

Present-day African analogue of a pre-European Amazonian floodplain fishery shows convergence in cultural niche construction

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Erickson [Erickson CL (2000) *Nature* 408 (6809):190–193] interpreted features in seasonal floodplains in Bolivia's Beni savannas as vestiges of pre-European earthen fish weirs, postulating that they supported a productive, sustainable fishery that warranted cooperation in the construction and maintenance of perennial structures. His inferences were bold, because no close ethnographic analogues were known. A similar present-day Zambian fishery, documented here, appears strikingly convergent. The Zambian fishery supports Erickson's key inferences about the pre-European fishery: It allows sustained high harvest levels; weir construction and operation require cooperation; and weirs are inherited across generations. However, our comparison suggests that the pre-European system may not have entailed intensive management, as Erickson postulated. The Zambian fishery's sustainability is based on exploiting an assemblage dominated by species with life histories combining high fecundity, multiple reproductive cycles, and seasonal use of floodplains. As water rises, adults migrate from permanent watercourses into floodplains, through gaps in weirs, to feed and spawn. Juveniles grow and then migrate back to dry-season refuges as water falls. At that moment fishermen set traps in the gaps, harvesting large numbers of fish, mostly juveniles. In nature, most juveniles die during the first dry season, so that their harvest just before migration has limited impact on future populations, facilitating sustainability and the adoption of a fishery based on inherited perennial structures. South American floodplain fishes with similar life histories were the likely targets of the pre-European fishery. Convergence in floodplain fish strategies in these two regions in turn drove convergence in cultural niche construction.

convergent evolution | cultural evolution | earthworks | historical ecology | tropical stream ecology

Fifteen years ago, in his studies of human-modified landscapes in the Beni savannas of Bolivia, Erickson (1) identified a particular form of zigzag earthwork in a 525-km² area of seasonal floodplain in the Baures region as vestiges of fish weirs. “A fish weir is . . . any structure constructed in water and acting as a funnel or barrier to direct fish into a trap or enclosure or to entrap fish behind it, where they can be easily harvested” (2, p. 5). Fish weirs are “. . . usually built in a flowing stream to funnel fish into a trap or built in a tidal flat to trap fish behind it as the tide goes out” (2, p. xv). The structures Erickson identified as vestiges of fish weirs are linear ridges of raised earth (now 1–2 m wide and 20–50 cm tall) that cross savanna floodplains from one forest island to another for distances up to 3.5 km, changing direction every 10–30 m. Erickson stated that “funnel-like openings, 1–3 m long and 1–2 m wide, are present where the structures form a sharp angle.” Erickson identified these gaps as passages where fish-catching devices were placed. Erickson's conclusions, based on the form of these structures and on their orientation, location, and association with other hydraulic earthworks,

were quite bold, because he lacked direct archaeological evidence of their function and because the ethnographic analogues he cited in support of his inferences all differ in important ways from the structures he described. Furthermore, examination of Connaway's world review of fish weirs (2) also turned up no close analogues (*SI Text*). This paucity of evidence leaves room for skepticism, and the only archaeological study of fish consumption so far conducted in the Beni llanos found assemblages to be dominated by species dwelling in slow-moving water (swamps, marshes, or ponds), with few or no remains of fish species that exploit flooding cycles and thus are likely to have been trapped in large numbers by weirs (3). However, weir-like structures appear to be absent from the area these authors studied, which is about 150 km southwest of Erickson's study area. Furthermore, no plausible alternative function of the features described by Erickson, and particularly of the funnel-shaped openings he described, has been suggested. That Erickson was able to make a compelling case despite the absence of close ethnographic analogues illustrates the validity of Binford's (4) statement that ascribing too much importance to ethnographic analogy prevents archaeologists from admitting “the possibility of dealing with forms of cultural adaptation outside the range of variation known ethnographically” (p. 13). However, although archaeologists should not allow their interpretive scope to be limited by the bounds of the ethnographic present, neither can they afford to ignore this invaluable source of

Significance

Erickson convincingly inferred a pre-European floodplain fishery unlike any present-day system he knew, illustrating the principle that archaeological inference should not be constrained by the range of cultural variation observed today. Our comparison of these inferences with observations from a present-day fishery in a similar environment suggests strong convergence in both the ecology of fish communities and the cultural means people have devised to exploit them, providing support for a predictive model of cultural niche construction. This conceptual framework emphasizes the synergistic action of human agency and environmental constraint in shaping patterns in the human use and management of ecosystems.

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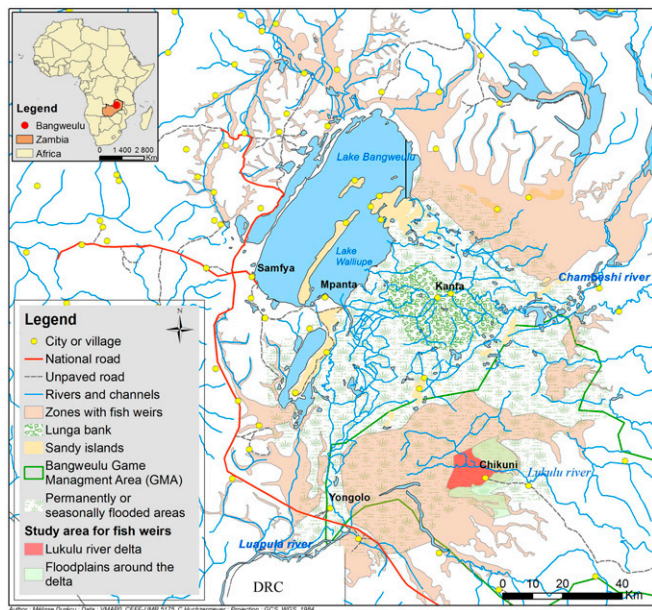


Fig. 2. Distribution of fish weirs in the seasonal floodplains of the Bangweulu basin, Zambia. See *Methods* and *SI Text* for sources and methods used to prepare the map.

and higher weirs in deeper parts of the floodplain. Deeper in the swamps, weirs of even greater height are built from vegetation.

The Zambian weirs can be up to 5 km long, traversing broad floodplains. Weirs sometimes zigzag but usually are more or less straight or curvilinear, running from one termitarium island to another. They are easily recognized by the presence of the frequent (every 2–10 m) fishways, which may be simple gaps or V-shaped structures (Fig. 3). Funnel-like openings (always oriented downstream with respect to the direction of water flow out of the floodplain) may be 1–8 m long and 1–2 m wide; simple gap openings are 1–2 m wide. Larger weirs are flanked by canals resulting from excavation of the earth to make the weirs and used for access by boat when nets and baskets are set, checked, and harvested. The excavation channels alongside the weirs also offer a slightly deeper habitat for fish and a route along which they can swim.

In the part of the Lukulu delta where most fieldwork was done (red area in Fig. 2), covering 129 km² of floodplain, exhaustive mapping based on a satellite image taken in May 2012 (Fig. S3) yielded a total of 328 km of fish weirs and thus a linear density of 2.55 km/km². Thus, although some uncertainty is associated with Erickson's estimates in Bolivia (see *SI Text*), the density of weirs (or their vestiges, in Bolivia) appears to be roughly comparable in the two sites (2.89 vs. 2.55 km/km² in the prehistoric and present-day fisheries, respectively).

Functioning of the Weir Fishery. For the archaeological system, Erickson's most fundamental inference—that the structures he observed were in fact fish weirs—was based on their form (particularly of the funnel-shaped structures), location, orientation, association with other earthworks, and (imperfect) ethnographic analogy. He excluded transport or water retention for flood-recessional farming as possible functions of the zigzag structures but considered that weirs, together with other hydraulic earthworks, could have been used to extend the period of flooding in some areas. Weirs are situated across areas that today are shallowly flooded in the wet season and functioned, he inferred, to trap fish that migrate from permanent water into seasonal floodplains to spawn and feed and then migrate back out of the floodplain to permanent water when

flood waters recede (14, 15). Today, floodplains in the Baures region are flooded for a period of 4–5 mo, from January/February to June (16). The duration of flooding is similar to that in the Bangweulu basin, reflecting the similar amount and seasonal distribution of annual rainfall in the two areas (Fig. S4). Depth of flooding is also similar, currently not greatly exceeding 1 m in the areas where fish weirs (or in Bolivia, their vestiges) are found (Fig. S5). Building, maintaining, and using earthen weirs would likely be prohibitively time-consuming and impractical if flooding were frequently much deeper than 1 m.

Erickson postulated that the fishery he described was highly productive, sustaining large populations in a seemingly marginal environment that today harbors few people. His claim of high productivity was based on a few reports of high fish biomass in river channels or ponds in seasonally flooded tropical savannas (17, 18). He also speculated that *Pomacea* snails, which are abundant in the area, could have been harvested in large numbers and that palms, also frequent around weirs today, provided both edible fruits and insect larvae. Nearby ponds, which Erickson assumed to be of artificial origin, could have held drinking water year-round, attracted game, and enabled dry-season persistence of fish and snails.

Erickson (1) considered the complex of weirs, ponds, and causeways to be “a form of intensive aquaculture” (p. 191) used to regulate water levels, extending the period of flooding by capturing the first rains and holding water longer into the dry season. As a perennial food-producing infrastructure, weirs must have been valuable and protected real estate, owned and inherited by clans and chiefly lineages. Like causeways, canals, raised fields, and other earthworks, they were durable investments in land created by modification of the landscape (19). Sustained high productivity justified the investment of labor required to build and maintain weirs. He also postulated that the system required social coordination. Landscape patterns suggested that both intercommunity cooperation and tension over fisheries and other resources may have occurred.

Considerable ethnographic information from the present-day Zambian weir fishery (*SI Text* and Fig. S6) can help us evaluate

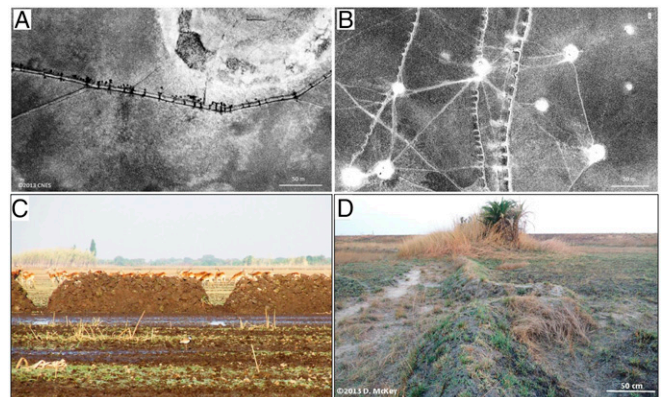


Fig. 3. Fishways, the simple gaps or V-shaped structures that are the characteristic features of earthen fish weirs in Bangweulu basin, Zambia, seen from the air (A and B) and on the ground (C and D). (A and C) Simple gap fishways. (A) Simple gap fishways seen from the air. Panchromatic satellite image by the Pléiades sensor, 12°02'S, 30°05'E, September 17, 2013 (Copyright 2013, CNES, Distribution Airbus DS, all rights reserved). (C) Simple gap fishways in a newly constructed weir in the Bangweulu basin. Behind the weir is a herd of black lechwe (*Kobus lechwe smithemani*). (Photograph copyright 2011, C.F.H.) (B and D) V-shaped fishways. (B) V-shaped fishways seen from the air. Panchromatic satellite image by the Pléiades sensor, 12°02'S, 30°09'E, September 17, 2013 (Copyright 2013, CNES, Distribution Airbus DS, all rights reserved). (D) V-shaped fishways seen from the ground. (Copyright 2013, D.M.)

Erickson's inferences and speculations about the functioning of the pre-European Bolivian system.

First, the present-day fishery is highly productive, and high harvest levels appear to be sustainable, because overall yield, although fluctuating, shows an increasing trend (13). Based on data gathered for an intensively studied area of 15 × 15 km around Chukuni, Huchzermeyer (11) estimated the annual yield of the weir fishery for local fishermen using a 22,500-ha floodplain to be 800,000 kg fresh mass of fish, or 35.5 kg·ha⁻¹·y⁻¹.

For the Bolivian fishery, estimates of yield are of course unavailable, and the figures Erickson (1) cites for potential productivity are expressed in a form that does not allow comparison with Huchzermeyer's (11) estimate for Zambia. Citing a reference (17), Erickson (1) writes that "yields of 1,000 kg per hectare per year have been recorded for shallow ponds in tropical savannas." This very high figure certainly represents the concentration in dry-season refugia of fishes from a much larger (but unknown) area of rainy-season floodplain and cannot be compared with Huchzermeyer's (11) estimate based on total floodplain area.

Secondly, weirs are indeed valuable real estate, perennial food-producing infrastructures that are owned and inherited. The perennial nature of earthen weirs warrants the considerable labor investment needed to construct and maintain them (*SI Text*). A person who builds an earthen weir when young can benefit from this initial investment throughout his life. The effort required to maintain a perennial earthen weir is probably much less than the effort that would be needed to build a new short-lived structure made of vegetation every year, a task that gets more difficult as the individual ages. Furthermore, a weir (or a section of weir) is inherited by the living descendants of the person who first built it and cannot easily be taken away from the lineage, because the "ancestor spirits" would keep that weir from having good catches unless it is used by their relatives (5). Weirs can remain operational for many decades, and there is no physical reason why they should ever be abandoned. Soils of the parts of the floodplain where earthen weirs occur are loamy in texture (20). Friable enough to allow easy working, they also are sufficiently clay-rich that weirs, held together by plant roots, are resistant to erosion. Furthermore, weirs are repaired regularly (*Fig. S6F*). The only cases known to us of weirs being abandoned are explained by conflict over ownership. In these cases, each feuding party is given a new area in which to build a weir.

Construction, maintenance, and use of weirs all require cooperation and coordination; access rights are regulated, and, as noted above, conflicts occur. Areas important for fishing are divided into tracts of land, each under the control of a traditional fishing chief known as a "*chipupila*" (*Fig. S6H*). These men are descended from notable people, and inheritance of the position is matrilineal. The *chipupila* determines where new weirs can be constructed, allocates fishing rights in the areas of water that drain through a weir, and mediates conflicts. Long fish weirs have multiple owners. Every owner assists with the construction and maintenance of a fish weir, and the gaps left in a weir for trap placement are individually owned. Formerly, the start of the fishing season and opening of new areas were surrounded by ritual, and the *chipupila* played a spiritual role ["fishing priests" (5)].

Thus, information about the present-day fishery supports Erickson's view of the archaeological fishery as capable of sustained high productivity and of weirs as structures inherited across generations, whose construction and use required social coordination. However, analysis of the present-day system suggests a technological/ecological basis for the system's sustainability that is different from, and simpler than, that proposed by Erickson.

The Ecological Basis of the Sustainability of the Present-Day Weir-Based Fishery. Erickson postulated that the archaeological fishery involved practices such as the management of water by using weirs,

ponds, and causeways to extend the period of inundation. Analysis of the present-day analogue suggests that sustained high harvest levels could have been achieved without such intensive management. In Bangweulu, weirs serve more to direct the movements of the fish across the floodplain than to control the hydrology.

Fish communities in Bangweulu include a large number of species that migrate seasonally into the vast floodplains for spawning and feeding (*SI Text*). Of 44 species recorded in the basin by Huchzermeyer (11), 25 occur in floodplain habitat. These species dominate assemblages and are the principal targets of the weir fishery. Different aspects of the fishery are illustrated in *Fig. S6*. At the start of the rains (December to February), fishways are left open to allow passage of in-migrating fish. Fish spawn, feed, and grow in the flooded plain, and weirs are tended and maintained. As soon as water levels begin to drop (April; see *Fig. S5*), the weirs are closed, and harvest begins, timed to coincide with massive out-migration of fish which are caught in large numbers in traps set in the fishways (May/June). As one area dries out, another becomes shallow enough to operate the weirs. Thus there is a gradual shift in the location of active weirs from March through to July/August, fishing on the same stock of juveniles as water draws through the various levels of plain and weir. The traditional high-current gear is a large funnel basket, without a valve, called "*kansa*" in the Bemba language (*Fig. S6 C and D*). When fishermen observe that flow rate is reduced, they place at the fishways smaller basket traps with a valve called "*imono*." Larger fish are smoke-dried, and smaller ones are usually sun-dried. Fish thus preserved can be stored for long periods.

The Bangweulu fishery is characterized by great resilience in the face of high harvest levels. The key to this resilience appears to be the life-history adaptations of fishes to seasonal floodplain environments. A large proportion of the individuals caught in weirs are juveniles (11, 12). Management discourses tend sweepingly to condemn the catching of under-sized and immature fish as wasteful and unsustainable, and the weir technique is considered illegal in the Bangweulu basin [although regulations are not enforced (21)]. However, the "growth-overfishing" concept often makes little sense, given the age-survivorship curve typical of most fishes (22) and particularly of seasonally breeding floodplain fishes. Warm, shallow, well-oxygenated, and relatively nutrient-rich water favors breeding in the high-water season, but severe competition and predation lead to high mortality of juveniles in the first dry season. The boom-and-bust conditions favor fish species that can mature after 1 y of life, start breeding at a small size, and have multiple reproductive cycles. Juveniles of the species captured by weirs at the end of the high-water season would suffer high mortality shortly thereafter, in any case (11). The harvest of this age class thus may have a limited effect on the reproductive potential of the population (23–25). Also, because the age distribution of fishing mortality with the weir technique mimics that of natural mortality in fishes of seasonal floodplains, selective pressures acting on the population are unchanged, conferring long-term resilience (cf. ref. 22).

There are limits to the sustainability of any harvest regime, and many questions about the limits of the weir fishery remain open. Although the harvesting of juveniles of fish species adapted to periodic breeding in floodplains should be sustainable at higher levels than for most fish species, the threshold level beyond which harvest no longer allows adult cohort renewal is unknown. Sustainability also requires relatively high adult survival. If too many adults, particularly large, highly fecund individuals, are harvested by weirs or other gear, the sustainability of the weir fishery would be compromised. We have no indication that fishermen adopt any conservation-motivated practices to spare adult fish; such practices would be unlikely to appear if resources are abundant. However, several factors may give larger fish a higher probability of surviving passage through the weirs. Because larger fish need deeper water to avoid predation, adults likely leave the spawning

ground before juveniles, at a time when higher water level allows them to swim (or jump, or in the case of *Clarias* spp., crawl) over weirs or through fishways not yet set with traps. Data on size-class-specific survivorship and the other open questions raised here are required to model the system's sustainability.

Evolutionary Convergence in Floodplain Fish Life Histories in Africa and South America. Lateral seasonal migrations such as those observed in Bangweulu are documented for many fish species in tropical floodplain rivers (26), and the combination of life-history traits described by Huchzermeyer (11, 12) is in fact typical of seasonally breeding floodplain fish species throughout the tropics, including those in South American floodplains [“seasonal strategists” (27) or “periodic” (P) strategies (28, 29)]. Of 71 fish species studied by Winemiller (27) in the Orinoco Llanos of Venezuela, 48 exhibited a P strategy, characterized by cyclic (often annual) reproduction, relatively long generation times, large clutches, and small investment per offspring. As in the Bangweulu floodplains, fishes identified as P strategists exhibit a characteristic burst of reproduction with the early rains, followed by gradual reductions in population size caused largely by predation on immature fish during the early dry season. In the Bangweulu wetlands, the reproduction of virtually all fish species is affected by the periodicity of this highly seasonal environment (Table S1). Following the classification of Winemiller and Rose (28), fish species with P strategies accounted for 57% of total biomass in that site (Table S2). Species with strategies intermediate between P and either “opportunistic” (O) or “equilibrium” (E) strategies accounted for a further 38%. No pure E strategist species was present.

In the Iténez-Guaporé watershed (the names are those applied to the same river in Bolivia and Brazil, respectively), within which Erickson's study area lies, experimental fishing conducted over a 2-y period (SI Text) (30) found that 43 fish genera together accounted for 96% of the fish biomass (Table S1). P strategists comprised 24 of the 43 genera and 49% of the biomass, followed by E strategists (eight genera, 26% of the biomass) and by species with strategies intermediate between E and P (I-E/P) (four genera, 17% of the biomass) (Table S2). Thus, as in the Bangweulu basin, a large proportion of the assemblage in this region, in terms of both richness and biomass, is comprised of fish that could have been targeted by the weir fishery.

Niche Construction, Ecological Inheritance, and Sustainability. Because the investment required in niche construction and maintenance is favored when the constructed environment remains productive over long periods and is inherited by the constructors' descendants, sustainability of the weir fishery is key to the system's functioning. We identify several features of the social regulation of weir use that enhance sustainability in the present-day Bangweulu fishery; these features are quite similar to those posited by Erickson (1) for the archaeological Bolivian fishery. We also identify ecological factors favoring sustained high harvest levels in the Bangweulu fishery. We propose that, in the two cases we compare here, sustainability is assured by the match between the way weirs are used and the life-history strategies of the fish they capture.

In both regions, similar physical environments and similar floodplain fish life histories drove convergence in the construction and use of weirs. Flooding regimes are similar in the two regions, with a large expanse of floodplain being predictably covered each

year (Fig. S5) with water that remains shallow enough to permit the operation of earthen weirs. In both regions, loamy or clay-rich soils (20, 31) and the organisms living in them contribute to making these structures resistant against erosion. Finally, in both environments many fish species respond to seasonal flooding in very similar ways, migrating into seasonal floodplains to spawn and feed and then migrating out as the water recedes. These similarities in ecosystem structure and ecological convergences, driven by natural selection in fish life histories and the functioning of fish populations, led to similar decisions by people in the two regions about how to exploit them. Thus, environmental similarities, natural selection, and human agency combined to drive strong convergence in how humans in these two regions constructed the fishing dimension of their ecological niche.

Methods

Our photo-interpretation of archaeological vestiges of fish weirs in the Baures region was based on images available through Google Earth and the World Imagery layer of ArcGis and were validated by comparison with Erickson's (1) mapping (SI Text and Figs. S1 and S2).

To map the distribution of habitats and land uses in the Bangweulu basin, we combined field observations, photo-interpretation of high-resolution multi-spectral images (Landsat 8, scene ID LC81710682014135LGN00; panned to yield an image of 15-m resolution), and analysis of a digital terrain model (data uploaded from the site EarthExplorer and assembled using ArcGIS 10.2.2; 30-m resolution), using supervised classification applied to predefined classes based on field observations. We then used very high-resolution images available through Google Earth to map the distribution of fish weirs within the region (Fig. 2). Within the area of the Lukulu delta where most field observations were conducted, we used Google Earth imagery, in addition to an image from the Pléiades sensor taken on September 17, 2013 [copyright 2013, Centre National d'Études Spatiales (CNES)], to map all fish weirs (Fig. S3) and calculate their linear density (kilometers of fish weirs per square kilometer). To examine changes over time, the distribution of weirs in this area was mapped on images taken on two different dates, May 9, 2012 and September 17, 2013. No earlier images of sufficiently high resolution are available for this area.

Observations of the construction, maintenance, and functioning of fish weirs in Bangweulu were conducted by C.F.H. during 5 y of fieldwork (11, 12). During this time, fish communities of the region were characterized by participatory observation of fishermen, experimental fishing, and opportunistic collection. Fish communities of the Baures region were characterized by similar methods (see SI Text for details).

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