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Geologic and hydrologic concerns about pupfish divergence during the last glacial maximum

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1. Introduction

Martin *et al.*'s [1] double-digest, restriction-site-associated DNA sequencing of Death Valley pupfish species (*Cyprinodon*) and new time-calibrated phylogenetic analysis provide estimated divergence ages for North American pupfish at two scales. On the larger temporal and spatial scale, Martin *et al.* conclude that the Death Valley pupfish shared common ancestry with: *Cyprinodon albivelis* Rio Yaqui, Mexico, which drains into the northern Gulf of California, at *ca* 10 kyr; *C. veronicae* and *C. alvarezi* from isolated springs in Nuevo León, Guzmán Basin, northeastern Mexico [2], at *ca* 17 kyr; and Atlantic coastal pupfish including those from the Yucatan Peninsula, Mexico, and the Bahamas (*C. artifrons*, *C. maya* and others) at *ca* 25 kyr. Martin *et al.* supported these genetic divergences and temporal estimates in their phylogenetic tree with these statements: 'these ages are consistent with increased population mixing expected from the formation of large pluvial lakes throughout North America during the most recent glacial period 12–25 thousand years (kya).' and it 'is not apparent how low-lying desert populations could have remained isolated within large inland seas . . . ' On the smaller scale, Martin *et al.* also conclude that introgression among pupfish species and subspecies of the 300 km-long Amargosa River of Death Valley occurred in the last 150 years.

We do not dispute possible introgressions along the Amargosa River in the last 150 years; however, the well-documented North American and Death Valley drainage basin histories of the last 25 kyr clearly demonstrate that the long-term divergence chronology proposed by Martin *et al.* is impractical. The temporal and spatial parameters defined by Martin *et al.* encompass 26.5–9 kyr, which is the last glacial maximum (LGM). We do not know, and Martin *et al.* did not offer, the dispersal path from the Gulf of Mexico to Death Valley. If dispersal is confined to waterways we estimate the shortest water dispersal path was about 3 000 km (Rio Grande to Gila River to Colorado River to Death Valley). This distance is not precise and, as we discuss below, the geologic evidence does not support the existence of such a dispersal path in the last 25 kya. Such a long path does, however, illustrate that the dispersal distance is relatively lengthy for a 5 cm-long fish.

Within those parameters, we focus on water (river or lake) as the most practical mechanism of 'overland dispersal' of fish. This is consistent with Darwin [3] who noted that lengthy dispersals of fish (e.g. 3000 km) are by water with short-distance dispersals by means other than water (e.g. live fish or ova moved by water spouts) being 'occasional' and 'accidental'. Waterbirds may disperse plants and invertebrates rapidly over large distances [3]; however, there are no documented cases of vertebrates or vertebrate eggs transported by waterbirds [4,5]. Conceivably, Native Americans may have transported pupfish a few kilometres, but it is impractical that they moved pupfish thousands of

kilometres over mountains where other edible fish were present. Similar to Darwin's conclusion, we do not consider water spout, waterbird or Native American transport of pupfish or ova over thousands of kilometres a practical dispersal scenario.

The isolation of fish species is apparent in the framework of the well-documented North American Great Basin palaeolakes and connecting rivers. The largest lake systems of Western North America during the LGM were palaeo-Owens River [6], Lake Lahontan [7] and Lake Bonneville [8]. Although covering thousands of km^2, these systems were hydrologically isolated by mountainous drainage divides hundreds of metres higher than the water bodies, which effectively prevented gene flow between fish populations. For example, Martin *et al*. show Death Valley connecting to the palaeo-Owens River system during the LGM by overflow of Panamint Lake into Death Valley. This is erroneous because lake shoreline deposits dated at 24–14 kyr in Panamint Valley are 90–100 m below the Wingate Wash spillway elevation [9]. Thus, the palaeo-Owens River did not spill into Death Valley during the LGM. The Death Valley drainage system did expand during the LGM when the sill of pluvial Silver Lake was breached at 12–11 kya and the Mojave River flowed into Death Valley [10]; however, even with this captured tributary, the Death Valley–Amargosa–Mojave drainage system was hydrologically insulated within the Great Basin during the LGM just as it is today [10]. Thus, fish in Death Valley during the LGM were effectively isolated from the rest of North America and fish dispersal to other areas was impractical.

Within the time frame presented by Martin *et al*., we assume that in the Gulf of Mexico, which is the likely source of a common ancestor, pupfish were relatively wide-spread at 25 kya. The shortest dispersal route to Death Valley is via the Rio Grande, then across the southern Rocky Mountains (greater than 2000 m above sea level) directly into the Gila River (*C. macularius* [2]), which drains into the Colorado River. The geologic evidence shows that, like today, there was no hydrological connection between the Gila River and Rio Grande during the LGM [11]. Alternatively, pupfish may have exited the Rio Grande drainage by the Mimbres drainage basin in southwestern New Mexico, which also shares a drainage divide with the Gila River. The geologic evidence shows that the Rio Grande flowed into the Mimbres basin up until 2.25 Mya, after which the Rio Grande flowed south into the Gulf of Mexico and the Mimbres basin was isolated and internally drained [12]. Therefore, there was no hydrologic connection from the Rio Grande to the Mimbres or Gila River basin during the LGM and pupfish could not practically disperse to the Gila River or Guzman basins from the Rio Grande during the LGM.

If pupfish somehow arrived at the Gila River from the Rio Grande, to reach the isolated springs of the Guzmán Basin, northwestern Mexico (*C. fontinalis*, *C. pisteri* and *C. albivelis;* only *C. albivelis* was studied by Martin *et al*.), Gila River pupfish must cross the southerly mountain divide [2]. Alternatively, Gila River pupfish went downstream to the Gulf of California, up the Rio Yaqui to the Rio Papígochic (*C. albivelis*), and then crossed a mountain divide from the south and into the Guzmán Basin to the isolated springs. We are not aware of any geological evidence for hydrological pathways across the mountain divides that encompass the Guzmán Basin [11] during the LGM, making gene flow by water to these springs impractical.

If pupfish somehow reached the Gila River, then a hydrologic connection to the Colorado River is established. Reaching Death Valley from the Colorado River, however, requires pupfish to cross 250 km of the Mojave Desert via a series of hydrologically isolated playas with intervening divides as high as 900 m above the basin floors. Geologists have hypothesized about a hydrologic connection between the Colorado River and Death Valley since the early twentieth century; however, the geologic data now show that a hydrologic connection between Death Valley and the Colorado River has not existed for over 3 million years [13–15]. Therefore, there was no hydrologic connection between the Colorado River and Death Valley during the LGM.

The biogeographical study by Martin *et al*. is dependent upon an understanding of both genetics and palaeogeography. Martin *et al*.'s 'large inland seas' of the LGM were, in fact, large, isolated lakes and pupfish dispersal across Western North America was physically impractical. The geologic data show that, during the LGM, the Death Valley–Amargosa–Mojave drainage basin was hydrologically isolated within the Great Basin with no demonstrated hydrologic connection with any other pupfish population for at least 3 million years.

When the geologic record is considered, it is apparent that during the LGM Western North American fish populations remained isolated (as evidenced by genetic divergence) because the pluvial lake and river systems were separated from each other by high mountain divides and did not form interconnected 'large inland seas'. We agree with Darwin that the only practical method of fish dispersal is by interconnected waterways. The numerous studies of Western North American palaeohydrology show that interconnected waterways did not exist during the LGM [6–19]. The absence of scientifically documented cases of fish transport by waterbird [4,5] or Native Americans across the thousands of kilometres between the Gulf of Mexico and Death Valley, or even the tens of kilometres across several waterless montane drainage divides between tributaries, renders non-waterborne modes of dispersal impractical and unlikely.

The geological implausibility of dispersal mechanisms during the LGM implied by Martin *et al*.'s molecular clock suggests that alternative hypotheses be explored. For example, the Laguna Chichancanab calibration point may be yielding mutation rates that are unrealistically fast. The assumption that Laguna Chichancanab desiccated prior to 8000 ± 200 years ago resulting in extirpation of pupfish within the basin may be incorrect; pupfish may have survived in other parts of the lake basin that did not completely dry. The geologic data [6–19], along with previous pupfish and springsnail genetic studies [2,20,21], suggest the Gulf of Mexico area was the likely ancestral origin of the Death Valley pupfish millions of years ago, not less than 30 000 years ago.

Data accessibility. This article has no additional data.

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