Lax Science Can Have Negative Impacts on Conservation: A Rebuttal to Lau and Jacobs (2017)

Richard C. Brusca
University of Arizona
rbrusca@desertmuseum.org

A recent paper by Lau and Jacobs (2017, PeerJ) negatively contributes to a critical conservation problem in the Gulf of California. Since ~2000, a small group of people have argued that decreased Colorado River flow has led to decreased productivity and health of the Upper Gulf, and even "ecosystem collapse" in the region. This group has clung to this idea despite the fact that there is little or no empirical evidence to support it, and despite the consistent flow of research from oceanographers and other researchers showing this not to be the case, and instead, showing that that the Upper Gulf's ecosystem, aside from poor fishing practices, is as healthy as ever (see recent summaries in Mercado-Santana et al. 2017 and Brusca et al. 2017, the latter reviewing the situation in considerable detail). Importantly, this unproven "flow-ecosystem collapse" argument has been the key leverage used for years, by fishermen and CONAPESCA (the government fisheries agency), to argue against the need for stronger fisheries regulations for the Upper Gulf (Villa-Ramírez 1993; Fleischer 1996; Fleischer et al. 1996; Bobadilla et al. 2011; Ramírez-León, et al. 2015). As a direct result of delaying better fisheries management in the region, gill-netting and bottom trawling has driven vaquita porpoise numbers so low that this rare marine mammal is now on the verge of extinction. Papers such as Lau and Jacobs (2017) only add fuel for those who argue that changes in the Upper Gulf's ecosystem due to reduced Colorado River flow, not illegal and unsustainable fishing, is the primary culprit in the demise of the vaquita.

Lau and Jacobs claim to show that: (1) Driven by past salinity gradients in the Upper Gulf of California, ecological speciation has occurred in the fish genus *Colpichthys*, resulting in two sister species in the northern Gulf; (2) Due to recent reduced Colorado River flows, introgression is now occurring between these two sister species; (3) Changes in the salinity gradient of the delta pose a risk for numerous sister species to lose their individual integrity and revert back to a single species; and, (4) These results have "worldwide implications for impacted estuary diversity."

Lau and Jacobs do show that there is an apparent zone of hybridization between the two fish species. However, this is the only fact that their data support. Their other claims are untested or unsupported, and many are clearly refuted by recent published research. Regarding those claims, the following concerns suggest lax reasoning and sloppy science that brings into question the ecological conclusions of the Lau and Jacobs paper.

First, the assumption that the fish species in question (*Colpichthys hubbsi* and *C. regis*) are actually sister species is unsubstantiated; Lau and Jacobs present no data showing this to be the case. Second, while speciation due to salinity gradients may be thought to have occurred in some places worldwide, Lau and Jacobs present no data showing that ancient or historic salinity gradients in the Upper Gulf of California were ever sufficient to drive ecological speciation. And third, they give no data in support of the idea that introgression in these two fish species (or

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any other species in the region) is a threat to the ecological integrity of the Northern Gulf or Colorado River Delta ecosystem. Specific details on these points are provided below. Note that Lau and Jacobs use the term "delta" for what is usually called the Upper Gulf of California, and it is the Upper Gulf to which I refer in the following comments.

Lau and Jacobs present no data in support of the argument that *Colpichthys hubbsi* and *C. regis* are sister species. Although Crabtree (1987) reported them to be sister species over 30 years ago, this was based on an outmoded allozyme data analysis, and of only 8 of the 100+ species in the family Atherinopsidae. This proposed relationship has never been tested, and a modern phylogenetic analysis of the species in this family has yet to be undertaken. *Colpichthys hubbsi* and *C. regis* are very different morphologically; so different, in fact, that Boyd Walker (of UCLA), who studied this group extensively, intended to place the then undescribed *C. hubbsi* in an entirely different genus (L. T. Findley, pers. com.). The species was ultimately described by Crabtree (1989), who placed it in the otherwise monotypic genus *Colpichthys*. Simply because there is some hybridization between them does not make them sister species anymore than hybrids among the various horse species imply sister-species relationships. To legitimately claim these two fishes are sister species, Lau and Jacobs need to first provide a well-supported phylogeny. Many gene sequences for this family are already in GenBank (e.g., Campanella et al. 2015), and this would be the most appropriate and straightforward way to determine the phylogenetic relationships of these two species.

The assumption that the putative origin of the two species was driven by salinity differences is not supported by any data Lau and Jacobs present. Further, if *C. regis* is known to tolerate very high salinities (as the authors note), why wouldn't it be generally euryhaline and also tolerate low salinities (e.g., ephemeral brackish-water periods in the northwest corner of the Upper Gulf)? Thus, another missing piece in this study is a salinity test of the two fish species, which would be one reasonable way to test their hypothesis. Instead of salinity, perhaps *C. regis* avoids the Upper Gulf because of the heavy suspended sediment load that characterizes the region (Thunnell 1998; Hernández-Azcúnaga et al 2014). Or perhaps by seawater temperatures, given that the shallow Upper Gulf gets so much colder than the rest of the Gulf in the winter (Lluch-Cota et al. 2007,;Brusca et al. 2017). A careful study by Lavín & Sanchez (1999) proposed that pre-dam salinities, during <u>high</u> flow periods, only slightly lowered the salinity, and only for short periods of time and in a highly restricted area of the northwest Gulf.

Lau and Jacobs cite eight papers in support of "ecological speciation" by salinity differences in "other silversides." But four of these papers refer to studies done on an entirely different family, Atherinidae, which has been shown by numerous studies not to be a sister group to Atherinopsidae, nor even to be closely related (e.g., Dyer & Chernoff 1996; Bloom et al. 2012; Campanella et al. 2015). Dyer & Chernoff's (1996) detailed morphological phylogenetic analysis (1996) found these two families to be the most distantly related of all families in the large order Atheriniformes (over 350 described species). The Bloom et al. (2012) molecular analysis showed these two families to be in different clades. The Campanella et al. (2015) dated molecular phylogenetic analysis showed the two families being separated by an ancient split, nearly 75 million years ago. And of the remaining four papers that Lau and Jacobs cite, two deal only with east coast inland populations of one atherinopsid genus (*Menidia*), and another is a theoretical paper. It appears that Lau and Jacobs were over-eager to generalize this previous work in a way that supports their own hypothesis.

The genetic introgression Lau and Jacobs document is minimal, and no good evidence is presented in support of the idea that: (a) introgression developed only post-damming of the Colorado River, or (b) that it is leading to dissolution of the species *C. hubbsi*. Their data represent a point in time, but what they have observed might have been going on for hundreds or thousands of years and have no consequence for the modern, post-dam evolutionary ecology of the two fish species in question.

Lau and Jacobs's claim that *Uca monilifera* and *Uca princeps* conform 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" is spurious. The citing of Brusca (1980) in support of this is simply not true; Brusca (1980) followed Crane (1975) and did not even recognize *U. monilifera* as a species. Crane (1975) sunk *U. monilifera* into a subspecies of *Uca princeps*—thus creating *U. princeps princeps* and *U. princeps monilifera*. The former ranges throughout the Gulf to Peru (and on the coast of west Baja), the latter ranges south at least to Guaymas (the type locality). Thus, neither is an Upper Gulf (nor "Delta") endemic. (The type locality of *U. princeps* is Corinto, Nicaragua.) Recent authors have re-elevated Crane's subspecies to species rank (Rosenberg 2001; Shih et al. 2016; WoRMS follows the latter). The only large phylogenetic analysis of the genus was Rosenberg 2001, but he did not include *U. monilifera* in his analysis. Thus, we have no idea if *U. princeps* and *U. monilifera* are sister species, or are even closely related. According to Ernesto Campos (pers. comm., 2018), who has studied this genus for a considerable time, *U. monilifera* appears to be most closely related to *U. major* or *U. maracoani*. And, according to Michael Rosenberg (pers. comm., 2018), *U. princeps* might well be a species cluster of two or more cryptic species.

The claim that, historically, the Upper Gulf received continuous freshwater flow from the Colorado River is incorrect. There is no evidence that fresh water from the pre-dam Colorado River ever continuously reached the Gulf of California (Brusca et al. 2017 addressed this in considerable detail, and see numerous earlier papers cited therein). Virtually <u>all</u> of the evidence suggests that the river's history has been, like most rivers in the Southwest, one of extreme variability. During most of the year, the amount of river water actually crossing the border into Mexico was greatly diminished, and most (or all) of that water was often captured by the various diversions, sinks, swamps, and lakes of the delta (e.g., the Salton Sea, Laguna Salada, Volcano Lake, Pescadero Basin, etc.) and never reached the Upper Gulf as surface water. During drought years this was certainly the case. And, for many periods the river emptied for years entirely into the Salton Basin or Laguna Salada, not into the Gulf at all. Even the flood months (snowmelts in the Upper Colorado River Basin), when the river flow was greatest, appear to have had a very limited effect on the salinity of the Upper Gulf, and only for three months (May to July, peaking in June). The only good estimate of this 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 used to divert 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 for a few weeks and extended only along the uppermost western shore of the Gulf

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for about 70 km (Lavín & Sánchez 1999). The idea of the Upper Gulf having "continuous freshwater flow" and being low salinity year-round in pre-dam years is simply erroneous.

The statement, "Prior to the completion of Hoover Dam in 1935, the water output at the delta was estimated to be 16 to 18 billion cubic meters per year (Stockton & Jacoby 1976)" is incorrect. The Stockton & Jacoby report did not reconstruct river flow to the delta, but for the Upper Colorado Basin, for the years 1512 through 1961, concluding that the mean annual flow over that entire period was 16.7 billion cubic meters annually (13.5 million acre-feet) at Lee's Ferry, near the Utah-Arizona border. Lee's Ferry marks the transition from the Upper Colorado River Basin to the Lower Basin. The river flows more than 1000 km beyond Lee's Ferry, through the hottest landscapes in the Southwest, before reaching the Gulf of California. Furthermore, Stockton & Jacoby is quite out of date; it has been superseded by numerous newer publications (e.g., Michelson et al. 1990; Hidalgo et al. 2000; Woodhouse et al. 2006; Meko et al. 2007), cited below. The latter reconstructs river flow from 762 AD to 2005.

Lau and Jacobs offer no evidence in support of their claim that reduction of river flow has resulted in "changes in the food chain" that have "imposed significantly different adaptive regimes on taxa in the Delta." This appears to be a misleading conclusion inferred simply because it supports their hypothesis. Their blanket acceptance of Rodríguez et al. (2001) and Rowell et al. (2008) is disturbing, given that Brusca et al. (2017) showed those papers to be flawed and Dietl and Smith 2016 further challenged the conclusions of Rodríguez et al. Dietl and Smith (2016) showed that of the mollusc species living in the area they studied in Upper Gulf today also lived there in the pre-dam era. There were 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). The major difference between the pre-dam and modern molluscan communities is that *Mulinia modesta* was the most common bivalve then, but is the second-most common bivalve today.

Scientific rigor is always important, but when a publication can have direct impact on conservation efforts, positive or negative, rigor looms especially large. The Lou and Jacobs paper is, unfortunately, another in a small body of work that has lacked scientific rigor but can been used to delay desperately needed conservation decisions in the Upper Gulf.

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