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Archaeozoological Papers in Honour of Ina Plug

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Archaeobiodiversity of Ichthyofaunas from the Holocene Sahel

Nadja Pöllath[†‡]*, Joris Peters*[‡]*, and Hélène Jousse*[§]

ABSTRACT. Taxonomic richness and biodiversity are useful measures to biologically characterise water bodies. When applied to archaeoichthyological samples from prehistoric sites in the northern Nilo-Sudanic ichthyofaunal Province of Africa, these parameters can help archaeologists understand the nature of the palaeodrainages that shaped the North African arid landscape in Holocene times. However, taxonomic composition of archaeoichthyological assemblages does not exactly reflect the natural fish population once inhabiting the water body. Indices of biodiversity based on faunal remains of anthropogenic origin should therefore be referred to as archaeobiodiversity indices (aD). Since Holocene water bodies cannot be characterised ecologically in sufficient detail on the basis of archaeobiodiversity indices alone, an approach is presented here that combines this parameter with a measure indicative of the type and quality of the local aquatic environment, namely the NISP ratio of Latidae to Clariidae in the assemblages. Latidae are known to prefer deeper, well-aerated open waters whilst Clariidae prosper in shallow, closed waters characterised by fluctuating temperatures and oxygen concentrations. Using this approach a classification of archaeological sites according to ichthyological diversity and predominant aquatic habitat can be attempted.

Introduction

Arid zones in northern Africa experienced considerable climatic change during the late Quaternary. The northward shift of the Intertropical Convergence Zone appears essential to explain the early Holocene Climatic Optimum since it brought about higher precipitation rates throughout much of the previously hyper-arid Sahara (Gasse and Roberts 2004). The rising ground water tables in the Early Holocene enabled sub-Saharan biomes to extend much further north, along (semi)permanent water courses some 1100 km in the central part of northern Africa and up to 600–800 km in its eastern part (Peters *et al.* 2007). Invertebrate and vertebrate taxa from Holocene anthropogenic contexts provide valuable information to reconstructing past economies and environmental conditions in arid zones. In this respect Holocene fish remains from the Sahara and Sahel are of particular interest because they testify the former existence of numerous water bodies which were connected to major river systems (Van Neer 1989). It is therefore not surprising to find traces of settlements associated with the extensive palaeodrainage systems that were active in the Sahara and the Sahel throughout much of the Holocene. However, if prehistoric human groups relied on fish as a source of proteins, it may have been in varying intensity depending on the local hydrological conditions. Larger, permanent water bodies could sustain human groups specialised in fishing, whereas at near temporarily flooded depressions, fishing may have been a seasonal, opportunistic activity. As could be illustrated by Linseele (2005:110) alternative economies can be evidenced in (pre)historic Sahelian West Africa. However, in order to minimise the impact of unpredictable events inherent to arid zones, complementary activities such as hunting, gathering and fowling may have been essential to avoid periods of food shortage, if necessary even an exchange with herders and farmers inhabiting the same region (Van Neer 2002). Besides elucidating the role of fish as a source of animal protein in the human diet, Holocene archaeoichthyological assemblages also allow insight into local ecogeographical conditions. These can be assessed by considering the present-day ecological requirements of the fish taxa identified and by evaluating species richness and abundance in the samples.

In this paper, dedicated to our distinguished colleague Ina Plug, aspects of fish biodiversity in Holocene anthropogenic contexts from the Nilo-Sudanic Province are considered. As such, the Holocene distribution of fishes in the arid zones of North Africa is the result of different interacting processes. These include, for example, the climatic or geological events that caused connection between, extension and/or isolation of river catchments, the changes in the

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overall size of the different river basins and the adaptations of the different fish taxa to disperse and survive in water bodies characterised by marked seasonal changes in water level and chemistry. Though fish bone assemblages provide valuable insights into the Holocene ichthyological record of the study area, their taxonomic composition in an assemblage appears not very appropriate to assess diversity in a true biological sense. Therefore, when discussing taxonomic diversity calculated on the basis of anthropogenic assemblages, the results obtained should be referred to as indices of archaeobiodiversity (aD).

In this paper the archaeobiodiversity in Holocene ichthyofaunas from the Niger, Chad and Nile systems are evaluated. Indices were calculated for fish bone assemblages exhibiting sufficient sample size (Figure 1). Archaeobiodiversity indices, however, are not as much informative as necessary relative to the ecology of a water body. Therefore an approach will be presented combining this parameter with a measure indicative of the type and quality of the local aquatic environment. This will enable a classification of sites from an ecological viewpoint.

The Sites and Their Ecogeographical Setting

Table 1 presents an overview of the archaeological sites and their dates of occupation considered in this study (Figure 1), as well as the number of fish bone specimens (NISP) per family. In addition, information regarding the ecogeographical setting of the sites and their archaeofaunas is also considered.

Niger River Basin

Archaeological sites yielding ample ichthyofaunal remains have been excavated in the Méma, a vast plain located to the west of the Inland Niger Delta in central Mali. The Inland Niger Delta, also known as the Macina, consists of a wide floodplain and a complex system of shallow lakes extending seasonally beyond the banks of the river. In former times the Macina also included the Méma depression. Here, the sites of Kobadi, Kolima and Akumbu are situated on the shore of a former lake (Table 2). They evidence the presence of human groups from the 2nd millennium cal. BC to AD 1400. Kobadi, the earliest site, seems to have been inhabited permanently (Jousse *et al.* in press). The site of Kolima-Phase I was inhabited contemporaneously with Kobadi, whereas Kolima-Phase II clearly post-dates it (Table 1) (MacDonald and Van Neer 1994). After a phase of abandonment people settled again on a water corridor shore, this time at Akumbu, a location which also witnessed two occupation phases (MacDonald and Van Neer 1994). During the prehistoric inhabitation of the Méma local hydrological conditions shifted from a large fluvial lake

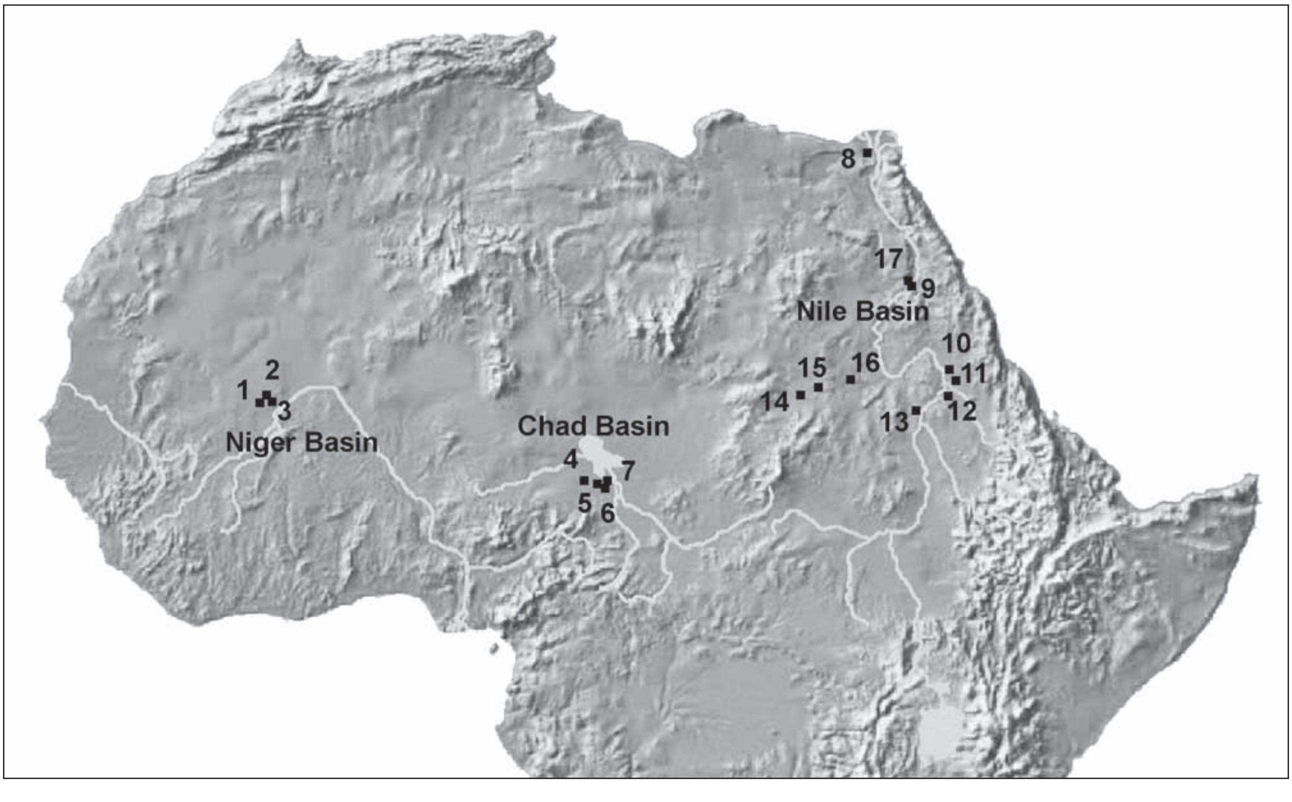

Figure 1. Localisation of the Holocene ichthyological record in three main river basins of northern Africa. See table 1 for corresponding numbers 1 to 16. No. 17 corresponds to Late Palaeolithic Wadi Kubbaniya.

Table 1. Overview of the Holocene ichthyofaunal assemblages under study, with their geographical position, chronological data, sample size and references.

Drainage basin/ Country	Map	Site - Level	Archaeological Dating	Site occupation	NISP Family level	Literature
Niger / Mali	2	Kobadi	Late Stone Age	1955–1415 cal BC	8876	Jousse et al., submit
	3	Kolima I	Late Stone Age	1700–1300 cal BC	764	MacDonald/Van Neer, 1994
	3	Kolima II	Late Stone Age	1300 to 500 cal BC	1410	MacDonald/Van Neer, 1994
	1	Akumbu Period a	Middle Iron Age	AD 600–1000	483	MacDonald/Van Neer, 1994
	1	Akumbu Period b+c	Late Iron Age	AD 1000–1400	39	MacDonald/Van Neer, 1994
Chad / Nigeria	4	Gajiganna (NA 90/5A)	Gajiganna Culture IIb	1500–1200 BC	389	Linseele 2005
	4	Gajiganna (NA 90/5BI)	Gajiganna Culture IIa/b	1500–1000 BC	810	Linseele 2005
	6	Kursakata (NA 93/46)	Late Stone Age	1000–700 BC	624	Linseele 2005
	6	Kursakata (NA 93/46)	Early Iron Age	700 BC–AD 300	16870	Linseele 2005
	7	Mege (NA 94/7-I)	Early Iron Age	550 BC–AD 50	1651	Linseele 2005
	7	Mege (NA 94/7-II)	Early / Late Iron Age	AD 50–700	534	Linseele 2005
	7	Mege (NA 94/7-III)	Late Iron Age	AD 700–1150	415	Linseele 2005
	7	Mege (NA 94/7-IV)	Late Iron Age–Recent	AD 1150–1983	328	Linseele 2005
	5	Ngala (NA 93/45-I)	Late Iron Age	?–7th cent. AD	397	Linseele 2005
	5	Ngala (NA 93/45-II)	Late Iron Age	8th–10/11th cent. AD	893	Linseele 2005
	5	Ngala (NA 93/45-IIIa)	Late Iron Age	10th–12th cent. AD	361	Linseele 2005
	5	Ngala (NA 93/45-IIIb)	Late Iron Age–Historical Period	14/16th–18th cent. AD	276	Linseele 2005
	5	Ngala (NA 93/45-IV)	Recent	19th–20th cent. AD	346	Linseele 2005
Nile/Egypt	8	Merimde	Predynastic	4700 ± 66–4311 ± 50 cal BC	9428	von den Driesch/ Boessneck 1985
	9	Elephantine	Old/Middle Kingdom	4–11th dynasty; 2600–1900 BC	10337	Boessneck/von den Driesch 1982; von den Driesch 1986
Nile/Sudan	10	Aneibis	Early Khartoum/ Khartoum Mesolithic	8000–6000 cal BC	1186	Peters 1995
	11	Abu Darbein	Early Khartoum/ Khartoum Mesolithic	8000–6000 cal BC	588	Peters 1995
	12	Ed Damer	Early Khartoum/ Khartoum Mesolithic	8000–6000 cal BC	2584	Peters 1995
	13	Jebel Umm Marrahi	Early Khartoum/ Khartoum Mesolithic	8000–6000 cal BC	1431	Gautier/Linseele/Van Neer 2002
Wadi Howar/ Sudan	15	Rahib 80/87	Dotted Wavy Line horizon	late 6th and 5th mill. BC	554	Jesse 2003
	16	Abu Tabari S02/1	Leiterband/herringbone pattern horizon	1st half of 4th mill. BC	4041	unpublished
	14	Djabarona 84/13	Leiterband horizon	1st half of 3rd mill. BC	3419	Van Neer/Uerpmann 1989; Keding 1997

connected to the main river (Kobadi, Kolima I) towards a system of smaller, isolated, more seasonal water bodies receiving water only during the rainy season or from inundations during the Niger floods (Kolima II, Akumbu-a). Today the Méma still carries water during the wet season, but this is due to local precipitation. In the absence of any connection with the River Niger fishes are absent from these seasonal pools.

Chad Drainage Basin

Sites of interest are located in north-eastern Nigeria, a region dominated by the presence of Lake Chad. About 90% of the lake's water supply stems from the Chari and Logone rivers. Their sources are situated more than 500 km to the south. Inhabitation of this area in north-eastern Nigeria only became possible after the retreat of Lake Mega-Chad around 2000 cal. BC. The earliest settlements are found in a geographical zone called the Bama Deltaic Complex (or Gajiganna area) (Linseele 2005:Table 3). Some low relief features were formed by previous deltas of the Yedseram and Ngadda rivers (Breunig *et al.* 1992). In its central section sand plains and clay depressions predominate, whereas flat, stabilised longitudinal dunes occur in the north and south-east. The clay depressions are believed to be the remnants of an ancient lagoon formed by the backwaters of Lake Mega-Chad (Breunig *et al.* 1993). During the rainy season they are filled with water and some of them even contain water year-round. Present-day Gajiganna, which gave its name to the archaeological complex, is a fairly recently founded Kanuri village. A group of four settlement mounds (NA 90/5A-D) is situated about 12 km to its east near pools which can still hold water until late in the dry season (Linseele 2005:19). Sites producing valuable samples of fish bones are Gajiganna NA 90/5A and NA 90/5BI.

About a thousand years after the formation of the Bama Deltaic Complex the flat lagoon clay plains known as the *Firgi* became accessible to human groups. This area is still inundated annually both by rainwater and by water coming from the major rivers. Even today, permanent inhabitation is only possible on land above the flood level. However, semi-permanent villages and seasonal camps close to or below flood level (after the waters have retreated) are frequented annually by pastoralists in order to exploit the extensive perennial grasslands sprouting after the floods. Three stratified sites pertaining to the so-called Chad Lagoonal Complex and situated within a 10 km radius of a 7 m high settlement mound (Kursakata) are of particular interest here, namely the settlement mound itself (NA 93/46), Mege (NA 94/7) and Ngala (NA 93/45) (Tables 1 and 4).

Table 2. Holocene fish assemblages (Family level) from the Niger basin (NISP).

	Kobadi	**Kolima I**	**Kolima II**	**Akumbu a**
Protopteridae	0	0	7	0
Polypteridae	15	9	5	0
Arapaimidae	263	47	23	4
Mormyridae	41	2	6	0
Gymnarchidae	128	7	3	1
Alestiidae	18	9	1	2
Citharinidae	11	12	3	3
Cyprinidae	67	31	7	1
Bagridae	1527	28	12	4
Clariidae	344	233	854	226
Mochokidae	856	52	23	77
Schilbeidae	19	0	0	0
Ariidae	1080	0	0	0
Channidae	1	2	6	0
Latidae	3749	44	40	74
Cichlidae	756	288	420	88
Tetraodontidae	1	0	0	3
Total	8876	764	1410	483

Table 3. Holocene fish assemblages (Family level) from Gajiganna in the Chad basin.

	Gajiganna NA 90/5A	**Gajiganna NA 90/5B1**
Polypteridae	1	28
Arapaimidae	1	36
Gymnarchidae	2	0
Clariidae	385	746
Total	389	810

Nile River Basin

The Holocene sites along the Egyptian Nile considered here are Merimde-Benisâlame and Elephantine (Table 5). Merimde is a Neolithic settlement near a former anabranch of the Nile some 45 km north of Cairo. Human inhabitation dates to the 5th millennium cal. BC (von den Driesch and Boessneck 1985). Domestic livestock provided most of the animal proteins to the site's inhabitants, followed by fish. Elephantine is an island situated near Aswan downstream the First Cataract. The fish bone finds excavated in the necropolis, which dates to the Fifth and Sixth Dynasties, and the Satet temple area, which dates to the Fourth–Eleventh

Table 4. Holocene fish assemblages (Family level) from Mege, Ngala and Kursakata in the Chad basin.

	Mege I	**Mege II**	**Mege III**	**Mege IV**	**Ngala I**	**Ngala II**	**Ngala IIIa**	**Ngala IIIb**	**Ngala IV**	**Kursakata LSA**	**Kursakata EIA**
Protopteridae	0	0	0	0	7	17	6	6	5	0	7
Polypteridae	57	6	1	0	29	64	20	2	8	122	3500
Arapaimidae	25	32	5	8	24	26	14	12	13	16	557
Mormyridae	0	4	0	0	1	2	0	0	0	1	11
Gymnarchidae	10	19	1	0	18	23	9	5	4	32	208
Alestiidae	0	0	0	0	0	0	0	0	0	0	4
Citharinidae	0	0	0	0	0	0	0	0	0	1	15
Cyprinidae	0	0	0	0	2	0	0	0	0	0	3
Bagridae	7	3	1	1	4	0	2	1	4	0	18
Clariidae	1534	375	386	309	219	636	262	229	276	415	10379
Mochokidae	6	2	1	1	6	6	5	5	4	0	36
Channidae	0	2	2	0	15	19	1	2	3	8	600
Latidae	8	8	3	4	49	85	30	8	18	18	451
Cichlidae	4	83	15	5	23	14	11	6	10	11	1028
Total	1651	534	415	328	397	892	360	276	345	624	16870

Table 5. Holocene fish assemblages (Family level) from the Nile valley in Egypt and Sudan.

	Merimde	**Elephantine**	**Abu Darbein**	**Aneibis**	**El Damer**	**Marrahi**
Protopteridae	0	0	4	50	46	1
Polypteridae	666	0	12	53	53	216
Arapaimidae	0	0	0	1	0	158
Mormyridae	208	158	42	44	145	14
Gymnarchidae	0	0	0	6	37	8
Alestiidae	26	163	4	0	70	0
Citharinidae	1	7	3	7	69	0
Cyprinidae	262	675	34	32	380	55
Bagridae	369	4644	57	51	256	42
Schilbeidae	6	0	0	0	0	0
Clariidae	4167	44	85	270	998	540
Mochokidae	1804	2508	311	470	269	66
Malapteruridae	7	0	0	1	1	0
Latidae	661	2126	32	176	217	239
Cichlidae	1147	9	3	22	42	89
Channidae	0	0	0	0	0	2
Tetraodontidae	104	3	1	3	1	1
Total	9428	10337	588	1186	2584	1431

Dynasties, have been lumped for this study (Boessneck and von den Driesch 1982; von den Driesch 1986). The faunal remains obviously represent domestic and consumption refuse and date between *c*. 2600 and 1900 BC.

Sites of interest along the Central Sudanese Nile include Aneibis, Abu Darbein, Ed Damer and Umm Marrahi (Table 5). The first three sites are located near the junction of the rivers Nile and Atbara, on the east bank of the Nile. The ceramics of these sites, the so-called Khartoum Mesolithic or Early Khartoum pottery, date them to the Mesolithic period. The ^{14}C-dates range from *c*. 8000 to 6000 cal. BC (for uncalibrated data see Haaland and Magid 1995, calibrated with OxCal 4.0; Bronk Ramsey 1995, 2001). The importance of aquatic resources in the diet of these Mesolithic groups is indicated by the considerable number of fish remains in the assemblages and the presence of reptiles, birds and mammals found in the same habitat (Peters 1995).

Most Mesolithic sites in the Central Nile valley excavated so far are located on the east bank of the river. Umm Marrahi is one of the rare west bank sites some 38 km north of Khartoum. Compared to the sites on the east bank of the Central Nile valley, fish must have been an even more important source of proteins (Gautier *et al.* 2002). Prehistoric settlements found near existing water bodies conceivably had hydrological conditions resembling the present-day situation. This seems to have been the case along the Holocene Nile, although a shift of the main river channel could be evidenced (Marcolongo 1983; Marcolongo and Palmieri 1988). Outside the Nile Valley, however, the situation was entirely different. For example in north-western Sudan the early Holocene optimum witnessed the formation of extensive drainage systems, the most important of these being the Wadi Howar. It was the northernmost tributary of the Nile extending 1,050 km from its upper reaches in the Ennedi and Jebel Marra mountains to its confluence with the main Nile north of Ed-Debba (Kröpelin 1993). Once connected, fish could migrate from the main Nile into the wadi system, which must have been perennial at times. However, increased aridity during the late Holocene of north-eastern Africa interrupted water supply from the upper (mountains) and lower (Nile) reaches, causing a compartmentalisation of the water body and, in the long run, desiccation.

The permanent availability of water in the Wadi Howar drainage throughout much of the Holocene made the landscape attractive to human groups as early as the 6th millennium cal. BC, first for hunter-gatherers and later for pastoralists with their flocks. Amongst the several hundred sites discovered in the Wadi Howar region by archaeologists of Cologne University, three sites are of interest here, namely Rahib 80/87, Abu Tabari 02/1 and Djabarona 84/13 (Table 6).

Rahib 80/87 dates to the late 6th and 5th millennia cal. BC and belongs to the Dotted Wavy Line horizon of the Eastern Sahara (Jesse 2003). The site is located on a lee dune at the Jebel Rahib foothills about 15 km north of the main riverbed of the Wadi Howar. Human subsistence at Rahib 80/87 was based on hunting, fishing and the gathering of wild plants.

Abu Tabari S 02/1 is situated in the lower section of the wadi about 260 km west of the main Nile on a north-east to south-west oriented low sand dune (Jesse 2006). Human inhabitation covers an area of 800 by 60–130 m, with several human graves on top and on the eastern margin of the dune. Site occupation dates to the first half of the 4th millennium cal. BC. Faunal analysis showed that human subsistence was based on cattle rearing, though fishing contributed significantly to the diet.

Human presence at Djabarona 84/13 post-dates that at Abu Tabari S 02/1, site inhabitation dating to the first half of the 3rd millennium cal. BC (Keding 1997). Situated on a dune at the southern bank of the middle section of the Wadi

Table 6. Holocene fish assemblages (Family level) from the Wadi Howar, western Nile basin.

	Djabarona 84/13	Rahib 80/87	Abu Tabari S02/1
Polypteridae	40	0	231
Arapaimidae	23	0	5
Mormyridae	14	0	28
Gymnarchidae	0	0	2
Alestiidae	11	0	16
Citharinidae	2	0	2
Cyprinidae	51	0	2
Bagridae	31	0	39
Schilbeidae	4	0	5
Clariidae	1189	426	1685
Mochokidae	172	6	629
Malapteruridae	0	0	0
Latidae	45	5	212
Cichlidae	1909	109	1164
Tetraodontidae	0	8	23
Total	3491	554	4043

Howar, its inhabitants had a similar mode of subsistence as that of Abu Tabari S 02/1.

In contrast to the Central Sudanese sites, the Holocene hydrological conditions prevailing at Rahib 80/87, Abu Tabari S 02/1 and Djabarona 84/13 are not well understood. The taxonomic composition of the ichthyofaunas suggests that larger (seasonal) water bodies were present either in the immediate vicinity of the sites or further away. In the latter case a seasonal connection must have existed.

Material and Methods

Material

All osseous remains obtained from the aforementioned sites result from human activities within the site catchment. The skeletal distribution of the different taxa as well as the absence of remains of exotic fishes implies that all ichthyofaunal assemblages considered here are of local origin. Taxonomic richness, size and habitat requirements of the taxa identified suggests that less selective fishing gear including nets, baskets and traps was mainly used, though hooks and harpoon points have been found, for example, at Kobadi (Raimbault 1994) and El Damer (Haaland 1995). Along the Sudanese Nile the use of boats dates as early as the 7th millennium cal. BC (Peters 1995).

As said, the bone accumulations represent the discarded leftovers from fish preparation and consumption. The density of fish remains in the cultural layers as well as their taxonomic composition vary from site to site, and fossilisation processes may have affected certain assemblages more than others. It is, nevertheless, assumed that the skeleton of a particular taxon will be affected similarly by these processes independently of whether embedded in sediments bordering the Niger, Chad and Nile or their tributaries. In other words, bones that tend to preserve well at one site conceivably did too at another one.

Serious bias may be introduced by the methods of recovery, particularly in the case of fish bones (Meadow 1980). Fish remains were generally obtained by dry-screening with a mesh <5 mm. As such, fish attaining sizes below 10 cm appear under-represented in most assemblages. Conceivably their skeletal elements are too small to be recovered systematically by the aforementioned technique, but the possibility cannot be entirely ruled out that such fish were consumed *in toto*, a practice still observed in fishing communities throughout Africa (personal observation by Joris Peters). Finally, since we have no indication that the fish bone assemblages were liable to any major anthropological filter such as food taboos, it can be postulated that they roughly reflect the fish composition of the associated watercourse, albeit impoverished (Morales Muñiz and Van Neer 1994).

Methods

Fish nomenclature in this study follows the terminology proposed in the FishBase (Froese and Pauly 2007). Identifying fish assemblages from sites in northern Africa requires good comparative collections, such as those available at the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels and the Staatssammlung für Anthropologie und Paläoanatomie in Munich. Most studies on North African Holocene fishes have been carried out with the aid of these collections. Since researchers working on such materials apply the same identification criteria and methodology, the datasets generated by them can be compared with sufficient confidence.

Different taxonomic levels may be attained when identifying fish remains from archaeological sites, exemplified here with the assemblage from Abu Tabari S 02/1 (Table 7). This is not surprising given the generally fragmentary nature of archaeofaunas and the fact that not all skeletal elements exhibit diagnostic features that enable identification to species or even genus level. Consequently, overviews of ichthyofaunal assemblages list different taxonomic categories (species, genus, family), for example *Clarias gariepinus*, *Clarias* sp. or indeterminate Clariidae. In most cases the lowest taxonomical level will comprise the majority of the finds. Thus, for reasons of compatibility and to maximise the exploitation of the available archaeoichthyological data, the taxonomic level of the family is considered the most appropriate for comparison.

‘Richness’ is the simplest way to characterise a community. This is done by counting the number of taxa present in an assemblage. Since in our database the fish bones are grouped into families, the term species richness, usually applied in biology, should be replaced by taxonomic richness. However, using this approach each taxon in the community will have the same weighting irrespective of its abundance. Richness is therefore very sensitive to rare taxa and will underestimate the relative importance of abundant taxa. It is also highly dependent on sample size, hampering the comparison between assemblages of highly differing sample size, which is the case in this study.

‘Diversity’ is a concept where both species richness and evenness are considered. Beyond its richness, the community organisation also depends on the relative abundance of the different taxa. The more a community is dominated by one or a few taxa, with low proportions left to the remainder, the less it is even and, in consequence, the less diverse. For biological samples, two diversity indices are usually applied to calculate the relative proportion of taxa related to the total number of taxa (Begon *et al.* 2006), namely the Shannon entropy and the Simpson index. Both take into account each taxon and its abundance, but the latter is very insensitive to rare species. While analysing archaeofaunal assemblages we found that both indices behave similarly, that is, the distance between the Shannon entropy and the Simpson index is more or less constant, except for assemblages showing very unequal distributions. We therefore decided considering only the Shannon entropy for this study.

The Shannon entropy depends on the assumption that the sample is a random one. Recently the Brillouin index was proposed for estimating diversity in archaeozoological assemblages (Zohar *et al.* 2001), which is to be preferred when dealing with non-random samples. Besides the fact that this index is inconvenient for large assemblages

Table 7. Detailed ichthyofaunal record of Abu Tabari S02/1, the respective highest level of identification achieved being highlighted in grey.

	Order	**Family**	**Tribe**	**Genus**	**Species**	**NISP**
	Polypteriformes	Polypteridae		*Polypterus* sp.		222
		Polypteridae			*Polypterus cf. bichir*	9
	Osteoglossiformes	Arapaimidae			*Heterotis niloticus*	5
		Mormyridae			*Hyperopisus bebe*	8
		Mormyridae indet.				20
		Gymnarchidae			*Gymnarchus niloticus*	2
	Characiformes	Alestiidae indet.				3
		Alestiidae		*Hydrocynus* sp.		13
		Citharinidae indet.				1
		Citahrinidae		*Distichodus* sp.		1
	Cypriniformes	Cyprinidae		*Labeo* sp.		2
	Siluriformes indet.					179
		Bagridae indet.				2
				Bagrus sp.		3
				Auchenoglanis sp.		30
					Clarotes laticeps	2
				Chrysichthys sp.		2
		Schilbeidae indet.				5
		Clariidae indet.				1553
				Clarias sp.		128
				Heterobranchus sp.		4
		Mochokidae		*Synodontis* sp.		571
					Synodontis frontosus	18
					Synodontis membranacaeus	1
					Synodontis schall	39
	Perciformes	Latidae			*Lates niloticus*	212
		Cichlidae	Tilapiini indet.			1164
	Tetraodontiformes	Tetraodontidae			*Tetraodon lineatus*	23
Fish, identified						**4222**
Pisces indet.						2743
Fish, total						**6965**

because factorials of figures surpassing N = 150 are very time-consuming to calculate, we believe that the archaeoichthyological assemblages considered in this study represent random samples, considering the fact that fishing was practised with a multitude of devices including nets, fences, baskets, harpoons, hooks and spears. The formula for the Shannon entropy is

$$H' = -\Sigma\ (n/N)\ \ln\ (n/N),$$

in which n = number of finds of a taxon (family in our case) and N = total number of finds. H' increases with richness and decreases with higher dominance by single taxa, so is positively correlated to evenness. The Shannon entropy was developed to describe the (un)predictability of information (= data) in information theory. If a data set has many equally distributed data, the likelihood of correctly predicting the next data is low; its unpredictability is high, as is its Shannon entropy. An entropy, however, is an index of diversity and therefore not equal to diversity (Jost 2006). Other sciences that use the Shannon entropy such as information theory or physics distinguish between the entropy of a community (as calculated on the basis of the entire set of data) and the effective number of elements. For biological data this means that the indices of diversity have to be converted into effective numbers of taxa, the resulting value being defined as the Shannon diversity termed ^1D (Jost 2006). The formula of conversion is

$$^1D = \exp\ (H').$$

Thus ^1D gives the effective number of taxa in an even community composed of equally common taxa. Since it is calculated on the basis of the taxonomic composition of archaeological assemblages, though, the Shannon diversity ^1D will be referred to as "archaeobiodiversity" (abbr. aD) in the following sections.

Prior to further analysis the samples had to be tested for their statistical validity. One approach to evaluating whether sampling efforts are sufficient is to calculate rarefaction curves, in which the number of taxa is plotted relative to sample size. This method is widely applied by ecologists, archaeobotanists, archaeologists and palaeontologists (Lepofsky and Lertzman 2005). In case a curve reaches its horizontal asymptote (plateau), additional sampling would not result in a significant increase in the number of taxa (for example Figure 2 for Djabarona 84/13). Rarefaction curves, however, are not always entirely suitable. The late Palaeolithic assemblage from Wadi Kubbaniya in southern Egypt (Gautier and Van Neer 1989) provides a good illustration of the limitations of the approach. This assemblage fails to produce feasible statistical results (Figure 2) since the rarefaction curve does not even approximate the horizontal asymptote. This is totally unexpected considering the amount of remains analysed (>90,000 specimens). One possible explanation for this unexpected result is offered by the rarefaction curves of two decidedly smaller assemblages from the Chad Lagoonal Complex, namely Mege (Phase IV) and Ngala (Phase IV) (Linseele 2005). Although sample size is similar for the two sites (NISP ~ 300), the rarefaction curves differ significantly (Figure 2): At the point where the rarefaction curve calculated for the Ngala IV assemblage shifts horizontally, the one calculated for Mege IV still continues to ascend. A closer look at the taxonomic composition reveals that remains of clariids dominate both assemblages. However, whereas other taxa are few at Mege IV (N = 5) and absolute frequencies are low (only 19 specimens), the Ngala IV assemblage yielded additional 13 taxa with altogether 69 specimens. Rarefaction obviously fails to produce feasible results if assemblages are characterised by extremely uneven distributions, which is the case at Wadi Kubbaniya (Gautier and Van Neer 1989:table 6.3). This suggests that rarefaction curves may not always be ideal for testing whether sample size suffices for statistical evaluation.

As shown by Soetaert and Heip (1990), diversity indices differ in their dependence from sample size. Indices sensitive to rare species demand more sampling effort than those attaching more importance to abundant species. The same authors also demonstrated that samples with low diversity are less affected by low sample sizes. Indeed, they could demonstrate that the Shannon diversity for their highly diverse sample of nematodes from a Mediterrean deep-sea transect (number of species = 202, number of individuals = 808) will already produce reasonable results with a size of the sub-sample of 200 individuals. Furthermore, indices highly sensitive to rare species like richness are likewise sensitive to sample size. The Shannon index is less affected by low sample sizes than richness but still more sensitive than the Simpson's Index. Since the fish bone assemblages considered here generally exhibit low diversities with 16 taxa at the most, and this in samples containing several hundred bone finds or more, it can be assumed that even smaller assemblages considered in this study will produce useful results. In order to test this assumption we subdivided the Abu Tabari 02/1 assemblage (NISP = 4022) randomly into a series of sub-samples yielding 100 bones each. We then calculated taxonomic richness and the aD-index starting with n = 100, to continue with n = 200, n = 300, etc. The resulting taxon accumulation curve (Figure 3) corroborates the conclusions of Soetaert and Heip (1990) (for the difference between taxon accumulation curve and rarefaction curve see Lepofsky and Lertzman 2005). The slightly higher values of archaeobiodiversity for the first

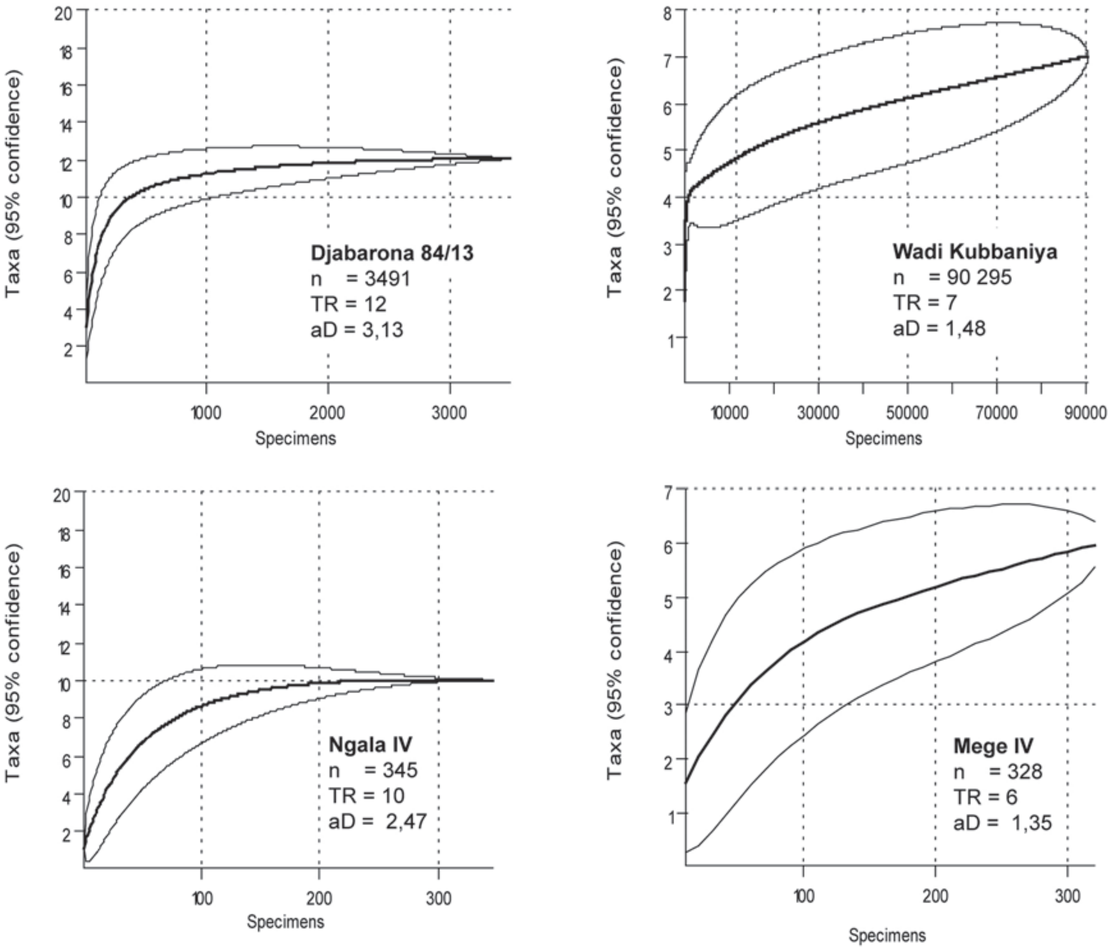

Figure 2. Rarefaction curves of four fish assemblages from the Nile and Chad basins, pointing out the relation of rarefaction to sample size and evenness. n = sample size, TR = taxonomic richness, aD = archaeobiodiversity.

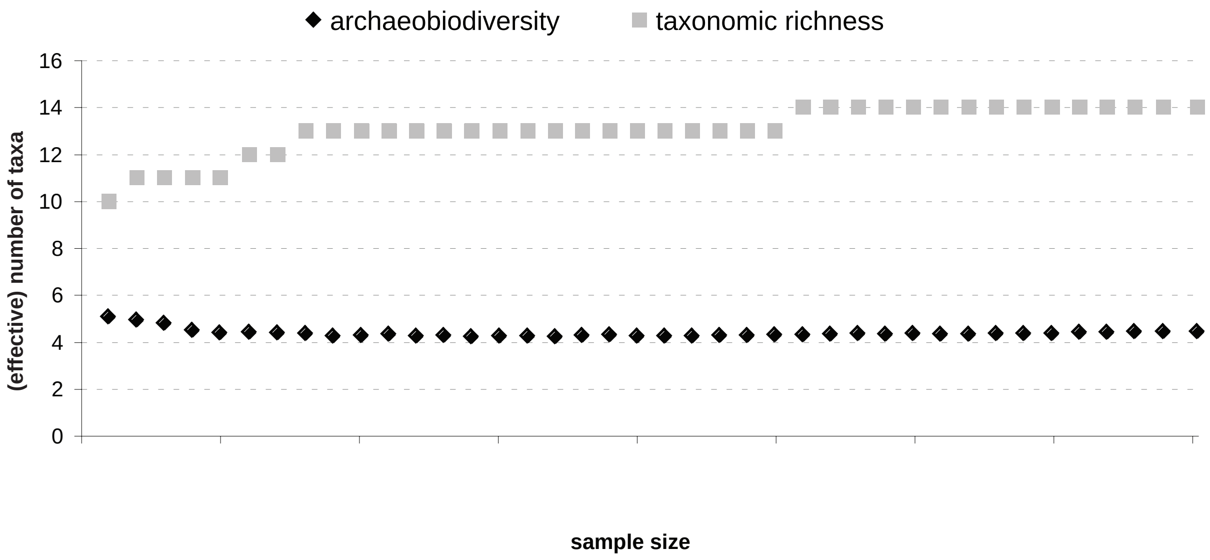

Figure 3. Taxonomic richness and archaeobiodiversity calculated for the Abu Tabari S02/1 assemblage, randomly sampled using steps of n=100.

sub-samples are obviously an artefact of the cumulative method. Values similar to the one obtained for the entire assemblage are encountered from n = 500 onwards, but a smaller sample may suffice if the total number of taxa evidenced is ten or less. As to taxonomic richness, if we accept a 5 to 10% error margin, Figure 3 illustrates that a sample size of n = 800 would suffice. We observed that assemblages with at least 300 identified specimens generally meet expectations. It should be stressed here that we are aware of the statistical problems arising when comparing assemblages with different sample sizes (Lepofsky and Lertzman 2005). However, our aim is not to compare sites individually but to trace patterns of a more general nature. All indices and rarefaction curves were calculated and plotted using PAST software, version 1.46 (Hammer *et al.* 2001).

Results and Discussion

Nilo-Sudanic Fish Families: Actual versus Holocene Presence

Due to late Quaternary climatic and geological events the different river basins of the Nilo-Sudanic Province were interconnected at times. This explains the similarities between their faunas (Hugueny and Lévêque 1994; Lévêque 1997;). The fact that the Niger lies at the intersection of the western and eastern Nilo-Sudanic basins accounts for its very rich fish fauna, totalling *c*. 220 species in contrast to 120 species in the Chad-Chari and 124 species in the Nile basin (Lévêque 1997:tab. 6.2; UNEP 2006), although the Niger ranks third in overall size (2,273,946 km^2) compared to Lake Chad with 2,381,635 km^2 and the Nile with 3,112,369 km^2. The conformity of the fish communities inhabiting the Nile and the Chad-Chari basins (85 species = 75% of the Nile fish community) strongly suggests that the two were still interconnected during late Quaternary times, conceivably during the early but possibly as late as the middle Holocene. The Nile and Niger ichthyofaunas have 78 species in common.

Such considerable overlap is also visible in the Holocene archaeoichthyological record of the present-day Sahel (Table 8; all data merged). Absence of families can be explained best by the small maximum sizes attained by its members and/or their limited distribution within the basin due to very particular habitat requirements. Families with species surpassing 15 cm are present in the anthropogenic assemblages of all three basins. This suggests that no food taboo existed against taxa of economic importance. Such a strong similarity also facilitates comparison of ichthyological assemblages throughout the Nilo-Sudanic Province.

Archaeobiodiversity

In some cases, taxonomic richness seems to decline with time in the archaeoichthyological record of the Late Holocene Sahel (for example Figure 4, Ngala). This is not surprising considering the early Holocene climatic optimum was followed by phases of oscillating climatic conditions and an overall trend towards increasing aridity. In the Inland Niger Delta, for example, it can be seen that archaeobiodiversity is highest at Kobadi, and that there is a significant decline in diversity in the course of site inhabitation at Kolima (Table 9, Figure 4). Between phase I and II most taxa decrease in numerical importance, except for the clariids and cichlids. The latter taxa can withstand the adverse conditions of seasonal waters and of small water bodies with low dissolved oxygen concentrations with limited water supply better than any of the other taxa. Their dominance in the Kolima II assemblage is therefore indicative of a desiccation of the local environment, and of an amplification of the seasonal fluctuation of water supply from the main Niger. Conceivably human subsistence practices had to be adjusted from an economy based largely on aquatic resources during the 2nd millennium cal. BC (Jousse *et al.* in press) towards a pastoralist mode of living in which fishing represented a seasonal activity in the 1st millennium cal. BC (MacDonald and Van Neer 1994).

In the Chad Basin the 2nd millennium BC Bama Deltaic Complex sites at Gajiganna (NA30/5A and 5B1) are characterised by a low taxonomic richness and archaeobiodiversity (Figure 4, Table 9). As to the Chad Lagoonal Complex, ongoing human exploitation of the natural resources and climatic change had a negative effect on archaeobiodiversity as is illustrated by the cultural sequence of Ngala (Figure 4, Table 9). At Mege, however, archaeobiodiversity is highest during occupation phase II which dates to the Early Iron Age. This phase coincides with Ngala I and Kursakata II, two other Early Iron Age assemblages that also exhibit high diversity indices. According to Brooks (1998), the period between ca. 300 BC and AD 300 corresponds to a dry phase, before ecological conditions improved during the following centuries, with relatively benign climate circumstances reigning between AD 300 and 1100. Whether the higher aD-indices in Early Iron Age assemblages relate to this climatic optimum is difficult to establish with available data. It is noteworthy, though, that the contemporaneous site of Akumbu-a (Figure 4, Table 9) also shows a much higher aD-index compared to preceding Kolima II. Thus, if the aforementioned explanation of better climatic conditions holds true for the Chad-Chari Basin, it conceivably also applies to the Inland Niger Delta. However, other explanations such as intensification of aquatic exploitation (annual vs. seasonal fishing), expansion of fishing grounds, and/or use of a more diversified set of fishing devices such as boats should not be discounted *a priori* explaining the higher aD-indices.

A comparison of taxonomic richness in Holocene Egyptian and Sudanese Nile assemblages reveals a similar pattern, likely due to the constancy of the hydrological conditions of the Nile River system. In almost all assemblages some 12 to 14 families have been identified, except for the site on Elephantine Island, situated just below the First Nile Cataract (Figure 4, Table 9): Although Elephantine Island produced a large assemblage in terms of its number of identified specimens (Table 5), only ten families could be recognised. This discrepancy can best be explained by the topography and hydrology of the Nile near Elephantine (Figure 4). Characterised by extensive granite formations the First Cataract is known to cause a channelling of the river and a strong current. As such, shallow sandy substrates and marshy, well vegetated habitats with slowly flowing or standing waters are absent near Elephantine Island. Consequently, essential

Table 8. Occurrences of fish families in the three river basins during Holocene and recent times. Note the high similitude of the ichthyological communities in northern Africa.

	Niger (Mali)		**Nile North of Khartoum**		**Lake Chad**	
	recent	**Holocene**	**recent**	**Holocene**	**recent**	**Holocene**
Protopteridae	x	x	x	x	x	x
Polypteridae	x	x	x	x	x	x
Anguillidae			x	x		
Clupeidae	x				x	
Arapaimidae	x	x		x	x	x
Pantodontidae					x	
Notopteridae	x		x	x	x	
Mormyridae	x	x	x	x	x	x
Gymnarchidae	x	x	x	x	x	x
Kneriidae	x					
Hepsetidae					x	
Alestiidae	x	x	x	x	x	x
Citharinidae	x	x	x	x	x	x
Cyprinidae	x	x	x	x	x	x
Bagridae	x	x	x	x	x	x
Schilbeidae	x	x	x	x	x	
Amphiliidae	x				x	
Clariidae	x	x	x	x	x	x
Malapteruridae	x		x	x		
Mochokidae	x	x	x		x	x
Ariidae	x	x				
Cyprinodontidae			x			
Aplocheilidae	x				x	
Poeciliidae	x		x		x	
Channidae	x	x		x	x	x
Latidae	x	x	x	x	x	x
Cichlidae	x	x	x	x	x	x
Gobiidae			x			
Eleotridae			x		x	
Anabantidae	x		x		x	
Mastacembelidae	x				x	
Tetraodontidae	x	x	x	x	x	

ecological requirements relative to food acquisition and reproduction (spawning grounds) are not met for taxa such as *Clarias*, Tilapias or *Polypterus*, explaining their (quasi-total) absence in the archaeoichthyological assemblage. Archaeobiodiversity, therefore, is lowest at Elephantine compared to that in other sites located on the Nile (Figure 4, Table 9). The latter nevertheless show considerable variation in taxonomic richness and diversity. This implies differences in local hydrological and ecological conditions, but an interpretation solely on the basis of the Shannon Diversity is problematic.

Compared to the Nile valley aD-indices of sites situated in the Wadi Howar drainage are, on average, lower (Figure 4, Table 9). The aquatic ecosystem did not provide a similar variety of habitats as present in the contemporaneous main Nile. The low archaeobiodiversity at Rahib 80/87 certainly relate to the 15 km distance to the main wadi channel. This implies that human occupation may have been seasonal following the inundation of the plains bordering the wadi. It should be noted that flood plains with low water levels are only attractive to fish taxa showing adaptations to cope with strong fluctuations in oxygen concentrations, water temperatures and salinity levels. The most tolerant taxa in this respect are clariids and tilapias (Van Neer 1989). Their abundance in the Rahib 80/87 assemblage is strongly indicative of such temporary habitat.

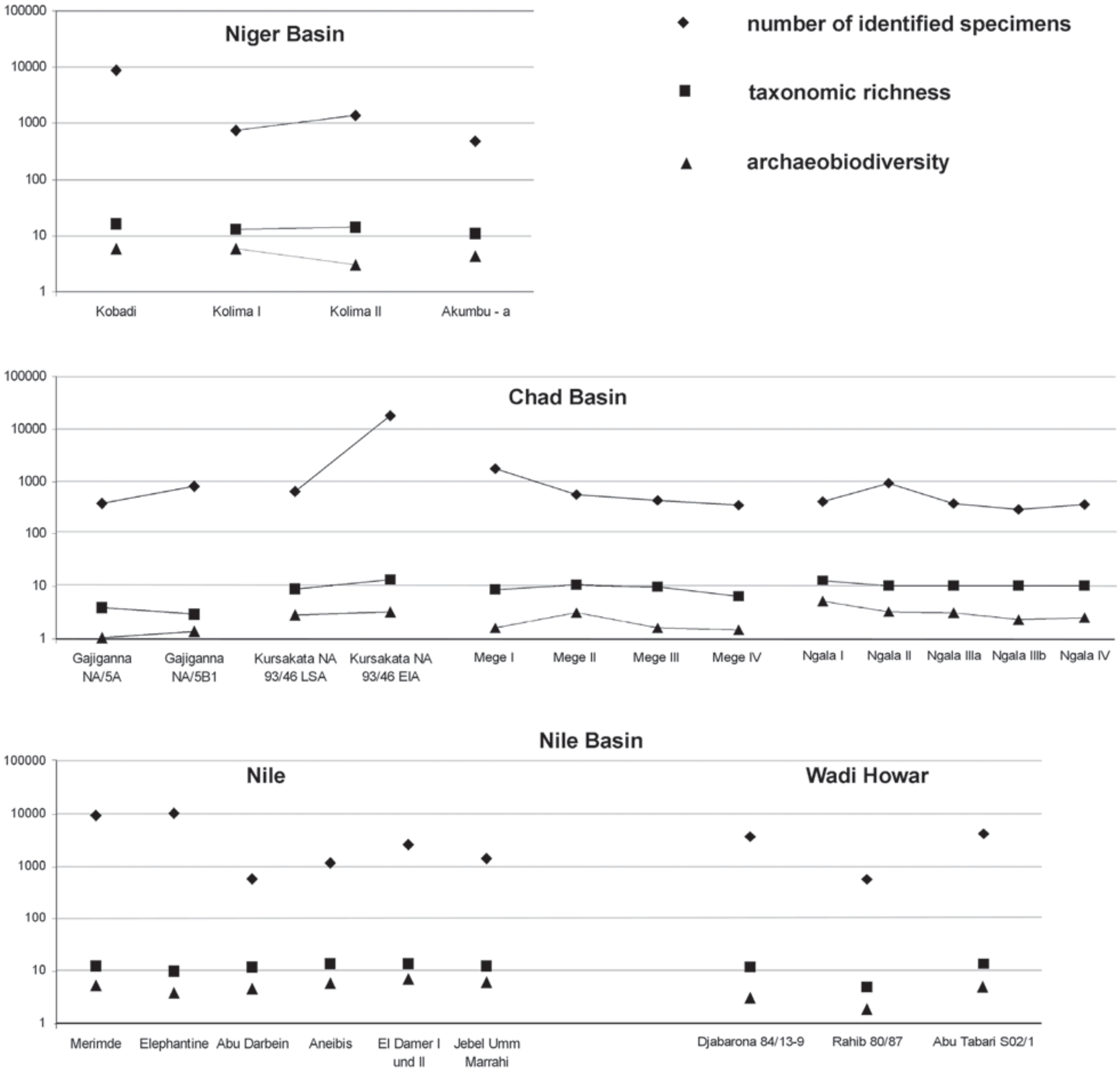

Figure 4. Sample size, taxonomic richness and archaeobiodiversity of the sites by river basins and regions (logarithmised). Records from the same site through time are connected by a line.

Archaeobiodiversity at sites located close to the wadi is clearly higher, implying a more diverse aquatic habitat. At Abu Tabari S 02/1, fishing likely extended beyond seasonal activities. The lower diversity at Djabarona compared to Abu Tabari can probably be explained by the fact that the 3rd millennium BC already witnessed increased aridity (Hoelzmann *et al.* 2001). No doubt, lower annual precipitation and higher evaporation rates in the upper and middle reaches of the wadi caused a decline in taxonomic richness of the ichthyofauna and affected the distribution of taxa within the wadi system.

Archaeobiodiversity and Ecology of Holocene Water Bodies

Ecosystems with high diversities are considered more stable than those exhibiting low diversities (Hamilton 2005). Therefore changes in abiotic and biotic characteristics will affect water bodies with low taxa biodiversity more severely. Good examples of this are aquatic environments exhibiting seasonally fluctuating water levels, such as the modern Inland Niger Delta, where a significantly lower diversity is observed at the end of the low-water period compared to the flood period (Laë 1995:fig. 5). The low diversities come about because ecologically more demanding fish species either leave the area or die due to unfavourable living conditions or predation. Thus, even in large river basins biodiversity will not be constant, a complicating factor for the interpretation of archaeobiodiversity indices based on assemblages that accumulated over years if not decades.

As was shown before, archaeobiodiversity indices may be useful for characterising past ecosystems, with higher indi-

Table 9. Taxonomic richness, archaeobiodiversity and Latidae/Claridae index of the Holocene ichthyological assemblages grouped according to the river basins.

		taxonomic richness	archaeobio-diversity	Latidae/Clariidae (ln)
Nile system	Merimde (n=9428)	13	5.45	-1.84
	Elephantine (n=10337)	10	3.95	3.88
	Abu Darbein (n=588)	12	4.79	-0.98
	Aneibis (n=1186)	14	5.88	-0.43
	El Damer (n=2584)	14	7.12	-1.53
	Marrahi (n=1431)	13	6.25	-0.82
Wadi Howar	Djabarona 84/13 (n=3491)	12	3.13	-3.27
	Rahib 80/87 (n=554)	5	1.96	-4.45
	Abu Tabari S02/1 (n=4041)	14	4.43	-2.07
Niger system	Kobadi (n=8876)	16	5.80	2.39
	Kolima I (n=764)	13	5.72	-1.67
	Kolima II (n=1410)	14	2.98	-3.06
	Akumbu a (n=483)	11	4.21	-1.12
Chad Lagoonal Complex	Mege I (n=1651)	8	1.44	-5.26
	Mege II (n=534)	10	2.85	-3.85
	Mege III (n=415)	9	1.43	-4.86
	Mege IV (n=328)	6	1.35	-4.35
	Ngala I (n=397)	12	4.95	-1.50
	Ngala II (n=892)	10	3.07	-2.01
	Ngala IIIa (n=360)	10	3.00	-2.17
	Ngala IIIb (n=276)	10	2.22	-3.35
	Ngala IV (n=345)	10	2.47	-2.73
	Kursakata NA 93/46 LSA (n=624)	9	2.97	-3.14
	Kursakata NA 93/46 EIA (n=16870)	14	3.38	-3.14
Bama Deltaic Complex	Gajiganna NA 90/5A (n=389)	4	1.07	—
	Gajiganna NA 90/5B1 (n=810)	3	1.39	—

ces implying more diverse aquatic environments. However, sites showing comparable values for taxonomic richness and Shannon diversity did not necessarily experience similar environmental conditions. A good illustration of this is provided by the assemblages from Elephantine Island and Ngala II, two samples with close archaeobiodiversity values (Table 5). Dominant taxa at Elephantine are *Bagrus*, *Synodontis* and *Lates*. These taxa demand good water quality with high oxygen concentrations and constant temperatures. In contrast, the Ngala II assemblage is dominated by clariids that are able to survive with low oxygen concentrations and highly fluctuating temperatures. Thus, in order to classify sites ecologically, archaeobiodiversity indices should be combined with another parameters indicative of the type and quality of the local water body, and hence of its ecology. One approach could be to calculate the ratio of taxa primarily associated with either open or closed aquatic environments and to plot this data against archaeobiodiversity indices. For the Nilo-Sudanic ichthyofaunal Province, the widespread Nile perch *Lates niloticus* (Latidae) and the air-breathing catfishes of the family Clariidae can be considered representative taxa from an ecological viewpoint. Adult Nile perch are confined to deep water (10–60 m) and need well-aerated habitats, whereas clariids generally prefer quiet waters such as lakes and pools. Clariids are widely tolerant of extreme environmental conditions because they possess accessory breathing organs enabling them to breathe air. In the Nilo-Sudanic ichthyofaunal Province, the Latidae are a monospecific taxon, whereas all species pertaining to the Clariidae overlap well in their ecological requirements. Furthermore, these two taxa are widespread and frequent in northern African archaeoichthyological records (see Tables 2–6). The Latidae/Clariidae ratio was calculated and then converted into natural logarithms to present the results in a graph (ln (Σ(Latidae)/Σ(Clariidae))). Assemblages lacking one of the two taxa are excluded from analysis.

Based on the results represented in Figure 5, the ratio of Latidae to Clariidae (vertical axis) combined with archaeobiodiversity (horizontal axis) causes a clustering of the different assemblages into three groups (for data see Table 9). Cluster 1 comprises assemblages that are characterised by a relatively high proportion of clariids and an archaeobiodiversity index of below 3.5. Cluster 2 comprises assemblages in which the ratio of latids to clariids is still in favour of the latter taxon, but with an archaeobiodiversity index surpassing 4.0. Cluster 3 includes assemblages in which clariids are decidedly less important than latids and with archaeobiodiversity indices ≥4.0.

Considering Cluster 1, it consists of the ichthyological assemblages of the Chad Lagoonal Complex (Mege I-IV, Ngala II-V, Kursakata LSA, EIA), the Inland Niger Delta (Kolima II) and the middle section of the Wadi Howar (Rahib 80/87, Djabarona 84/13). The dominance of clariids

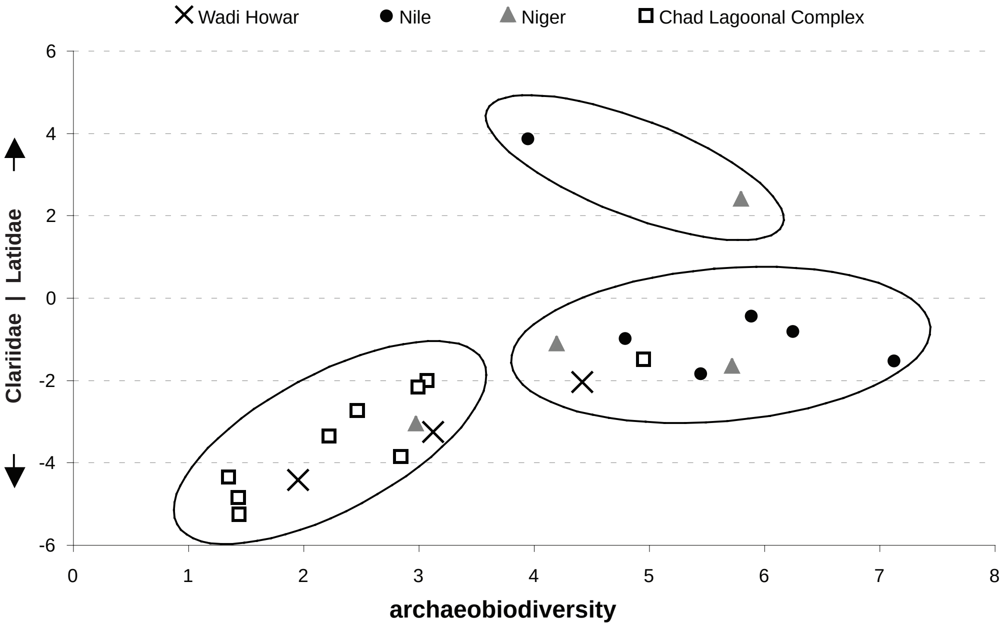

Figure 5. Relation between archaeobiodiversity and the Lates/Clariidae index within the archaeoichthyological assemblages. Cluster 1 depicts shallow seasonal waters, cluster 2 water bodies with highly diverse habitats and good water quality, and cluster 3 comprises sites near well-oxygenated, deeper water bodies.

and overall low archaeobiodiversity indices suggests that the main feature of the aquatic ecosystems were rather shallow waters, partly of temporary nature, with relatively poor oxygen conditions and relatively low habitat diversities. The positioning of Rahib 80/87 and Djabarona 84/13 in this graph implies a similar kind of environment for the middle Wadi Howar, conceivably with a more diverse aquatic habitat near Djabarona 84/13, given its higher archaeobiodiversity index.

Cluster 2 groups all Central Sudanese Nile sites, the Egyptian Nile Delta site of Merimde, Kolima I and Akumbu-a in the Inland Niger Delta, the Chad Lagoonal Complex site of Ngala I, and Abu Tabari S 02/1 on the lower Wadi Howar. The more balanced ratio of clariids to latids as well as the overall higher taxonomic richness implies considerable habitat diversity. Indeed, a characteristic feature of the assemblages arranged in this cluster is the presence of taxa confined to a variety of aquatic environments associated with fluvial and flood plain conditions, as could be expected for sites located near extant major water bodies. However, the classification of Abu Tabari S 02/1 in cluster 2 is rather unexpected and hence of interest, particularly if considering the site's present-day location in the desert to the west of the Nile. Presumably, the 4th millennium cal. BC lower Wadi Howar experienced hydrological conditions that were more or less comparable to those prevailing near Ngala I, Akumbu-a and Abu Darbein.

The third cluster includes two assemblages in which latids outnumber clariids by far. Elephantine Island is a special case since its particular ecogeographical setting account for the relative low archaeobiodiversity index (see above). At Kobadi the taxonomic richness and high archaeobiodiversity can be explained by the location of the site on the shore of a former lake, receiving a fresh water supply from the main Niger on a permanent basis. The fact that the site's inhabitants captured Nile perch and giant catfish (*Arius gigas*) surpassing 1.8 m indicates a water body of considerable depth. This would also explain the presence of the African manatee *Trichechus senegalensis* at Kobadi (Jousse *et al.* in press).

In sum, by combining archaeobiodiversity indices with a measure of local hydrological conditions, here expressed by means of the ratio of Clariidae to Latidae, a general classification of sites according to their palaeoenvironments are possible. Such an approach seems particularly useful for ecologically classifying Holocene sites located away from any extant fluvial system in present-day North Africa, a region which once experienced intensive human occupation and exploitation along the extensive drainage systems originating during the post-Pleistocene climatic optimum.

Concluding Remarks

Diversity indices are valuable and useful to characterise prehistoric fish communities and environments since they are an indication of habitat richness. However, diversity indices alone are difficult to construe relative to other important ecological characteristics of water bodies such as water chemistry, current velocity or depth and size. Additional parameters are necessary to trace these palaeoecological aspects, an example of this being the ratio Latidae to Clariidae in an assemblage. Plotted against the Latidae/Clariidae ratios, the aD-indices will cluster in several groups, each of these corresponding to a different kind of aquatic environment. For sites located near extant water bodies with known ecologies this approach may be unsurprising, but for those ancient settlements situated at a considerable distance of any major river system, as is the case for the Wadi Howar sites, their position in the graph clearly helps to reconstruct the local environment and to trace changes in the aquatic environment with time.

To a certain extent, taphonomic and statistical biases may limit the utility of the approach presented here. Moreover, a calculation of aD-indices using higher taxonomic levels such as genus and species would allow more detailed characterisation of the anthropogenic assemblages, and hence, of the ecology of ancient water bodies. Yet a further refinement of such approaches to evaluate faunal assemblages, in particular those aiming at a site-by-site comparison, will likely necessitate more elaborate statistical tools as well as a secure testing of validity of sample size.

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References Cited

Begon, M., C.R. Townsend, and J.L. Harper. 2006. *Ecology: From individuals to ecosystems*. 4th edition. Malden: Blackwell Publishing.

Boessneck, J., and A. von den Driesch. 1982. *Studien an subfossilen Knochen aus Ägypten*. (Münchner Ägyptologische Studien 40.) Mainz: Verlag Philipp von Zabern.

Breunig, P., A. Garba, D. Gronenborn, W. Van Neer, and P. Wendt. 1993. Report on excavations at Gajiganna, Borno State, Northeast Nigeria. *Nyame Akuma* 40:30–41.

Breunig, P., A. Garba, and I. Waziri. 1992. Recent archaeological surveys in Borno, Northeast Nigeria. *Nyame Akuma* 37:10–17.

Bronk Ramsey, C. 1995. Radiocarbon calibration and analysis of stratigraphy: The OxCal program. *Radiocarbon* 37(2):425–430.

Bronk Ramsey, C. 2001. Development of the radiocarbon calibration program OxCal. *Radiocarbon* 43(2A):355–363.

Brooks, G.E. 1998. Climate and history in West Africa. In *Transformations in Africa: Essays on Africa's later past*, ed. G. Connah, 139-159. London: Leicester University Press.

von den Driesch, A. 1986. *Fische im Alten Ägypten: Eine osteoarchaeologische Untersuchung*. Documenta Naturae 34. München: Buchhandlung Kanzler.

von den Driesch, A., and J. Boessneck. 1985. *Die Tierknochenfunde aus der neolithischen Siedlung von Merimde-Benisâlame am westlichen Nildelta*. München: Institut für Paläoanatomie.

Froese, R., and D. Pauly. (eds.) 2007. *FishBase*. www electronic publication. www.fishbase.org. 04/2007.

Gasse, F., and N. Roberts. 2004. Late Quaternary hydrologic changes in the arid and semi-arid belt of northern Africa. Implications for past atmospheric circulation. In *The Hadley Circulation: Present, past and future*, ed. H.F. Diaz and R.S. Bradley, 133–162. Berlin: Springer Verlag.

Gautier, A., and W. Van Neer. 1989. Animal remains from the Late Palaeolithic sequence at Wadi Kubbaniya. In *The prehistory of Wadi Kubbaniya: Stratigraphy, palaeoeconomy, and environment*, ed. F. Wendorf, R. Schild, and A.E. Close, 119–161. Dallas: Southern Methodist University Press.

Gautier, A., V. Linseele, and W. Van Neer. 2002. The fauna of the Early Khartoum occupation on Jebel Umm Marrahi (Khartoum Province, Sudan). In *Tides of the desert: Gezeiten der Wüste*, ed. Jennerstrasse 8, 337–344. (Africa Praehistorica 14.) Köln: Heinrich-Barth-Institut.

Haaland, R. 1995. Bone artifacts: Production technique and function. In *Aqualithic sites along the rivers Nile and Atbara, Sudan*, ed. R. Haaland and A.A. Magid, 123–136. Bergen: Alma Mater.

Haaland, R., and A.A. Magid. 1995. Radiocarbon dates. In *Aqualithic sites along the Rivers Nile and Atbara, Sudan*, ed. R. Haaland and A.A. MAgid, 47–51. Bergen: Alma Mater.

Hamilton, A. 2005. Species diversity or biodiversity? *Journal of Environmental Management* 75(1):89–92.

Hammer, Ø., D.A.T. Harper, and P.D. Ryan. 2001. PAST. Palaeontological statistics software package for education and data analysis. *Palaeontologia Electronica* 4(1):9.

Hoelzmann, P., B. Keding, H. Berke, S. Kröpelin, and H.-J. Kruse. 2001. Environmental change and archaeology: Lake evolution and human occupation in the Eastern Sahara during the Holocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* 169:193–217.

Hugueny, B., and C. Lévêque. 1994. Freshwater fish zoogeography in West Africa: Faunal similarities between river basins. *Environmental Biology of Fishes* 39:365–380.

Jesse, F. 2003. *Rahib 80/87. Ein Wavy-Line-Fundplatz im Wadi Howar und die früheste Keramik in Nordafrika*. (Africa Praehistorica 16.) Köln: Heinrich-Barth-Institut.

Jesse, F. 2006. Cattle, sherds and mighty walls: The Wadi Howar from Neolithic to Kushite times. *Sudan & Nubia* 10:43–54.

Jost, L. 2006. Entropy and diversity. *Oikos* 113(2):363–375.

Jousse H., H. Obermaier, M. Raimbault, and J. Peters. In press. Late Holocene economic specialisation through aquatic resource exploitation at Kobadi in the Méma, Mali. *International Journal of Osteoarchaeology* 17.

Keding, B. 1997. *Djabarona 84/13: Untersuchungen zur Besiedlungsgeschichte des Wadi Howar anhand der Keramik des 3. und 2. Jahrtausends v.Chr*. (Africa Praehistorica 9.) Köln: Heinrich-Barth-Institut.

Kröpelin, S. 1993. *Zur Rekonstruktion der spätquartären Umwelt am unteren Wadi Howar (Südöstliche Sahara / NW-Sudan)*. (Berliner Geographische Abhandlungen 54.) Berlin: Selbstverlag des Geomorphologischen Laboratoriums der Freien Universität Berlin.

Laë, R. 1995. Climatic and anthropogenic effects on fish diversity and fish yields in the Central Delta of the Niger River. *Aquatic Living Resources* 8:43–58.

Lepofsky, D., and K. Lertzman. 2005. More on sampling for richness and diversity in archaeobiological assemblages. *Journal of Ethnobiology* 26(3):175–188.

Lévêque, C. 1997. *Biodiversity dynamics and conservation: The freshwater fish of tropical Africa*. Cambridge: University Press.

Linseele, V. 2005. Domestic livestock, subsistence strategies and environmental changes in Sahelian West Africa during the past 4000 years: Evidence from archaeofaunal remains. Ph.D. dissertation, University of Leuven.

MacDonald, K.C., and W. Van Neer. 1994. Specialised fishing peoples in the Later Holocene of the Méma (Mali). In *Proceedings of the 7th meeting of the ICAZ, Fish remains working group, Tervuren*. ed. W. Van Neer, 243–351. (Annales du Musée Royal de l'Afrique Centrale, Sciences Zoologiques 274.) Tervuren: Musée Royal de l'Afrique Centrale.

Marcolongo, B. 1983. Late Quaternary Nile and hydrology of the Khartoum-Sabaloka region (Sudan). *Origini* 12:39–40.

Marcolongo, B., and A.M. Palmieri, 1988. Dynamics of natural environment in the Geili area. In *El Geili: A Middle Nile environment 7000 BC–AD 1500*, ed. I. Caneva, 35–47. (Cambridge Monographs in African Archaeology, BAR International Series 424.) Oxford: BAR.

Meadow, R. 1980. Animal bones: Problems for the archaeologist together with some possible solutions. *Paléorient* 6:65–77.

Morales Muñiz, A., and W. Van Neer. 1994. Species abundance models as potential discriminators of natural and anthropogenic paleo-ichthyocenoses with a case example from African sites. In *Archaeo-ichthyological studies. Proceedings of the 6th meeting of the ICAZ Fish Remains Working Group,* ed. D. Heinrich, 386–394. (Offa 51.) Kiel: Institut für Ur- und Frühgeschichte der Christian-Albrechts-Universität.

Peters, J. 1995. Mesolithic subsistence between the 5th and the 6th Nile cataract: The archaeofaunas from Abu Darbein, El Damer and Aneibis (Sudan). In *Aqualithic sites along the rivers Nile and Atbara, Sudan*, ed. R. Haaland and A.A. Magid, 178–244. Bergen: Alma Mater.

Peters, J., N. Pöllath, and F. Jesse. 2007. Tierknochen als Archiv für Klima, Landschaft und menschliche Mobilität: Das Beispiel Ostsahara. *Nova Acta Leopoldina NF* 94(348):73–83.

Raimbault, M. 1994. Sahara malien: Environnement, populations et industries préhistoriques. Ph.D. dissertation, Université de Provence, Aix-Marseille.

Soetaert, K., and C. Heip. 1990. Sample-size dependence of diversity indices and the determination of sufficient sample size in a high-diversity deep-sea environment. *Marine Ecology Progress series* 59:305–307.

UNEP, 2006. *Africa's lakes: Atlas of our changing environment*. Nairobi, Kenya: United Nations Environment Programme.

Van Neer, W. 1989. Recent and fossil fish from the Sahara and their palaeohydrological meaning. *Palaeoecology of Africa and Surrounding Islands* 20:1–18.

Van Neer, W. 2002. Food security in western and central Africa during the late Holocene: the role of domestic stock keeping, hunting and fishing. In *Droughts, food and culture: Ecological change and food security in Africa's later prehistory*, ed. F.A. Hassan, 251–273. New York: Kluwer Academy.

Van Neer, W., and H.-P. Uerpmann. 1989. Palaeoecological significance of the Holocene faunal remains of the B.O.S.-missions. In *Forschungen zur Umweltgeschichte der Ostsahara*, ed. R. Kuper, 309–341. (Africa Praehistorica 2.) Köln: Heinrich-Barth-Institut.

Zohar, I., T. Dayan, E. Galili, and E. Spanier. 2001. Fish processing during the early Holocene: A taphonomic case study from coastal Israel. *Journal of Archaeological Science* 28:1041–1053.