therefore, if we accept the assumption that they would not have occurred naturally in Parita Bay during the relevant time period (7000-500 BP), in a practical sense it is allowable to accept the Panamic region as the geographic universe of our comparative fish skeleton collection. The fact that this collection possesses specimens of all the 18 described species of catfish, all 24 grunts, and 40 of the 46 sciaenids that have so far been formally recorded in this region boosts our confidence in the validity of species-level identifications (as we comment later, there is likely to be a 19th undescribed ariid species).

It is important, of course, to be aware of advances in taxonomy and zoogeography and to revise identifications and quantifications accordingly. Three new species, which have recently been added to the Panamic inshore fish fauna, have proved to be abundant in some parts of Panamá Bay: *Arius cookei* (Ariidae), *Sphoeroides rosenblatti* (Tetraodontidae), and *Paranebris bauchotae* (Sciaenidae) (Walker & Bussing, 1996; Chao, Béarez, & Robertson, 2001; Acero & Betancur, 2002). We have identified *Arius cookei* and *Sphoeroides rosenblatti* in Parita Bay archaeofaunal samples (Table 1; Figure 5). We presumed that the former taxon was an undescribed species on the basis of its osteology several years before it was described, listing it as *Arius species A* or *B* – a hypothesis that was confirmed independently by fish taxonomists (Bussing & López, 1993). When *S. rosenblatti* was described, we revised all archaeological tetraodontid bones in order to check for its presence. Materials attributable to this species had been identified as *Sphoeroides* sp. We have not yet checked to see whether *P. bauchotae* is present in Parita Bay archaeofaunas.

Incorrect identifications of the fish that provide the skeletons used by archaeozoologists are known to occur and may insidiously go unnoticed for a long time. We have had the advantage of being able to consult with specialists in the case of difficult or new species for which preserved specimens are available at the Smithsonian Tropical Research Institute (STRI) in Panamá. Even so, our overconfidence has generated some noxious mistakes, the most important of which was to underestimate the diversity of Panamic corvinas (Sciaenidae: *Cynoscion*). Our failure to identify correctly one species in modern fish catches, *C. praedatorius*, meant that we had to revise earlier identifications of all sciaenid bone samples. Another mistake, which was recently identified by a Colombian ichthyologist, Ricardo Betancur, was the inclusion under one species, *Arius osculus*, of skeletons that are clearly from *two* very similar species, one of which accords with the original description of *A. osculus*, while the other appears to be an undescribed species. At a later date, we will have to reanalyze the archaeological material that has been listed under *A. osculus*.

The fact that the distribution and abundance of food fish species within a coastal system may change through time in response to biotic, abiotic, and historical factors should be considered when pre-Columbian and present-day fishing records are compared. For example, one inshore marine catfish, the gloomy catfish (*Cathorops hypophthalmus*), is extremely abundant today – it comprised more than 80% of the catches in an intertidal trap we studied in the 1990s in an estuarine inlet at the edge of Parita Bay – but it is rare in archaeofaunal samples (Cooke, 1993, 1996; Cooke & Tapia, 1994b; see Figure 7 for the trap's location). Although we must be aware that this discrepancy may give a false impression of the magnitude of the change in abundance – in light of the aforementioned osteological underrepresentation of this and other *Cathorops* species, which we comment on below – we hypothesize that *C. hypophthalmus* may have increased recently because of the anthropogenic eutrophication of Panamá Bay. With twice the number of gill-rakers than those of the other TEP ariid catfish, it probably feeds mostly on plankton.

OSTEOLOGY, PHYLOGENY AND ECOLOGY

Molecular studies indicate that the species of many TEP genera are very ancient. Even so, the ease with which they can be separated osteologically varies greatly within families and genera, and also vis-à-vis individual elements of the skeletal anatomy. For example, although the snook (*Cen-*

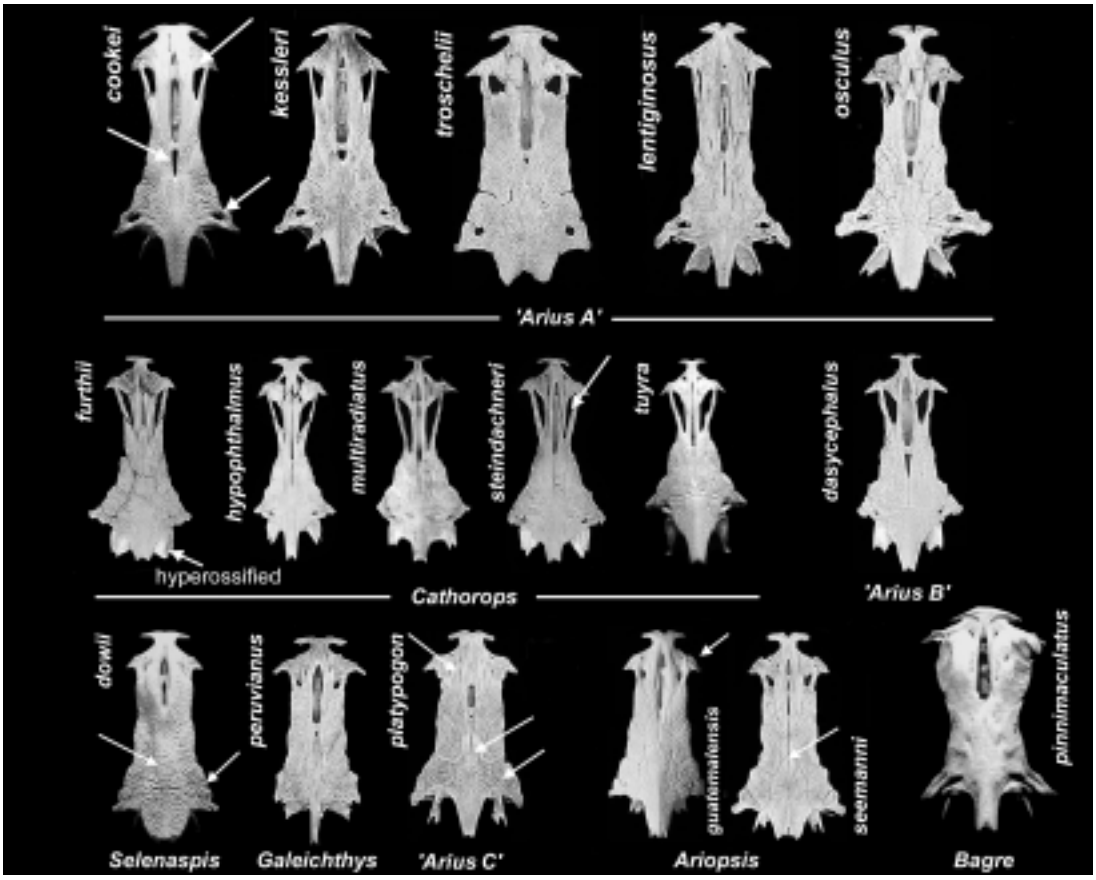

FIGURE 2

In spite of their confusing external appearance, the tropical eastern Pacific marine catfish (Ariidae) can be differentiated generically and specifically on the basis of their neurocranial anatomy although the accuracy with which individual species can be identified from a single bone element varies among genera, and must be determined empirically. Features that are taxonomically significant at the generic level are highlighted with arrows (i.e., the "fontanelle" anterior to the supraoccipital and posterior to the supraethmoid; the space between the prefrontal and frontal, and the orifice – or lack of it – between the supracleithron, sphenotic, and scale bone). The congo catfish (*Cathorops furthii*) is the only described TEP species of this genus that has hyperossified epiotics, which permit identification even when fragmented. All illustrated species occur in Parita Bay except the Peruvian catfish (*Galeichthys peruvianus*), which appears to be restricted to waters cooled by the Peruvian current. Two species that also occur in Parita Bay, the Chihuil catfish (*Bagre panamensis*) and flathead catfish (*"Arius A" planiceps*) are not illustrated. The phylogenetic relationships among species formerly attributed in the TEP to *Arius* are currently under revision by R. Betancur, whose provisional groupings ("*Arius A, B,* and *C*") we have honored. (Photos of skulls by R.G. Cooke, not to scale. For size details, see Cooke, 1993, 1996).

tropomus) diverged during the Pliocene and before (Tringali *et al.*, 1999), the six TEP species look outwardly so similar that they are difficult to differentiate without detailed laboratory analysis (especially *C. viridis* from *C. nigrescens*, and *C. armatus* from *C. robalito* and *C. unionensis*). Certain well-preserved bone elements can be diagnostic to species, but they are few in number. A similar situation affects the snappers (*Lutjanus*), whose TEP species, being more ecologically heterogeneous than snook species, are more informative about the habitats in which prehistoric people fished. That we have not yet identified the golden snapper (*Lutjanus inermis*), blue-and-gold snapper (*L. viridis*), or Pacific red snapper (*Lujanus peru*) in modern inshore fish catches in Parita Bay during 25 years of observations, and that we have identified only one element of the last-named species in archaeofaunal samples (at Cerro Juan Díaz), accord with these three species' preference for reefs and deep water over rocks, and their concomitant reluctance to enter turbid estuaries.

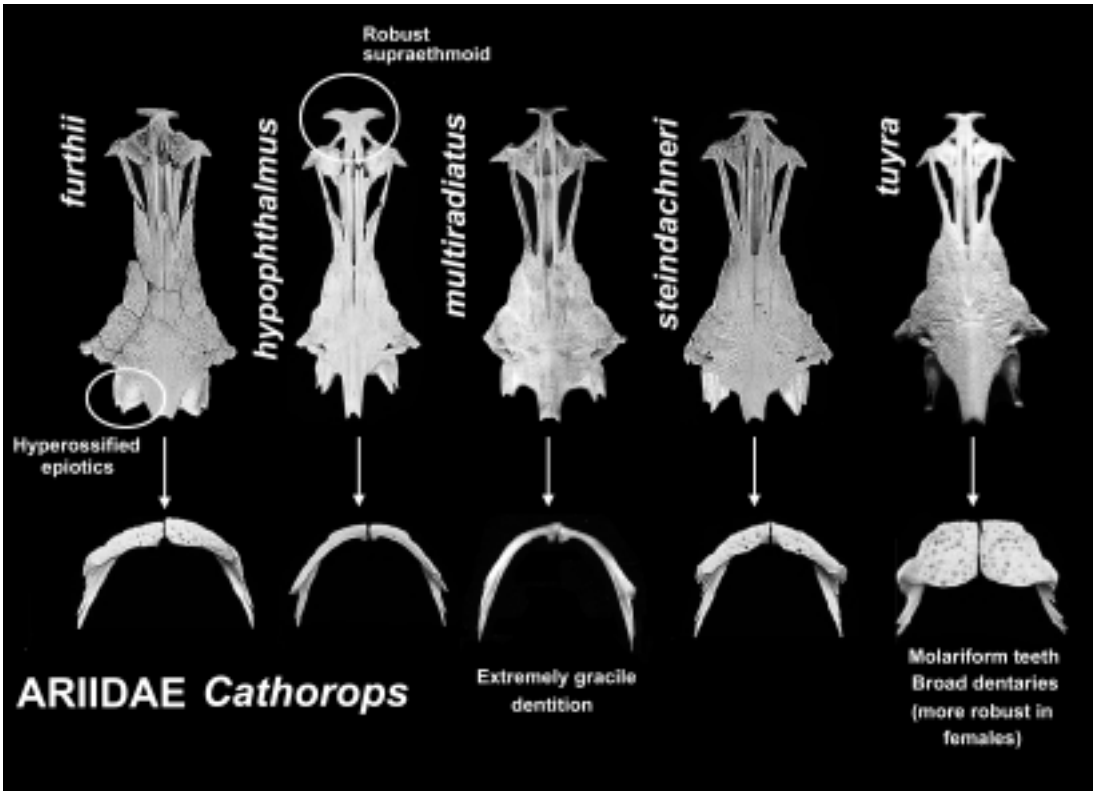

FIGURE 3

The dentition of TEP *Cathorops* species reflects dietary differences among species: the extreme molarization of the teeth of *C. tuyra* and broadness of the dentaries and palatine tooth patches are appropriate for grinding molluscs. The gracile dentition of *C. hypophthalmus* and *C. multiradiatus* is presumably related to a planktivore diet, although this has not, to our knowledge, been determined by stomach content analysis. *C. furthii* differs from its congeners with respect to the hyperossified epiotics and from *C. hypophtalmus* regarding the robust supraethmoid.

On the other hand, the two widespread TEP species of threadfin (*Polydactylus approximans* and *P. opercularis*), which outwardly look so similar that a quick identification in the field is often a wrong one, are remarkably divergent osteologically, so that most of the elements of the skeletal anatomy, including vertebrae, are sufficiently diagnostic to permit the differentiation of these two species even on the basis of highly fragmented materials.

Even if the ecology and behavior of species like the TEP snook and threadfins are so similar that identifying them correctly does not greatly enhance our *interpretations* of inshore fish faunas and prehistoric fishing methods, it is important to try to separate them from the point of view of *quantification*. Six snook bones from six different body parts, which would give an MNI of 1 at the genus level, can obviously represent six different individuals.

In other genera, osteological idiosyncrasies may be more marked in one species than among its congeners. This is true for the small congo catfish (*Cathorops furthii*), which is quite divergent from the other five described TEP species in this genus. Even tiny fragments of some of its bones can be readily identified – especially the hyperossified epiotics (Figure 3). This situation must mask the real abundance of the other four species, many of whose bones can be differentiated from *C. furthii*, but with less confidence from each other. Therefore it is possible that the notable abundance of *C. furthii* at one Parita Bay site (Monagrillo) reflects this osteological-cum-taxonomic bias (Figure 5).

The marine catfish (Ariidae) – the most frequent family in many TEP archaeofaunal samples

(Cooke, 1992) – look so similar outwardly that their taxonomy is in disarray. Nevertheless, they exhibit many species-specific osteological characteristics, which can be identified by carefully comparing archaeological and modern samples (Figure 2; Cooke, 1993, 1996). There are 21 described or soon-to-be described species in the TEP; probably there are several more. Skull morphology, cladistics, and mtDNA studies by Colombian ichthyologist Ricardo Betancur are demonstrating that one genus, *Arius*, contains at least three phylogenetically distinct lineages in the TEP (grouped provisionally as "*Arius A*," "*Arius B*," and "*Arius C*"). One genus formerly considered monotypic (*Sciadeops*) belongs to "*Arius A*" (Betancur *et al.*, in preparation). One TEP species, *Galeichthys peruvianus*, is found only in waters adjacent to the cool Peruvian current. The others are all tropical and inshore; but their ecologies and behaviors are remarkably different. The Panamanian catfish (*Arius lentiginosus*), as its common name implies, has been recorded only in Panamá. We have seen it only once in 25 years. But it is present in an archaeofaunal sample – Cerro Mangote – deposited between 5,000 and 7,000 years ago (Cooke & Ranere, 1999). Perhaps it was commoner then because water conditions were different.

Some marine catfish osteological differentiation appears to be trophic even though we are ignorant of field studies of the feeding behavior of the six currently recognized TEP *Cathorops* species, which we present as our example. The Tuyra catfish (*C. tuyra*) has a striking molariform dentition and greatly expanded dentaries (especial-

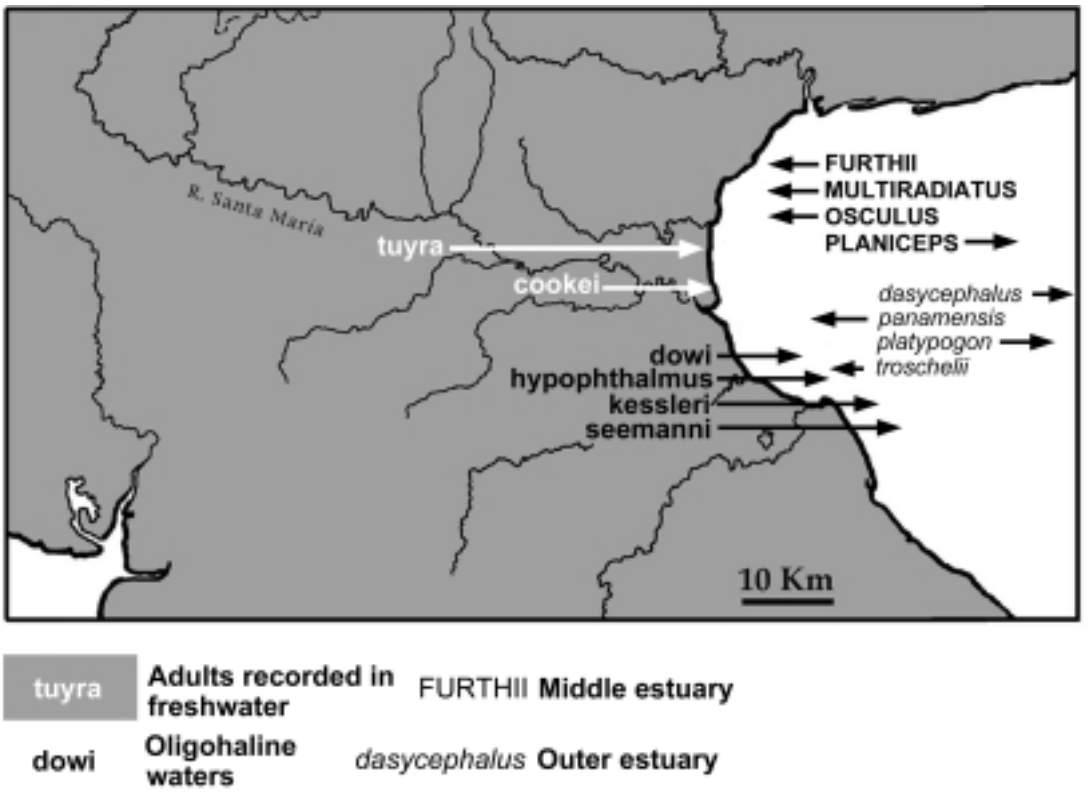

FIGURE 4

Schematic summary of the habitat preferences of marine catfish (Ariidae) around the Parita Bay littoral. We have identified four groups of species that, on the basis of catch records from an intertidal fish trap (Cooke & Tapia, 1994 a), marine fish movements in the River Santa María (Cooke & Tapia, 1994 b), and artisanal fish catches, are most abundant as adults in (a) the upper estuary (including completely fresh water); (b) the oligohaline stretches of rivers, and river mouths; (c) the middle estuary (mudflats, mangrove-fringed shores, and the mixing zone); and (d) the outer estuary, where water is more constantly saline, clearer, and/or deeper. The arrows indicate that the species in question move readily into the adjacent habitat. "*Arius B*" *dasycephalus* and "*Arius C*" *platypogon* appear to be the species that frequent the deepest water in the TEP. There is not enough information on "*Arius A*" *lentiginosus* to infer its habitat preferences.

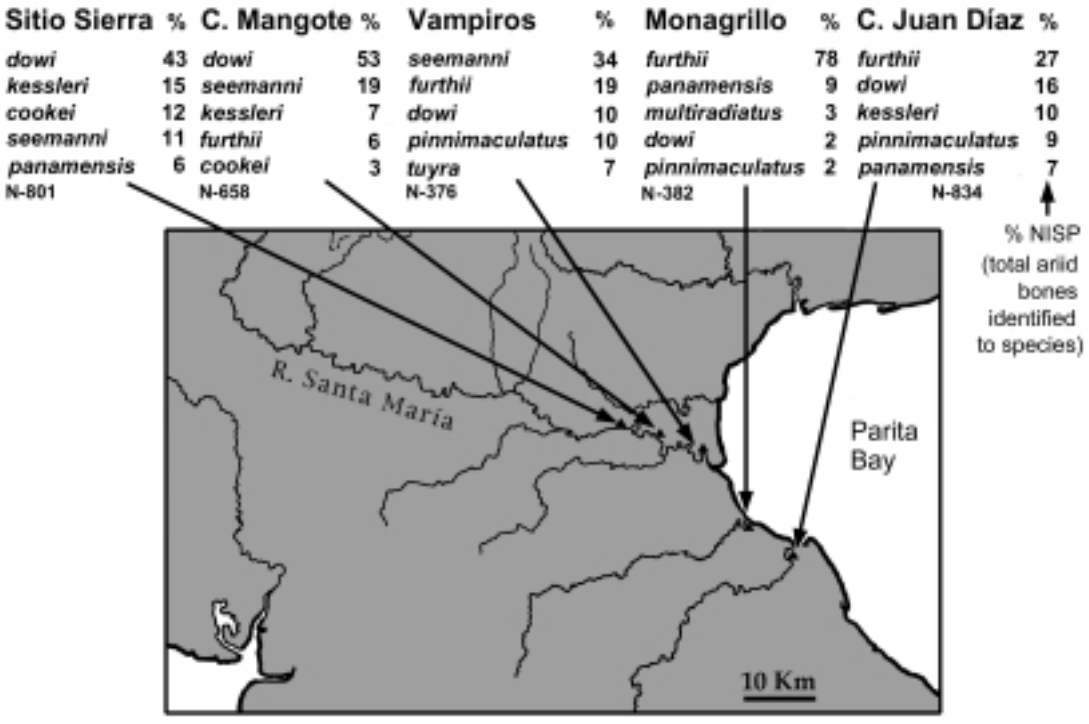

FIGURE 5

Abundance of the five most frequently caught marine catfish (Ariidae) species at five pre-Columbian sites around Parita Bay, expressed as % NISP (i.e., the total number of ariid bones in each sample or group of samples that we identified to species).

ly in females). Gut contents observed during specimen preparation suggest that it specializes on mollusks. Catch data along the Santa María river suggest it spends a large part of its adult life in completely fresh water (it has been recorded 60 Km from the sea). The gracile dentition of its congeners, the many-rayed catfish (*C. multiradiatus*) and gloomy catfish (*C. hypophthalmus*), and the latter species' large gill-raker count, point towards a planktonic diet (Figure 3). We surmise that the Tuyra catfish has experienced a very ancient symbiosis with the brackish water shellfish genus *Polymesoda*, abundant in archaeofaunal samples in Parita Bay, which we have often observed in *C. tuyra* gut samples.

WHERE DID PEOPLE FISH IN PRE-COLUMBIAN TIMES?

If we can identify fish bones to species and know something about each species' distribution in inshore waters, we can use these data to help us infer which habitats were being used by prehistoric fisherfolk. In Figure 5 we summarize the distribution of the five most abundant marine catfish species at five Parita Bay archaeological sites. Figure 4 presents schematically our interpretation of the habitat preferences of the 18 locally available species, based on fish catch data obtained at a tidal trap on the shore of Parita Bay between 1991 and 1993 and marine fish distribution in the tidal stretches of the River Santa María (Cooke & Tapia, 1994 a, b), complemented by 30 years' informal observations made on artisanal and shrimp-boat catches during trips to obtain comparative specimens in Parita and Panamá Bays. All nine top-ranked species are inshore or riverine; none of the species that prefer the deeper, outer estuary, was commonly taken, i.e., "*Arius B*" *dasycephalus*, "*Arius C*" *platypogon*, or "*Arius A*" *troschelii*. At two sites situated along the main course of the Santa María river, Sitio Sierra and Cerro Mangote, *Arius cookei* has a high rank – predictably, because this species is fished in the main channel today,

from the mouth to at least 20 Km inland (Cooke & Tapia, 1994a). At Cerro Mangote, where the fish bones thrown onto kitchen middens between 7000 and 5000 BP point towards a fishing strategy directed towards large, non-shoaling taxa, the commonest marine catfish species is the brown catfish (*Selenaspis dowi*) (Cooke & Ranere, 1999), which grows to a large size (SL > 1 m) and is particularly abundant in the oligohaline stretches of rivers and in mangrove channels. Conversely, the Monagrillo ariid sample (ca 4600 BP) is dominated by the small (SL < 30 cm) congo catfish (*Cathorops furthii)*, a shoaling species, which moves into shallow waters. Aerial photographs indicate that Monagrillo was situated at the time of its major occupation alongside a now-silted lagoon and close to the mouth of the Parita River, which would have been appropriate habitats for this species (Willey & McGimsey, 1954; Cooke, 1995).

The distribution of croaker or corvina species (*Cynoscion*) also epitomizes the inshore and riverine orientation of pre-Columbian fishing practices around Parita Bay. Figure 6 summarizes the frequency of *Cynoscion* species caught at five sites on the basis of the frequency of the bones that we have identified to species. Predictably, the deep-water *C. nannus* and the striped corvina, *C. reticulatus*, which shoals some distance offshore and is common in shrimp boat catches made beyond the mixing zone, are absent. The white corvina (*C. albus*), which moves into the oligohaline stretches of the river, apparently to spawn (Cooke & Tapia, 1994b), represents over half the identified bones. Two other species, which are frequent in the turbid plume of the estuary, but more rarely enter the tidal river – *C. stolzmanni* and *C. phoxocephalus* – together comprise 31% of the sample.

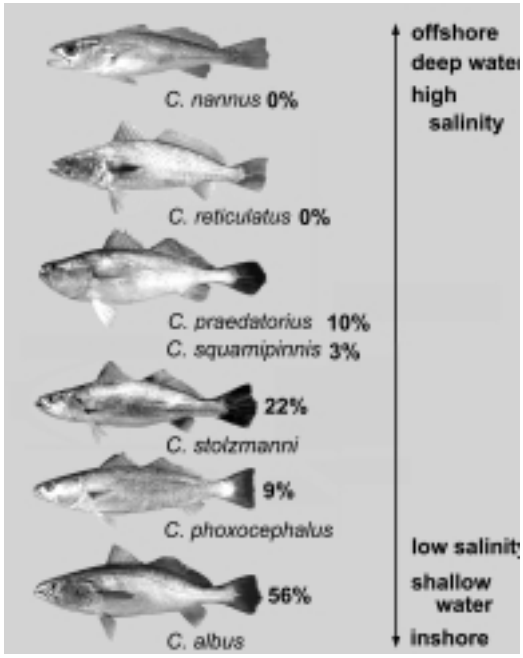

FIGURE 6

The corvina (*Cynoscion*) species in Parita Bay are fished in different areas of the estuary. This figure compares the region-wide abundance of these species (expressed as % of all *Cynoscion* bones identified to species pooled from five sites [N = 281]) with a hypothetical schematization of their habitat preferences based on observations of fish caught in an intertidal fish trap (Cooke & Tapia, 1994a), of fish movements in the River Santa María (Cooke & Tapia, 1994 b), and of catches by local fishers. *C. albus* is the species that most frequently moves into the oligohaline stretches of rivers. *C. reticulatus* is rarely caught in the mixing zone. *C. nannus* is found in deep water well offshore. *C. phoxocephalus* and *C. stolzmanni* are abundant in the turbid mixing zone. *C. praedatorius* appears to prefer clearer, deeper water than these two species. (Photos of fish courtesy of D. Ross Robertson and the Smithsonian Tropical Research Institute, Panamá).

FISHING TECHNIQUES

In 9 of the 10 Parita Bay sites we have not found evidence for fishing gear – a fact that indirectly supports the hypothesis that tidal traps and weirs would have been used for the provision of much freshly consumed and salted and dried fish in pre-Columbian times (Cooke, 2001). The exception is Cerro Juan Díaz, where a line of small stones with holes found in a refuse dump suggests their use as weights for nets or lines (Mayo, 2004). This site is located at the southern edge of Parita Bay where the turbid water plume is narrower than at the center of the estuary and where sandy beaches stretch southwards to the southern tip of the Azuero Peninsula (Cooke & Sánchez, 1998). Fish species distribution in the five archaeofaunal samples that have been studied reflects the proximity of these geological features (Jiménez, 1999; Jiménez & Cooke, 2001). The best indicator that the people who obtained fish for Cerro Juan Díaz made sorties in boats to fish into deeper waters beyond the turbid mixing zone, probably with hook and line, is the frequency of one of the TEP *Pomadasys* species, the Panamanian grunt (*Pomadasys panamensis*), which local fisherfolk catch today with hooks in water between 6 and 15 fathoms deep. This shoaling species is much more prevalent in the sample of *Pomadasys* bones at

Cerro Juan Díaz than are those of its congeners, *P. bayanus* and *P. macracanthus*, which are abundant along tidal rivers and are the commonest species of this genus at Cerro Mangote and Sitio Sierra located along the main channel of the River Santa María (Figure 7). The spotted rose snapper is the most frequent *Lutjanus* species in the Cerro Juan Díaz samples. Since it frequents coral reefs and sandy substrates, it was probably fished with hook and line on the same sorties that brought in catches of the Panamanian grunt.

TRANSPORT OF FISH

The archaeofaunal data from the 10 studied sites indicate that fishing in Parita Bay concentrated on the middle and upper estuary (tidal rivers, mangrove channels, pools in high tidal flats, intertidal mudflats, sandy beaches, and small rocky islets close to shore). Predictably, there is no or little input from pelagic species that swim a considerable distance offshore or from others that prefer coral reefs or rocky substrates. That does not mean, however, that all the fish species consumed or used ritually during the pre-Columbian period were obtained in close proximity to every site. The inhabitants of Cueva de los Ladrones, located at 300 m above sea level and 25 Km from the present-day coastline, consumed small inshore marine fish during the Early Ceramic A period in the regional sequence (4500-3000 BP) (Table 1; Cooke, 2001). Marine catfish bones have been recovered 60 Km from the Parita Bay coast. At Sitio Sierra, which between 1800 and 1500 BP would have been about 13 Km from the sea along the freshwater tidal sector of the Santa María river, about 70% of the fish consumed during this period were of marine origin (Cooke & Ranere, 1999).

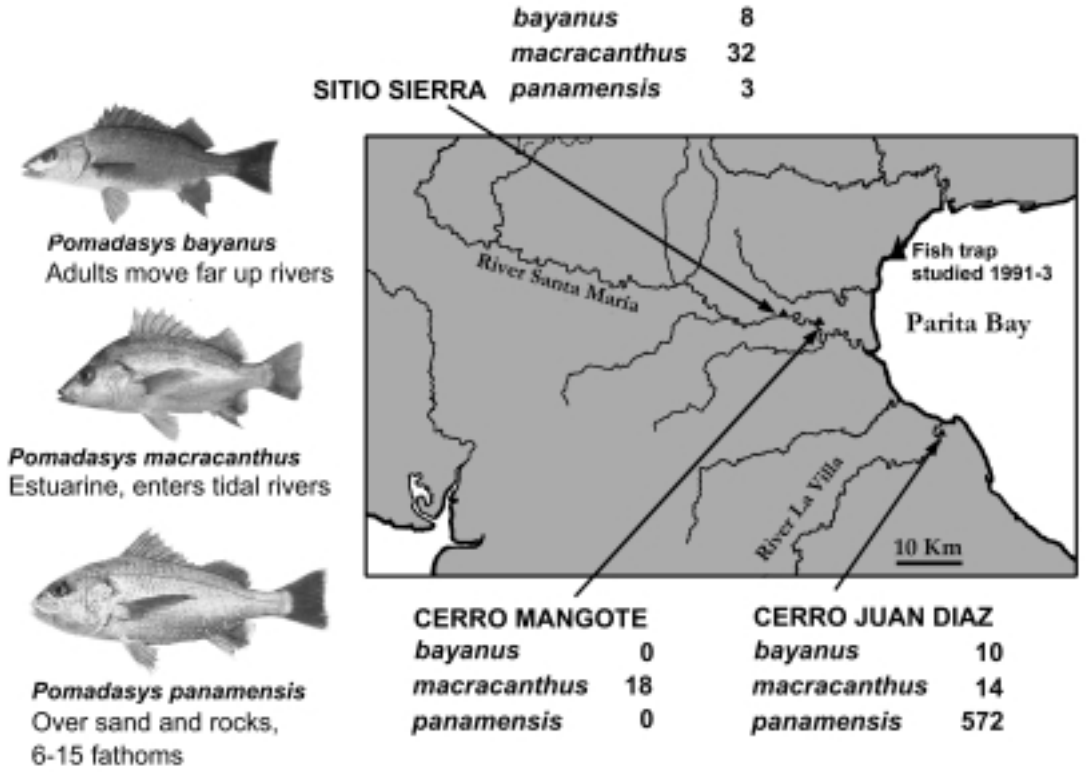

FIGURE 7

Abundance of three widespread grunt (Haemulidae: *Pomadasys*) species at three pre-Columbian sites around Parita Bay, Panamá (*P. bayanus*, *P. macracanthus*, *and P. panemensis*) (numbers of bones identified for each species). (Photos of fish courtesy of D. Ross Robertson and the Smithsonian Tropical Research Institute, Panamá).

The four most frequent marine species avoid the turbid waters of the mixing zone of the estuary, but move into sandy bays and into river mouths during the dry season: thread-herrings (*Opisthonema*), Pacific moonfish (*Selene peruviana*), brassy grunts (*Orthopristis chalceus*) and Pacific bumpers (*Chloroscombrus orqueta*). In order to fish them, Sitio Sierra's inhabitants would have had to make canoe journeys in excess of 20 Km (taking into account the river's meanders). It is more likely that these and other marine fish that do not enter the tidal river were brought to the site in a preserved state – perhaps being exchanged for other produce in the markets the Spanish observed in this area of Panamá in the early 1500s. Ethnoarchaeological data suggest that salting and drying was the method used to preserve them (Zohar & Cooke, 1997). We are currently investigating a rock shelter located at the mouth of the Santa María with a view to testing the hypothesis that it was this site that provided preserved fish for Sitio Sierra and other villages located about every 3 Km along the lower course of the river during the last 2,000 years of the pre-Columbian period (Cooke & Ranere, 1984; Pearson & Cooke, 2002; Cooke, in press).

SUMMARY

A lot of work has gone into building up a comparative collection of fish skeletons from the Panamic region of the eastern tropical Pacific in order to identify archaeological bone samples from Parita Bay pre-Columbian sites as accurately as possible. To achieve this, we have worked closely with such taxonomists and fish biologists as William Bussing, Arturo Acero, and D. Ross Robertson. We have been mistaken about some details of taxonomy and have sometimes made erroneous identifications, not only of fish in present-day catches, but also of archaeological specimens. These have taken time to rectify. The presence and/or frequency of the 150-odd marine species we have identified (Table 1) are consistent with the present-day environmental characteristics of Parita Bay. Nevertheless, the distribution and abundance of individual fish species at sites occupied along this rapidly changing littoral zone during the period 7000-500 BP confirm the exploitation of specific habitats at specific points in time, and help us define how far the pre-Columbian population traveled to obtain fish (or how extensive their exchange contacts were) as well as the practices and techniques they used for fishing. Our analysis has been particularly useful for reconstructing fishing practices at sites where the topography has changed radically because of marine transgression and coastal progradation. Even if people did not travel far from shore in order to fish for food and ritually important animals, a few species, such as the Panamanian grunt and spotted rose snapper, which live in deeper water and whose efficient capture would have required hook and line or sophisticated nets, were important at those settlements, which were in a position to exploit these resources effectively, making short boat trips beyond the estuarine mixing zone.

Comparing archaeological bones visually with those of specimens in a comparative collection is, obviously, an empirical process and intrinsically subjective. Thus the accuracy and dependability of the species-level identifications that rely on that process are open to question. We point out that, just as Passerine bird diversity at the species level is difficult to ascertain with fragmented bone samples, so is the identification of many fish species. We show here, however, that making the effort to differentiate fish species provides details about regional and diachronic fishing patterns that cannot be achieved with less precise taxonomy.

ACKNOWLEDGMENTS

We are grateful to two reviewers whose comments were most useful. We appreciate Ricardo Betancur's allowing us to refer to unpublished data on marine catfish taxonomy. Philippe Béarez kindly provided the specimen of *Galeichthys peruvianus.* We have benefited greatly from the taxonomic expertise and zoogeographic and ecological knowledge of William Bussing, Arturo Acero, Ricardo Betancur, and D. Ross Robertson. Thanks are due also to the Walcott Fund of the Smithsonian Institution for providing funds for the archaeozoological project in Parita Bay for several years.

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