A Reply to Jacobs and Lou (2018)

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Jacobs & Lau (2018) have published a 20-page response to a 7-page rebuttal I wrote to their recent paper in PeerJ (Lau & Jacobs 2017; Brusca 2018). Although they threw everything they had at it, even in 20 pages they failed to correct any of the errors I pointed out in my rebuttal. Hence, I would not bother to reply to their response, except for the fact that (as with their initial paper) they misquote and misrepresent what I have written. To be as clear as possible, I presented 5 specific points in my rebuttal:

(1) Lau & Jacobs (2017) based their entire study on an assumption that the two fishes they studied (*Colpichthys hubbsi* and *C. regis*) were sister species, but they failed to provide any evidence in support of this. Their response does nothing to remedy that. In their response, they mention that they have an unpublished phylogenetic analysis, based on unpublished mitochondrial DNA sequences, that supports the sister group relationship. While reporting results from unpublished analyses is a sloppy approach to doing science in and of itself, they did not even go as far as mentioning this unpublished evidence in their original paper. Their statement that my rebuttal posited these two fishes belonging in different genera is simply not true; I made no such claim. I only noted that, not only did they fail to provide any evidence that they were sister species, but that other researchers have had the opinion that the two species are not closely related. Until someone tests this hypothesis, it remains unresolved. I am not an ichthyologist and I don't personally have an opinion, nor a stake in whether or not these species are sister taxa. But until they are shown to be, and the peer community has an opportunity to evaluate the data that may or may not support that hypothesis, it remains simply their opinion.

(2) I challenged their claim that the salinity of the Upper Gulf (where their study was based) has changed dramatically since the construction of dams on the Colorado River, a claim that was not supported by any data they presented. Their response also offers no evidence of significant salinity change, and previous research has cast doubt on the idea of significant salinity gradients developing in the Upper Gulf during from Colorado River flow (Lavín and Sánchez 1999).

(3) Their response still presents no evidence that these alleged sister species were driven to ecological speciation due to salinity gradients in the Upper Gulf. It is merely speculation. Simple salinity tolerance tests of the two species would go a long way in supporting or rejecting that hypothesis. The idea that *C. hubbsi* evolved in and was restricted to low-salinity pre-dam habitats is not supported by their presence today in the Upper Gulf and delta's high salinity environment.

(4) My rebuttal argued that their claims of *Uca monilifera* and *Uca princeps* conforming to the same pattern as *C. hubbsi/C. regis*, and that "*Uca monilifera* may also be at risk of loss through introgression from their proximally distributed congeners," were spurious. If Lau & Jacobs have evidence that these two fiddler crabs are sister species, and that introgression is taking place, then they should have presented it in their paper. Again, their response claims they have an unpublished phylogenetic analysis of unpublished mitochondrial sequence data for four species of *Uca* that supports a sister relationship between the two they discuss, but the evidence they provide is unconvincing and the *Uca* specialists I consulted with and report on in my rebuttal do not consider them to be closely related. Their purported unpublished evidence is unconvincing since, although they do not list all of the four species they analyzed, one that they do list is an Atlantic species, so they could not have analyzed more than three Gulf species. But, there at least 7 described species of *Uca* in the Gulf of California (and probably several more undescribed species) (Brusca, online, May 2017). This is another idea of theirs that needs testing and exposure to the daylight of peer review. Personally, I doubt that mitochondrial sequences alone will be able to satisfactorily resolve the phylogeny of *Uca*, and suggest to Jacobs and Lau they consider using nuclear DNA.

(5) Their original paper offered no evidence in support of their claim that reduction of Colorado River flow has resulted in "changes in the food chain" that have "imposed significantly different adaptive regimes on taxa in the Delta." Their response adds nothing new in support of that claim.

I can only urge Lau & Jacobs to read my rebuttal more carefully. It is not about impacts of fisheries, as they claim. Nor is it about Gulf productivity, as they also claim. My rebuttal is about sloppy science, and the potential harm it can cause.

Their statement that I confuse the Colorado River Delta and the Upper Gulf of California is incorrect. It is the other way around. Neither their original paper nor their response explicitly defines the boundaries of the delta and the Upper Gulf. However, the Upper Gulf is clearly defined by topography, oceanography, and convention. Even the Government of Mexico, including its National Park Service, recognizes its boundaries (hence, the "Upper Gulf of California and Colorado River Delta Biosphere Reserve"). All one needs to do is look at any map, any atlas, or better yet at the Mexican Government's Geographic Services INEGI map series. The area around and north of Montague Island is where the Gulf becomes deltaic, and the delta extends from there roughly to the US border or, in an historical sense, into the Mexicali Valley (Sykes 1937). Figure 1 in their response is correctly labeled in this regard, although they don't acknowledge this. Cohen et al. (2001) considered the final 19 km of today's Colorado River to be the beginning of the intertidal zone, because near the junction of the Colorado River and Río Hardy riparian vegetation is dominated by non-native saltcedar (*Tamarix ramosissima*), indicating a fresh or brackish-water environment; whereas the final 19 km of the river is dominated by the endemic marine grass *Distichlis palmeri*, indicating true tidal-flat habitat. I agree with Cohen et al. During times of substantial river flow, the delta has historically extended its influence down the east coast of the Baja California Peninsula, south to around the latitude of San Felipe. Lavín & Sánchez's (1999) study of the 1993 flood release clearly defines these boundaries oceanographically. But, the sampling regime and analysis used in the Lou & Jacobs (2017) paper extended from the lowermost region of the delta (the area around Montague Island) south as far as Yavaros (southern Sonora; their Figure 1). However, they did correctly identify their "deltaic sites" and "delta edge" sample sites (their Table 1).

To the best of my knowledge, there are no historic, pre-dam measurements of Colorado River water entering the Upper Gulf, nor even crossing the US-Mexico border, nor of pre-dam salinities in the Upper Gulf (but see below). The best estimate of the effects of pre-dam Colorado River flow on the Upper Gulf is the Lavín & Sánchez (1999) study of the 1993 flood release. This occurred at a time when the river flow across the delta had become highly channelized, preventing the river's waters from reaching any of the previous sinks it formerly diverted to—so virtually all of the water crossing the border into Mexico went straight to the Gulf. And, even given this maximum-flow situation, the effect was minimal; salinity decreased from 35.4 to 32.0 parts per thousand for a few weeks and extended only along the uppermost western shore of the Gulf for about 70 km (from Montague Island to San Felipe). This is the most accurate, data-driven delineation that I am aware of for the effect of the river on the Upper Gulf. Thus, to the best of our knowledge the maximum penetration of the delta into the Gulf region, historically, was likely from the mouth of the river (Montague Island) to San Felipe, only on the northwest side of the Gulf, and probably only during very high flow periods. The idea of the entire Upper Gulf having continuous freshwater flow and being low salinity year-round in pre-dam years is simply not supported by any data I am aware of.

The accusation that I claimed, "there were no historic environmental influences of the river" is also not true. I have never made such a claim; in fact, just the opposite. What I specifically argued in my rebuttal is that the salinity influence (the focus of Lau & Jacobs's paper) of the pre-dam (pre-1935) river on the Upper Gulf was likely far less than some have argued, and that there is little or no evidence that a post-dam salinity increase has substantially impacted the environment of the Upper Gulf.

The suggestion in their response that fishing in the Upper Gulf "will likely lead to the imminent extinction of Totoaba" is the exact opposite of what I, and many others, have argued for years. I did not allude to anything of the sort in my rebuttal and, in fact, Brusca et al. (2017), which is not cited in the References section of their response, summarize current data that indicate just the opposite—that totoaba are not in any threat of extinction (hence recent calls to open a sport fishery for the species). Actually, I don't even mention totoaba in my rebuttal to the Jacobs and Lau paper.

Lau & Jacobs's assessment of pre-dam river flow into the Upper Gulf is inaccurate. Their insinuation that the flow at Lee's Ferry (the dividing line between the Upper and Lower Colorado Basins) is equivalent to what entered the delta is completely unsubstantiated. (Measurements at Lee's Ferry estimate Upper Colorado River Watershed discharge.) And further, water crossing into Mexico (or "entering the delta") is not the same thing as water entering the Sea of Cortez. My point was that they should have looked at actual pre-dam water flow as close to the border as possible if they wanted to estimate historical flow to the Gulf, rather than using reconstructed (from tree-ring data) estimates of flow a thousand kilometers upriver at Lee's Ferry. Jacobs & Lau present three river flow data graphs in their response. As with their original paper, they seem to be unclear where these flow measurements were taken. The first graph (Nowak 2011) is an unpublished thesis reconstructing "annual basin water supply." Presumably this is an estimate for Lee's Ferry, but Jacobs & Lau do not state where the data are from. The second graph is from Cohen et al. (2001), which in turn takes its pre-1935 data from Figure 3 in Morrison et al. (1996), the latter which does not provide a source for their data other than the statement, "Flow of the Colorado River Below all Major Dams." These data are most likely from the Yuma gauge, the last on the river at the time (thus it is not flow into the delta, as Jacobs & Lau claim). The third graph is from Lavín & Sanchez (1999) who used USGS river gauge data from Yuma for their pre-1935 data; this graph is useful and relevant. However, the data go back only to 1904. Jacobs & Lau's argument that the Lavín & Sanchez graph shows "continuous flow" has little to do with how much water reached the Gulf, because that flow measurement was made in Yuma. For example, it shows high flow during 1905-1907 when we know that the entire river flowed into the Salton Sink and created the Salton Sea. Point being, just because water flows at Lee's Ferry or Yuma does not mean it is reaches the Upper Gulf of California.

The argument made by Brusca et al. (2017) and others has been that over the 5-million year history of the river there have been long periods of no flow, or greatly reduced flow to the sea (Bright et al. 2016). Thus, the ecosystem is historically adapted to broadly fluctuating river flows and elevated salinities. This is what is relevant to hypotheses of new species evolving in the Upper Gulf (such as proposed by Lau & Jacobs 2017)—unless Lau & Jacobs are proposing the speciation event took place in the twentieth century!

Below I provide historical river flow data for the Yuma area, which is probably as close as we'll ever get to knowing how much water reached the delta before 1935. We may never know with certainty how much water reached the Gulf, but it was far less than what flowed past Lee's Ferry or Yuma, and even less than what crossed the US/Mexico border.

THE NOT-SO MIGHTY COLORADO RIVER

Numerous workers (including Sykes 1937 and Brusca et al. 2017) have argued that the Colorado River's flow to the Gulf, over the 5-million year history of river, has been highly variable, including long periods of no flow or greatly reduced flow to the sea. Flows in the Lower Colorado River, in particular, are dynamic and unstable, historically varying from zero to 6000 $m^3 s^{-1}$ depending upon rainfall and snowmelt in the watershed (Sykes 1937, Rhodes et al. 1984, Glenn et al 1996). Tellman et al. (1997) said, "It has long been a highly unpredictable river carrying more than 29.6 X 109 m3 (24,000,000 a.f.) of water . . . . in some years and less than 6.2 X 109 m3 (5,000,0000 a.f.) in others." Tellman et al. (1997) described Native American farmers who relied on the Colorado River struggled with the unpredictability of the river and, "in some years there was too much water, and the seeds could not germinate; in other years too little water came to create a good flood field."

To the best of my knowledge, no data are available for Colorado River flows across the border to Mexico prior to construction of Hoover (Boulder) Dam in 1935, and probably not before construction of Morelos Dam in 1950. The graph of estimated Colorado River flow into Mexico "at Morelos Dam," 1914 to 1935, by Tellman et al. (1997, p. 145) shows annual flow across the border to fluctuate from ~2.5 X 109 m3 to 27.1 X 109 m3 (~2,000,000 to ~22,000,000 a.f.), with most years being below 24.7 X 109 m3 (20,000,000 a.f.), with the exception of an early 1930s flood year (~58,000,000 a.f.). However, Tellman et al. do not provide a source for their data and Morelos Dam wasn't built until 1950! In conversation with Barbara Tellman (11 April 2018), she could not recollect the source of those data. Her best guess was that it was either from one of the gauges on the river at Yuma, or further upstream (e.g., Lee's Ferry).

Based on US Bureau of Reclamation data, Glenn et al. (1996, Figure 2) estimated a mean of ~21 X 10^9 m^3/year flow across the border for the 28 years prior to 1935 (ranging from ~9 to ~30 X 10^9 m^3/year). However, the actual source of these data were not provided by Glenn et al. (1996), and is cited only as "Bureau of Reclamation (B. Williams, Pers. Corr.)." It is likely that these data came from a Yuma gauge.

The USGS has had a gauge on the Colorado River at Yuma since 1895, and the Southern Pacific Company installed one on its bridge at Yuma in 1878. Cory (1913; Table 4) published data from these gauges for the period, 1894 to 1911. The mean flow of these 18 years, which included several flood years, was 15.3 X 10^9 m^3/year.

Thomson et al. (1969) also reported on pre-1935, USGS data on river flow at their Yuma gauge. Average annual flow for the years 1902 to 1934 was 18.6 X 10^9 m^3 annually (15,094,000 acre-feet).

Lavín and Sánchez (1999) plotted USGS flow data from 1904 to 1935 at Yuma, Arizona. Their data generally ranged from 7.9 X 10^9 m^3 annually (250 m^3 per second) to 47.3 X 10^9 m^3 annually (1500 m^3 per second), with occasional peaks of 75.7 X 10^9 m^3 annually to 98.6 X 10^9 m^3 annually (and one year of 115 X 10^9 m^3 annually; 1921).

Using any of these flow estimates, or an average of 15 to 20 X 10^9 m^3 annually past the city of Yuma, it is obvious that the Colorado pales in comparison to other large American rivers. For example, the Mississippi River discharges 554 X 10^9 m^3 annually to the Gulf of Mexico, and the Columbia and Fraser Rivers discharge 236 X 109^9 m^3 and 110 X 10^9 m^3 annually to the Pacific, respectively. Even Niagara River discharges 183 X 10^9 m^3 annually to Lake Ontario. (Geraghty et al. 1973; Oxford 2009). The Colorado River flow is practically insignificant in comparison. And this is flow estimate for Yuma; as Brusca et al. (2017) and others have shown, the actual amount of this water annually reaching the sea has varied from nothing to a lot.

Many tree-ring reconstructed studies, including Nowak (2011) and others I cited in my rebuttal, have also shown that severe multi-year, decadal, and multi-decadal periods of widespread drought occurred in the Upper Colorado River Basin over the 20th century.

It is this variability that I, and others, have argued led to adaptation of Upper Gulf marine life to fluctuating salinities. But, as Lavín and Sánchez (1999) showed, even at flood flow volumes, the amount of dilution in the Upper Gulf is very small and circumscribed. For all these reasons, salinity is an unlikely candidate to drive speciation in the Upper Gulf of California. The salient argument in my rebuttal was that even full river flow did not create brackish water conditions, nor even significantly widespread, low-salinity conditions, in the Upper Gulf of California. If Jacobs and Lau really believe that episodic salinity gradients from 35.4 to 32.0 parts per thousand is enough to cause ecological speciation and a subsequent hybridization barrier, my bet is they will have a hard time proving it.

Despite all this, Jacob and Lau's response was correct on two things. First, as for "proscribing what type of science should and should not be considered worthy for publication," I did offer a plea that science should be accurate, measured, and grounded in scientific rigor. As I tried to show, their paper was none of these things. And second, they are correct that my view of the Dietl & Smith (2016) paper differs from theirs. Dietl & Smith (2016) showed that all of the mollusc species living today in the area they studied (at Montague Island) also lived there in the pre-dam era. There were also no significant differences between the two communities in terms of taxonomic similarity (Jaccard-Chao Index) or rank-order abundance of species (Spearman's rank-order Abundance Index). They found one major difference between the pre-dam and modern molluscan communities—*Mulinia modesta* was the most common bivalve during pre-dam times, but is the second-most common bivalve today. This is important evidence of little or no impact on the delta's benthic molluscan faunas pre- and post-dam.

Altogether, Jacob & Lau's response to my rebuttal of their paper amounts to no more than angry rhetoric and defensive hyperbole. No substantive new data were offered in support of their hypothesis of salinity-driven ecological speciation and subsequent introgression due to changes in river flow.

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