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Conflict in the Colorado Delta - A response to Brusca (2018)

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Abstract:

In his enthusiasm to highlight the impacts of fisheries in the Gulf of California, Richard Brusca (Brusca 2018) attacks our paper which is about a largely separate issue, makes false claims, does a disservice to his own cause, and undermines science. Brusca sets out to defame our work because, as he states, he fears that third parties will misuse work of this type in fisheries management. This is unfortunate. Brusca's effort to manipulate and suppress scientific work because he fears managers will use it inappropriately is overt and chilling. We respond to Brusca's numerous and varied criticisms in as much detail and in as measured a way as we can muster.

In the form of a "preprint" in PeerJ Richard Brusca (Brusca 2018- online on 24 March 201), takes exception to our paper (Lau and Jacobs 2017) on the hybridization of the Colorado Delta endemic silverside and its Gulf congener.

Brusca's effort to undercut our work, "Lax science can have negative impacts on conservation: A rebuttal to Lau and Jacobs (2017)" is polemical and nothing if not wide ranging, as are his misleading characterizations of the Colorado Delta and the river that once sustained it. He:

- 1) Forces our work onto his primary concern which involves productivity of the Northern Gulf and overfishing. Our work is not about this. It is about the risks to ecologically maintained species in the face of environmental change.
- 2) Falsely conflates Delta and Gulf habitats in service of his argument – that environmental changes have been inconsequential. The Gulf and Delta are actually distinct if connected geomorphic entities that support distinct biodiversity and it is essential for our work as well as effective understanding of process in the region to treat them separately.
- 3) Attacks our taxonomic usage – here we respond with our own data in a fairly direct way and will seek to publish these results expeditiously
- 4) Mischaracterizes our claims about river flow.
- 5) Makes every effort to deny the historic reality of Colorado River flows and their now much-diminished environmental influence in the Delta.

We respond to these points in detail further below.

Brusca also insists that we are part of a scientific cabal advocating for the importance of river flows relative to fishery impacts. If there is such a cabal it is even smaller than Brusca claims as we are not part of it.

More critically, Brusca here attempts to proscribe what types of science should and should not be considered worthy for publication. He argues that anything that distracts from a fixed idea of what is important in the Gulf is not merited due to its potential for misuse by managers. This attitude undermines science as it insists on a singular focus at the expense of any other agenda. Furthermore, Brusca is arguing that if science does not aid one side in a policy debate it is inadmissible and should not be published. This turns the use of science as an honest assessment tool for managers upside down.

We elaborate themes enumerated above under major headers below.

1) Brusca forces our work onto his primary concern which involves productivity of the Northern Gulf and overfishing. Our work is not about this.

Our publication is about ecological species and their potential loss due to habitat change in the Delta and is attached to broader concepts of biodiversity, not productivity. We use the word "productivity" once in the paper in reference to Brusca's previous combative arguments. We referenced this in an effort to point out that we were discussing a separate point and were not

talking about productivity of the Gulf. The intent here was to effectively avoid *this* conflict which Brusca had already engaged in with other parties. Thus, Brusca has made a point of bringing this conflict to us - which we were explicitly trying to avoid.

If it were not for this spurious attack, we might have time to agree with some of his more obvious and well supported points — for example that fisheries are currently a primary direct and critical threat to Northern Gulf species, and that these fisheries are leading to the imminent extinction of the world's smallest cetacean (the Vaquita) and will likely yield a similar outcome for the Totoaba. However critical the impacts from fisheries are, they do not preclude the possibility of additional impacts, nor does the importance of productive oceans preclude important biological connections between the Delta and Gulf. For example, some fishes move between these habitats through their life histories. More to the point, there is no evidence that *Colpichthys*, the genus we studied, is substantially impacted by fishing, but we document interspecific introgression into the Delta endemic species in the genus. This observation implies that a component of Delta endemic biodiversity is potentially at risk from an additional factor distinct from fishing. For investigating these ideas Brusca implies that we are guilty of contributing to the extinction of the Vaquita:

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.

Here Brusca places management discussion and science itself in a zero-sum game. In this view any research in the region on any other topic besides documentation of fisheries risk is a menace due to its potential to distract managers. The further implication is that large areas of scientific research should not be published. And those that do have the temerity to publish stand accused of driving species to extinction. *This sort of commentary seems inappropriate in a scientific journal.*

Our work treats potential risks to species due to changing Delta environments based on the observation that we found hybridization of the Delta-associated *C. hubbsi* and non-Delta *C. regis* species in recent samples, and that hybridization was not evident in earlier museum specimens. This, combined with knowledge that hybridization can eliminate species, is why we found this topic of scientific and applied conservation interest and published it. The taxon we investigated has been minimally studied beyond its description as a species. This is also the case for many species in comparable circumstances around the world where river flows to deltas are being drastically reduced following the pattern in the Colorado River. In our paper we call for more work and attention to this matter. That this is distinct from Brusca's passions should be increasingly evident below.

2) Brusca falsely conflates Delta and Gulf habitats in service of his argument - that there were no historic environmental influences of the river.

Gulf and Delta have dramatically different meanings in the English language and the geographic region under discussion. By equating these Brusca changes agreements into disagreements, makes false claims about our work and underpins his misrepresentation of the Delta.

Brusca states the following:

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.

The Gulf and Delta are actually very different, though connected, geomorphic entities that support distinct biodiversity. Given their disparate natures, processes that effect one system significantly will have more limited effect on the other and vice versa. For example, a delta contains less water than a gulf, thus adding significant amounts of fresh water within the Delta can have significant effect in generating a salinity gradient. When more fresh water is present the salinity gradient moves downstream, in this case, usually towards the Gulf. In the absence of freshwater input much of the Delta becomes hyper-saline and dries out, producing salt flats. Adding the same amount of fresh water to the open waters of the Gulf will have a more limited effect. Thus, equating the Delta and the Gulf is inappropriate. *Much of Brusca’s commentary revolve around this fundamental misdirection.*

Use of the word Delta was intentional in our work, and we made a very explicit point not to use the term Upper Gulf. The “Upper Gulf” is ambiguous geomorphically, as it has been applied to a variety of areas in the literature (see Fig. 1). In some cases, it is associated with the biosphere reserve boundary. This use of the term captures the waters north of a line between San Felipe and Puerto Peñasco. In other cases, different lines are drawn well South of San Felipe and North of Puerto Peñasco. In either case, the definition captures a substantial region of open Gulf waters of varying depth where marine fishery activities are extensive, and where fisheries management efforts are concentrated. This area is Brusca’s focus, but not ours. It also includes estero habitat beyond the Colorado Delta proper where the more widespread *C. regis* occurs. Thus, the distinction we draw between Delta and Gulf is important to our research. Based on all available samples and those from museums, *C. hubbsi* is not a creature of the open Gulf. We collected *C. hubbsi* exclusively from channels within the Delta (Lau & Jacobs 2017- e.g. Esteros-Segundo, Tercero, Chayo and Santa Clara), and have more recent observations 40 km above the river mouth in the Estero of the Colorado. These collections and the available museum records associate *C. hubbsi* with the Delta and its channels (Fig.2). Thus, treating the situation as Brusca does is inappropriate for the question we addressed.

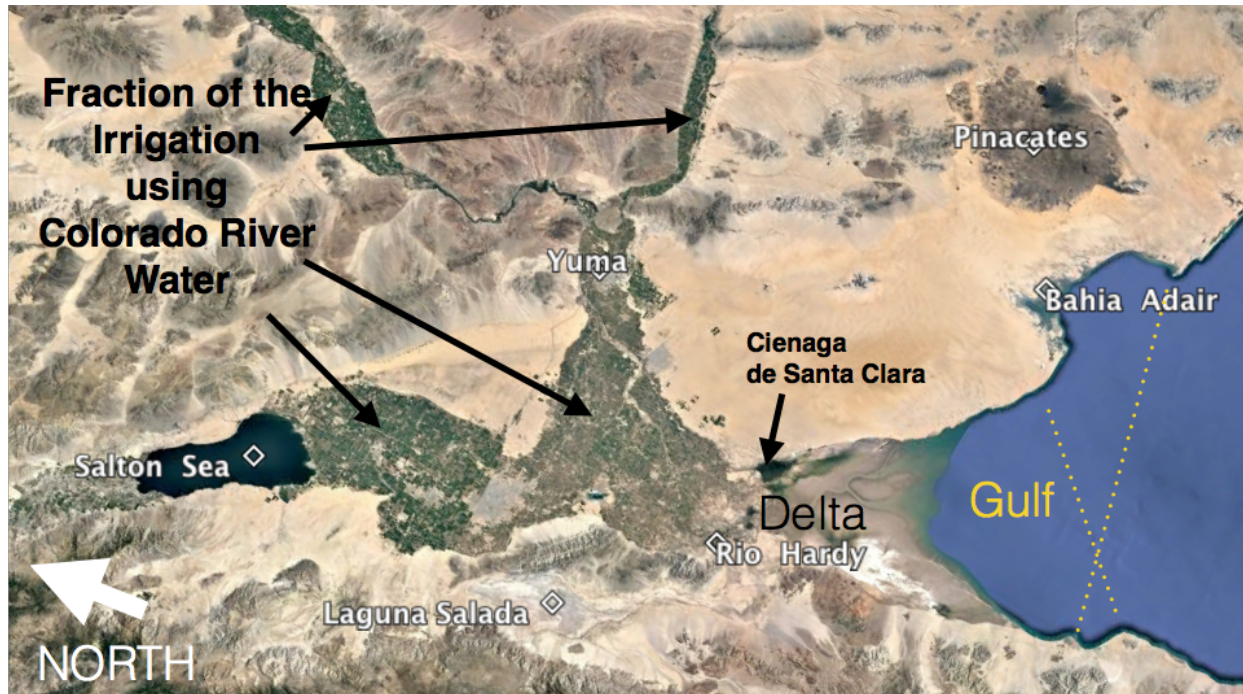


Figure 1. Shows a Google Earth image of the region under discussion with several of the locations mentioned in the text highlighted. Note that in the 19th century there was regular steamboat traffic from the Gulf to Yuma and upstream on the Colorado. The former channel is dry and overgrown today. Note that the small amount of brackish water entering the Delta at the Cienega de Santa Clara has a dramatic effect on vegetation observable even at this scale. Several times the amount of water used in this image would have entered the Delta in the 19th century prior to development of irrigated agriculture and urban use in the region. Yellow dotted lines highlight variable boundaries of the “Upper Gulf” as employed in the literature.

Brusca’s conflation of Upper Gulf and Delta is fundamentally misleading. Within the Delta salinity gradients exist even with the minimal flows permitted today [e.g. Cienega de Santa Clara (Glenn et al. 2013)]. Furthermore, although, we discuss salinity gradients in our paper, we also consider the possibility that other ecological factors are important to the ecological distinction of *C. hubbsi*, including the loss of sediment supply. After all, the Delta itself is a flat-topped silt deposit produced by the flow of the river. Fresh water and fresh sediment reached across the delta top to the delta front during high seasonal flows which no longer exist (Figs. 3-5). This is what built the Delta. In considering the Delta environments, it is important to realize that in addition to riverine processes there is a very high tidal range here approaching 10 meters. This has produced a number of estuary channels leading into the Delta. Furthermore, the Delta top floods tidally over large regions especially during the highest tides of the year, and historically tidal movements were observed well up the Rio Hardy (Sykes 1937). Thus, historically, it was difficult to keep fresh and salt waters from mixing in the Delta; this is now accomplished in part by dikes and barriers that prevent high seasonal and storm tides from penetrating into the agricultural lands that now cover much of the Delta, and of course, by the much reduced movement of freshwater into and through the Delta as discussed further below.



Figure 2. Sample localities for silversides of genus *Colpichthys* in the northern portion of the Gulf and Colorado Delta: *C. regis* red pins. *C. hubbsi* yellow pins. Some of the sites are also mentioned in discussion of fiddler crabs of the genus *Uca*.

Brusca claims that we did not consider sediment or other variables in ecological separation of the species we studied. However, the first three sentences of our introduction (Lau & Jacobs 2017) show that he misrepresents:

Damming and water extraction in river systems are accelerating around the globe (..), impacting estuarine and deltaic settings downstream (..). Physical changes include loss of freshwater, elimination of peak flood flows, loss of sediment supply, and alteration of the nature and position of salinity gradients (..). Such changes necessarily influence the adaptive context under which local species evolve, potentially reducing the selective pressures maintaining species differences and placing ecological species at risk of elimination through introgression. (references removed)

In contrast Brusca states that:

*Instead of salinity, perhaps *C. regis* avoids the Upper Gulf because of the heavy suspended sediment load that characterizes the region.*

There are 3 problems with just this small part of Brusca's presentation. 1) It does not recognize that *C. regis* occurs in the other esteros of the "upper gulf", however defined (Fig. 2). 2) It does not recognize that we were already considering sediment as an environmental variable with the potential to impose selective differences relevant to the distinction between the two species we examined as the previous quote and other text demonstrates. 3) It does not recognize that sediment as well as water is trapped by dams. And thus, if sediment is an important variable it is also affected in terms of quantity, quality, and distribution by the same anthropogenic process. Other authors have published on this vis a vis the "Upper Gulf" [(e.g. Carriquiry et al. 2001) which we cite in our original work]. We immediately recognize this point in our introduction.

3) Taxonomy

In his enthusiasm to attack us from a taxonomic perspective, Brusca makes numerous mutually contradictory claims that are incorrect and/or irrelevant to our argument.

Colpichthys – Brusca does not dispute that we've identified hybridization between *Colpichthys regis* and "*Colpichthys hubbsi*". However, he nevertheless posits that these species belong in different genera and are not sister taxa. Given the hybridization, this is a surprising claim, as intergeneric hybridization is more unusual than that between named congeners. Thus, if Brusca's claim were true it would make our work more remarkable without changing the interpretation. However, the claim conflicts with previous taxonomic usage—which Brusca champions elsewhere in his comments when it is convenient to his argument. In addition, it is in conflict with unpublished phylogenetic analysis of data we and others have generated, and the inference in our publication regarding the likely Pliocene age of the species separation inferred from sequence data reported in the paper itself.

The details- Brusca bases his claim on an unpublished ichthyological remembrance suggesting that prior to the description by Crabtree (1989), other parties intended to apply a different generic name to *Colpichthys hubbsi*. Early in our work we were concerned about the relationship of these fishes and their closest relatives in the region. We generated sequences and performed a mitochondrial sequence-based assessment of this matter, much as Brusca suggested we now do. *Colpichthys regis* and *Colpichthys hubbsi* were analyzed along with their eastern Pacific relatives within Atherinopsinae, including the Gulf Grunion (*Leuresthes sardina*) and Topsmelt (*Atherinops affinis*) sequences we generated. We included GenBank sequences from *Leuresthes tenuis* and *Atherinopsis californiensis* as well as other outgroups. In those analyses both *Leuresthes* and *Colpichthys* are monophyletic. The species pairs within each genus are sisters. The monotypic genera *Atherinops* and *Atherinopsis* are sister taxa. We did not report this because it was not novel to find named genera to be monophyletic. Now that there is more interest in this issue we will revisit, reanalyze and publish these data.

Uca – Brusca makes a broad range of comments regarding our mention of *Uca monilifera* as a Colorado Delta associated species. In our paper we mention *U. monilifera* in passing as aspects of its delta biogeographic pattern suggests potential risks comparable to those associated with the hybridization we demonstrated in *Colpichthys*. Thus, we are forced into a defense of a very

minor component of the published work that is attacked from many mutually contradictory angles.

Brusca's multiple arguments include: a) that *Uca monilifera* is not a species, but a subspecies of *Uca princeps*; b) the contrary opinion that *Uca monilifera* is unrelated to *Uca princeps*, but instead is related to species found in the Atlantic, and c) that the original description of *U. monilifera* is from further south in the Gulf and thus is not associated with the Colorado Delta. Here we respond to each of these varied points - and stand by our argument.

a) We have extensive estuarine collections from the Gulf of California and the outer coast of Baja California (Swift et al. 2011; Ellingson et al. 2014; Dolby et al. 2016; Dolby et al. 2018) as well as unpublished mitochondrial sequence data from *Uca* from these collections that speaks to some of these issues. These data demonstrate that a genetically distinct *U. monilifera* is found exclusively in the Northern Gulf centered on the Delta.

The details - Our collections include 32 sampling localities where we recovered fiddler crabs of genus *Uca* (sensu Shih 2016). These are in all cases either *U. princeps* or *U. monilifera* (we use species rank following Shih 2016 herein). The sample distribution ranges from Nayarit through the Gulf of California to the outer coast of Baja near Punta Eugenia. From the 32 sampling localities we generated 170 CO1 partial sequences; 58 of these contained a set of related haplotypes unique to the Northern part of the Northern Gulf, in contrast, haplotypes from outside the Northern Gulf lacked geographic structure regardless of whether they were from the Southern Gulf or the outer coast of the Baja California Peninsula. The broad lack of genetic structure reflects a tendency toward dispersal and panmixia that is to be expected in Crabs which typically have highly dispersive planktonic larvae (e.g. Felder & Staton 1994; Silva et al. 2010). In contrast the set of related haplotypes restricted to the Northern Gulf is an unusual pattern.

All male crabs outside of the Northern Gulf had an enlarged orange major chela, with proximal tuberculate ornament consistent with descriptions of *U. princeps* (e.g. Crane 1975, pg. 556 Plate 19 A-D). Striking blue *U. monilifera* are abundant in mid intertidal habitat in the esteros within the Delta (Estero (Ramada) Segundo, Estero (Ramada) Tercero, Colorado Main Channel, E. Chayo, E. Santa Clara). Of the 60 sequences generated from the Northern Gulf, 34 were from these localities explicitly within the Delta and all male crabs observed in the Delta were blue with a smoother, broader chela typical of *U. monilifera* as shown in Crane, pg. 555 Plate 18 E-H). Of the remaining 26 individuals sequenced from the Northern Gulf, 19 /19 from Estero Percebu, the nearest collection separated from the Delta on the Baja side, and 5/5 from Bahia Adair showed the Northern Gulf exclusive haplotypes we attribute to *U. monilifera* (4/5 of these are phenotypically consistent with *U. monilifera*). One individual from Bahia Adair shows an interesting intermediate morphology between *U. monilifera* and *U. princeps*, but had a Delta *U. monilifera* mitochondrial haplotype. The remaining two specimens, from locations North and South of Puerto Peñasco, are orange individuals with *U. princeps* morphology; they have haplotypes related to those recovered from crabs sampled outside the Northern Gulf. In sum, there is a clear geographic pattern reflected in the morphology and genetics of *Uca* populations in the Northern Gulf.

These observations are consistent with a genetically and morphologically distinct entity, currently referred to as *U. monilifera*, in the Northern Gulf with a range centered on the Delta where it is abundant. Slight

overlap of species but minimal interbreeding is consistent with the combination of dispersive larvae typical of crabs combined with sexual selection maintaining species separation. Fiddler crabs are well known for mating associated with the large distinctly colored chelae used in courtship. Brusca in (1973) considered this entity to be a distinct species; following Crane (1975) in 1980 he considered it a subspecies; more recently in monographic work Shih et al. (2016) assigned it full species rank. Based on its genetic distinction combined with morphological differences, and ready diagnosability it likely merits species rank, but this is not critical to our argument. The occurrence of the Bahia Adair individual with intermediate morphology could suggest some level of interbreeding in the face of sexual selection. Thus, a future concern about introgression similar to our current findings regarding *Colpichthys* is plausible. We conveyed this concern only briefly in Lau and Jacobs (2017), but will return to it and publish it given the expressed interest in this issue.

b) At one point we had similar concerns to those Brusca reports from his colleagues, that *U. monilifera* might not be an immediate relative of *U. princeps*. This is reasonable, given that Rathbun, when she originally described *U. monilifera*, found it similar to the southern Atlantic species *U. maracoani* - similarities included the smooth chela (Rathbun 1914). However, our unpublished sequence data demonstrate that this is not the case.

The details- Neighbor-joining trees of our mitochondrial data combined with GenBank sequences of 4 of the species in the *Uca* clade (sensu Shih 2016) including *U. maracoani* show that *U. monilifera* and *U. princeps* are closely related to each other and substantially sequence divergent from these other taxa. Brusca also brings up the possibility that the widespread *Uca princeps* could be a complex containing other cryptic taxa. This is possible but more sampling between Nayarit and Peru would be needed to demonstrate this. However, our primary point here is to support our general argument that *U. monilifera* is an easily diagnosed (not cryptic) and genetically distinct entity strongly associated with the Colorado Delta.

c) The location of the *U. monilifera* type locality in Guaymas well south of the current distribution is referred to by Brusca as a contradiction to our argument. We do not find it so. This observation, although the formal type locality, is known to be anomalous relative to all other observations of *U. monilifera*. Given this, likely explanations include: *i*) *U. monilifera* was and is abundant and dominant in the Delta and its appearance elsewhere is a function of larval dispersal from this primary source consistent with its limited distribution in adjacent habitats and increasing rarity at increasing distance. Thus, an instance of long distance dispersal may have led to recovery of *U. monilifera* at the nominal type locality in Guaymas. *ii*) There has been a reduction in range due to loss of peripheral distribution through time, perhaps associated with reduction in the primary larval source in the Delta. *iii*) Lastly, there is some suggestion in the available published literature that the type locality is from a mixed lot and is actually from the Northern Gulf. All of the above are consistent with our interpretation and available knowledge regarding locality data.

The Details - I spoke to Brusca about this taxon over a dozen years ago early in our collection efforts on the Gulf. My recollection is that he found it mysterious that that *U. monilifera* had not subsequently been reported anywhere near the type locality in Guaymas. Thus, Brusca understands that the type locality is not representative of recent observations of the distribution. He reported observing a few individuals in

the inferno channel @ 200 km North of Guaymas as the most southerly subsequent observation, but also communicated that that they were very unusual there. Consistent with Brusca's communications, we did not find *U. monilifera*, but only *U. princeps* individuals in terms of morphology and sequence at Laguna Soldado adjacent to Guaymas, at Kino Bay 140 km to the North of Guaymas, and at Animas on the west side of the Gulf at comparable latitude.

The *U. monilifera* population in the Colorado Delta are widespread as discussed above, with some landscapes having impressive numbers of displaying crabs at @meter intervals over very large areas of intertidal flats (e.g. E. Chayo). Thus, the exceptionally large intertidal habitat of the Colorado Delta supports what appears to be extremely large *U. monilifera* population. As a consequence, Delta sources likely dominate *U. monilifera* larval production. Crab larvae spend a number of weeks in the plankton and disperse very effectively over long distances (e.g. Felder and Staton 1994). Thus, we infer that the populations outside the Delta in the Northern Gulf that we recovered in Percebu and Bahia Adair are largely sourced from the Delta. Rare observation of *U. monilifera* further south in the inferno channel or possibly even the type location in Guaymas are consistent with the patterns observed. Our observations may also prove consistent with the counterclockwise typical summer circulation of the Northern Gulf (e.g. Lavín et al. 2014). The Baja Coast where Percebu is located experiences such seasonal currents from the Delta region and only *U. monilifera* were observed there. Whereas the observations of *U. princeps* at sites on the Sonoran Coast of the Northern Gulf are consistent with more frequent flows from the South and a southern larval source for this species in the region.

Rathbun (1914) described *U. monilifera* from material collected by Captain Stone as from Guaymas with no other comment on locality. Stone's collections were made in the late 1850s during a wide-ranging mapping/real-estate scam exercise that included the entire Sonoran Coast. Elsewhere in the literature Stones' collection locations at Guaymas and "Pinacati" bay are routinely mentioned together (e.g. Carpenter 1873) as though lots from these localities were not held separate. Pinacati Bay presumably refers to an area in the Northern Gulf adjacent to the Pinacate volcanics in the region between Bahia Adair and Puerto Peñasco in the Northern Gulf where we and others (Brusca 1973) collected *U. monilifera*. Thus, the type may have been from the Northern Gulf (see Fig. 1 for general locations, Fig. 2 for collection locations in the Northern Gulf.)

Use of other examples of silverside — Brusca objects to our use of "silversides" beyond *Colpichthys* as examples of ecological speciation in response to salinity gradients. Stating that we cite only 8 papers, finding this inadequate and noting that some of these taxa are more distantly related than others. We respond to this by emphasizing that we intended to demonstrate that salinity gradient driven ecological speciation is a previously recognized phenomenon in estuarine and delta systems worldwide, and that examples are found in the silversides. We make no precise phylogenetic claims so phylogenetic proximity is not an issue. Examples we cited include those within the New-World silversides more closely related to *Colpichthys*, such as the genera *Odontesthes* and *Menidia*, ranging to the more geographically and phylogenetically distant Old-World silversides. These examples demonstrate that this is a geographically widespread and repeated phenomenon. We also note that we are only looking at geographically and environmentally adjacent (parapatric) sister species. There are many more examples of lineages that have evolved between fresh and salt water including within

relatively closely related New-World silversides (Campanella et al. 2015). Thus, we are at a loss as to what Brusca is on about here – it seems to exhibit his general modus operandi to attack us from an any conceivable angle he can conjure up.

4 & 5) Mischaracterizes our claims about river flow, and makes every effort to deny the historic reality of Colorado River

Brusca misrepresents our statements regarding the flow of the Colorado, but more importantly his characterization of the Colorado River and its historic flows is fundamentally biased. He: A) misleads regarding our claim of continuity of flow to the Gulf; B) claims that the Delta was historically fully disconnected from the Gulf in most years; C) argues that Colorado River waters rarely made it to the Delta in significant amount in contrast to many hydrological analyses; D) claims that biological/ecological processes have not changed in the Delta and adjacent Gulf since the diversion of fresh water and elimination of flood flows.

A) Brusca misleads regarding our claim of continuity of flow to the Gulf

Brusca states that we claim that freshwater was "continuously flowing to the gulf". What we said was far more qualified:

In the 19th century, the Delta received continuous freshwater flow and extensive flood water during the spring and summer melting of mountain snows in the headwaters (Lau and Jacobs 2017, p.2, emphasis added).

Thus, our statement is circumscribed in time and expressly admitted of dramatic seasonal and flood variation in flow, and only claims continuity of flow in the melt season. Our use of the 19th century places our baseline prior to most major anthropogenic manipulations of the river. And although we did not claim direct flow to the Gulf, in the 19th century the connection along the historic main channel of the Colorado was continuous and flows were large (as discussed further below). The main river channel supported regular steamboat traffic from the Gulf to Yuma involving many boats between 1850 and the advent of rail transport to Yuma in 1877 (Sykes, 1937). Sykes then navigated and mapped the channel in 1891 and reports continuity of the channel to the Gulf until 1909. This, followed the period of artificial diversion of the Colorado to the Salton Basin during which the historic main channel function was lost. Thus, in the 19th century there was direct conveyance of a significant portion of Colorado River to the Gulf of exactly the kind that Brusca denies.

B) Brusca claims that the Delta was historically fully disconnected from the Gulf in most years

To make this argument, he invokes filling of *i)* Laguna Salada, *ii)* Volcano lake & Pescadero "Basin", and *iii)* Salton Basin:

...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.

As noted above the main channel connected the river to the Gulf in the 19th century avoiding these issues entirely. Thus, prior to 1906-1909 these claims are directly falsified by Sykes (1937). However, discussion of these claims is of use in understanding the range of historical flow behaviors in the Delta. It is also important to note that to varying degrees these same features were part of the complex set of interacting bodies of water that supported the ecology and biology of the Delta.

The Details-

i) Laguna Salada occasionally occupied a structural depression that extends westward from the edge of the Colorado Delta into the Baja California Highlands behind the Cocopa Mountains, which partially protect it from interaction with the Delta. This elongate basin was connected to the Colorado only by overland flow across the Delta floodplain. Historically, it only received flow during specific flood years [e.g. 1894-5, 1905-6, 1910-11 (Webster 1913); 1923, 1929 1932 (Sykes 1937)] when the whole Delta plain was largely inundated. Given its peripheral position on the far western edge of the Delta and the historic absence of a persistent channel to the basin, Laguna Salada was not in a position to capture a large fraction of Colorado flow in the Delta even in flood years when flows were widespread across the landscape. Given the lack of a channel, and contrary to Brusca's claims, it was not in a position to interfere with the connectivity or mixing of marine and fresh waters in non-flood years.

However, starting early in the 20th Century efforts began to maintain a channel to Laguna Salada. These became effective in the 1970s (Jimenez et al. undated) when a channel was built, and sustained to Laguna Salada, from the lower Rio Hardy which currently serves as an agricultural drain on the western side of the Delta. In addition, a 15km dike was extended across the western Delta flat to the south of the channel further isolating the western Delta from the influence of the highest tides. Today these artificial structures do capture some of the remaining agricultural sump water and likely limit connectivity of the minimal flows from agricultural drainage on the western side of the Delta with the Colorado Estuary and the Gulf. The Laguna Salada system often contains marine fishes speaking to intermittent connection to tidewater and movement of fish through the system. However, the primary problem is the overwhelming reduction of freshwater entering the Delta system as a whole which we will return to below.

ii) Volcano lake was historically fed by local geothermal springs and a variety of flows westwards of the 19th Century channel of the Colorado. The Pescadero drainage also passes to the west to the Rio Hardy. This flow orientation became more active in the 20th Century (Sykes 1937). Volcano lake was accessible by boat from the Colorado Estuary during the 19th and early 20th centuries (Sykes 1937). Thus, this shallow system is part of a range of varied connections by which fresh water flowed across the Colorado fan and Delta flood plain and ultimately mixed with waters of the Gulf. These basins were not large or deep (and perhaps not basins at all in the case of the Pescadero) and are now subsumed into parts of the agricultural drainage partly connected to the Rio Hardy today. Historically, prior to levee construction in the Delta, they supported freshwater flow in the Delta and provided the integrated habitats connected in complex and changing ways where fresh and salt waters had an opportunity to mix, as waters moved in channelized and non-channel flows across this landscape to the Rio Hardy, the estuary of the Colorado and the Gulf (Sykes 1937).

iii) In contrast to the Volcano lake and Laguna Salada, whose total volume represents small fractions of the average annual historical flow of the Colorado, the Salton Basin is large. However, there is no

evidence for significant flow to, or filling of, the Salton basin for the last several hundred years prior to 1905. Only minor flows in flood years went to the north prior to this date. This is an additional reason why we were careful to limit our comparisons to the 19th century. This is prior to the artificial diversion of the Colorado to the Salton Basin in 1905, that formed the Salton Sea, and post dates the last filling of Paleo-lake Cahuilla (Waters 1983).

The Salton trough or basin is a northward extension of the tectonic rift valley that also contains the Gulf of California to the south. It is effectively separated from the Gulf by the alluvial fan and delta of the Colorado which has been depositing sediment there since the Pliocene. The Salton basin extends some 280 ft below sea level. As was demonstrated by artificial manipulation and canal failure during the Flood of 1905, the Salton basin is more than sufficient in scale to absorb much of the Colorado River flow for multiple years.

What effects earlier variation in distribution of flow between the Salton basin and Gulf and how this affected changes in environments and the movement of fish across this landscape during episodes of lake filling earlier in the Holocene is unknown. However, lake filling, which was thought to take on the order of 10 to 20 years, was a temporary condition (Waters 1983). Once the lake filled it overflowed across the delta to the Gulf, potentially increasing the habitat available. This is in contrast to the anthropogenic reduction in flow to the Delta which has been maintained for over 80 years and is intended to go on indefinitely.

Whether there could have been earlier episodes of hybridization elicited by lake filling events during Holocene and Pleistocene is currently unknown. It is potentially testable using more comprehensive genomic approaches, which we are implementing. We do know that: 1) there was orders of magnitude more water entering the alluvial fan and Delta of the Colorado prior to the diversion of nearly all Colorado flow to human use, 2) that the limited available museum material lack evidence of hybrid morphology, 3) that current hybridization is active, recognizable morphologically and genetically, and that this has occurred since all flow has been diverted. Lastly very little migration/hybridization is needed to eliminate the genetic distinction between populations or species (e.g. Wang 2004). Thus, that we observe F1 heterozygotes, as well as introgression across the range with modest sampling suggests a significant threat to the species, *Colpichthys hubbsi*. Brusca's claim that this hybridization is insignificant has no obvious basis or merit.

C) Brusca argues that Colorado River waters rarely made it to the Delta in significant amount in contrast to many hydrological analyses.

Brusca takes exception to our use of the historic figure for the flow emanating from the upper basin at Lee's Ferry and then goes on to imply that such waters were greatly diminished in their flow to the South:

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.

However, any implication that evaporation impeded historic flow to the Mexican border and Delta more than modern flows is misplaced. Water still flows to near the border where it is conveyed to agricultural uses in California, and Mexico. Evaporation loss is now much greater

than it was historically due to the large surface area and warmer waters of the impoundments along the Colorado. Thus, a quantity of equivalent to or greater than all the water diverted for other uses by people once flowed to the Delta (Fig 1).

In addition, observations at Lee's Ferry do not include tributaries entering the Colorado below this point such as the Little Colorado, Virgin, and Gila Rivers, which are known to have contributed to flooding in some years in the Delta (Sykes 1937) prior to damming and diversion of, or downstream of these drainages.

Brusca also states that:

..river's history has been, like most rivers in the Southwest, one of extreme variability.

The Colorado is variable in flow. But it is decidedly different in scale and therefore continuity than other rivers in the region. Thus, in those senses it is not like other rivers in the Southwest. Historically, in terms of flow in its lower reaches it was certainly the largest river between the Sacramento and the Rio Grande. In the flood years it was the largest river in terms of flow between the Colombia and the Mississippi. These amounts of water were delivered to the Delta and had ecological impacts across the Delta.

To make the points that water historically entering the Delta was massive, had some degree of continuity despite variation, and was roughly equivalent to the water extracted for human use today we present figures modified from three works that report measured historic flows and or reconstruct flows at or near the Mexican border close to the upstream end of the Delta.

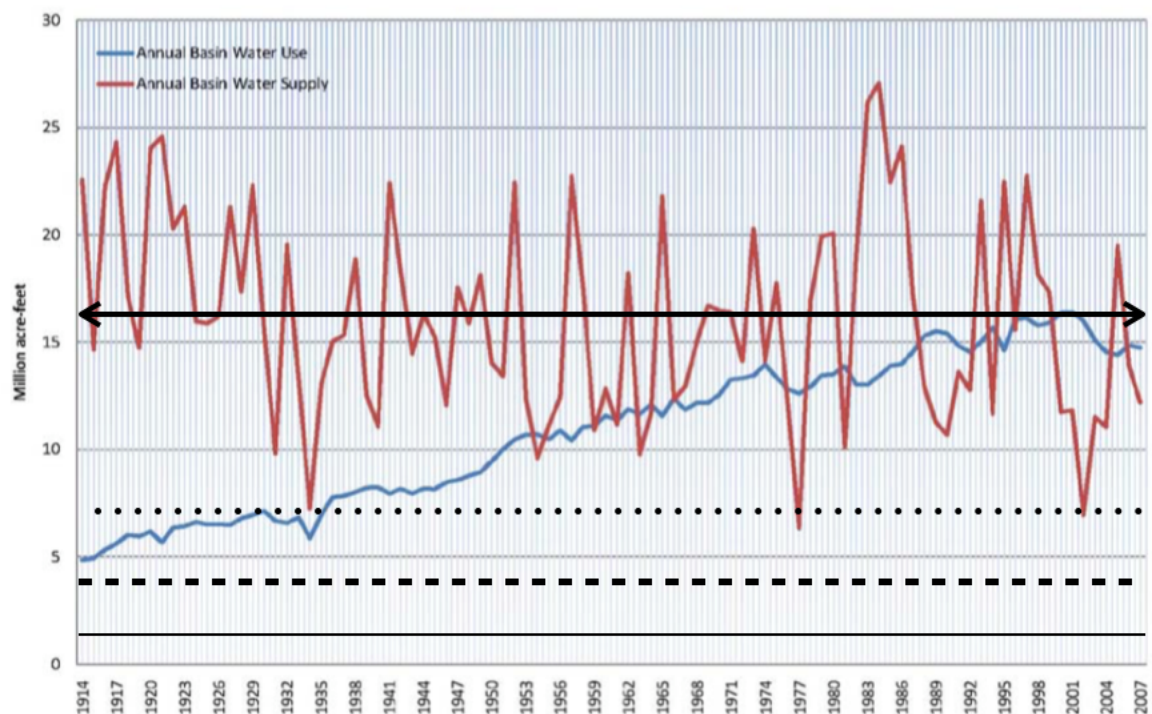


Figure 3. Water that once was available to the Delta and is now diverted and consumed (after Nowak 2011, Figure 54)). This is a reconstruction of annual flow provided by the Colorado River basin in red, and anthropogenic diversion and consumption of that water in blue, from 1914 to 2007, reconstructed at Imperial Dam. The horizontal lines added show various allocations of the river water by compact. The bottom line, at 1.5 million acre-feet, is the amount of water level allocated to Mexico, used primarily in agriculture, a tiny fraction of which returns to the Rio Hardy in brackish form after use. The dashed line is the 4.4 million acre-feet allocated to California, while the dotted line is 7.5 million acre-feet allocated to the lower basin states. The solid line with black arrows is the 16.5 million acre-foot total allocation of water to all users. As Brusca indirectly pointed out, this allocation is in excess of the water produced by the upper basin in many years, leading to a variety of accommodations – especially in low water years. These details are modest relative to the more important point for the Delta – virtually every drop of water (and sediment) that once flowed there is now gone.

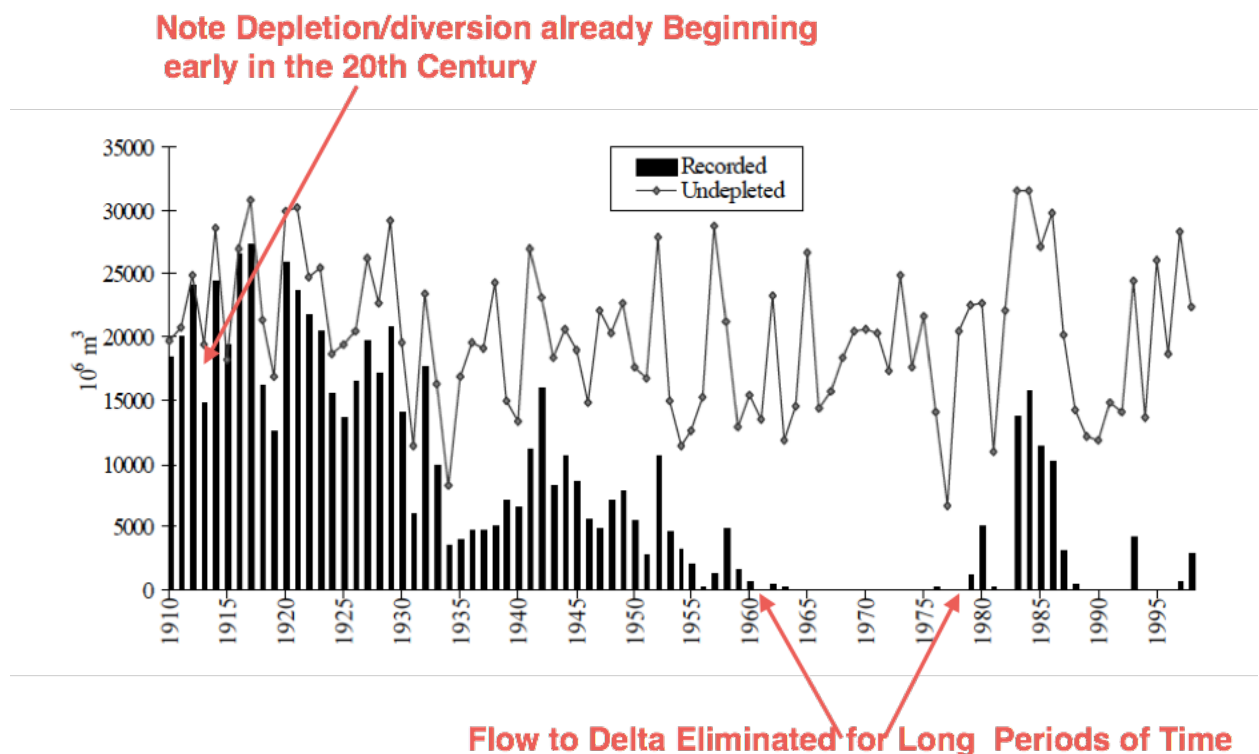
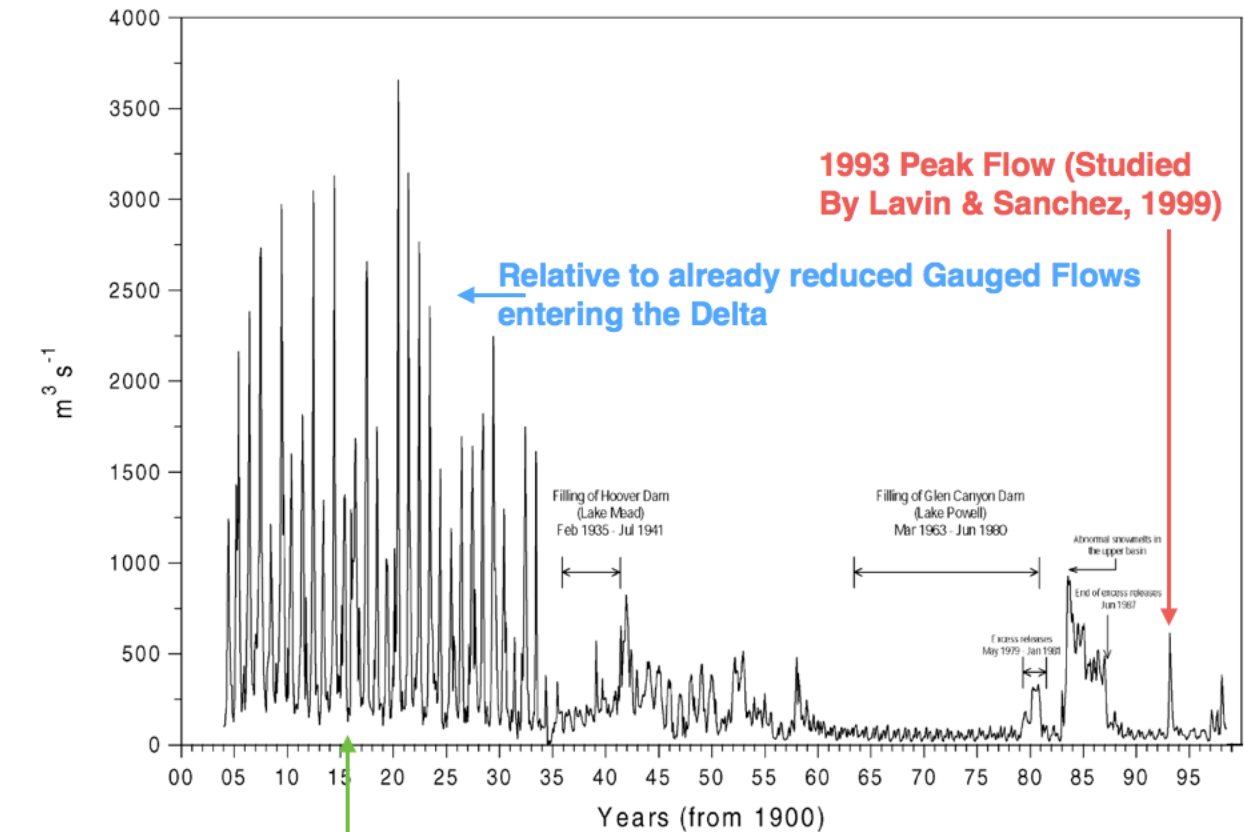


Figure 4. This figure (modified from Cohen et al. 2001) reports the annual flow entering the Delta as measured in millions of cubic meters (there are 1233 cubic meters in an acre-foot, the unit used in the previous graph). The continuous line is a reconstruction of what the flow would have been in the absence of removal by damming and diversion. Note that by the 1910s flows were already

significantly reduced by diversion, and by the 1960s no flow was regularly reaching the delta.



Gauges Demonstrate Continuity of Flow

Figure 5. The above graph, modified from Lavín and Sánchez (1999), authors to whom Brusca gives his approval, provides a continuous graph of gauged flow in the lower Colorado approaching the Delta. This figure accompanies salinity measurements and reconstruction in the northernmost gulf associated with the 1993 flow event marked in red. This isolated flow going across a desiccated and hypersaline environment that it had to wet was sufficient to reduce the salinity along the Delta front away from the river's mouth by 5 parts per thousand. This 1993 peak is comparable to the minimal, not the maximal, flow in many years in the early 20th century, a time when a portion of the flow was already diverted. These data and the analysis of Lavín and Sánchez (1999) provide very strong support for expansive low salinity conditions in the Delta during the 19th and earliest 20th century consistent with wide-spread freshwater/ riparian flora reported by Sykes (1937). It also would suggest substantive and frequent reductions in salinity in the uppermost Gulf along the Delta front Consistent with changed ecology (see below).

D) Brusca claims that biological/ecological processes have not changed in the Delta and adjacent Gulf despite the diversion of fresh water and elimination of flood flows.

Determining ecological conditions in the past is difficult in the absence of Museum collections to record the fauna present. This is the case in the Colorado Delta in the late 19th and early 20th century. One approach to such a question is to compare the living shelled organisms in the study area with the shell remains in historically deposited sediments - a so called live-dead comparison. Towards the end of his reply Brusca makes a number of comments regarding Dietl and Smith (2016). These authors conducted a live-dead comparison at the mouth of the Colorado River Channel where it enters the sea. Brusca claims that these authors demonstrate ecologic stasis. However, the authors report the opposite. In the abstract they state:

The increase in these metrics in the live relative to the chenier (dead) assemblage reflects a shift in the estuary from brackish to full marine conditions after damming and water diversions reduced freshwater flow to the estuary during the twentieth century. [emphasis and (dead) added].

Furthermore, the first sentence of the conclusions of this paper reads:

We conclude that the CRE bivalve community has undergone substantial ecological change in response to damming and water diversions along the Colorado River during the twentieth century.” (CRE= Colorado River Estuary)

Thus, Brusca’s interpretation of this paper is the exact opposite of the conclusions of Dietl and Smith (2016) themselves.

P.S. Lastly, in rereading Brusca 2007 after the above draft was completed we find many of the arguments regarding Delta environments that we present in response to Brusca (2018) were espoused by Brusca in 2007. So in some sense this can be viewed as Brusca vs Brusca. We are much more in tune with the perspective of Brusca of 2007 than the polemical attack of 2018.

In Conclusion

Brusca highlights the impacts of fisheries in the Gulf of California and we are in complete agreement that this is a fundamental problem. However, our paper is about a substantially distinct issue. Despite or perhaps because of this difference in purpose, Brusca felt it necessary to bring everything he could to bear against our work. As we demonstrate above, his approach is aggressive and substantially misleading on many points. In our view Brusca’s approach is sufficiently extreme and biased that it does a disservice to his cause, a cause which we largely share. Brusca fears that third parties will misuse work of this type in fisheries management. Efforts to suppress or manipulate how scientific results are communicated to society undermines the public’s confidence in the integrity of our institution. In our view efforts to constrain topics of scientific discourse as a function of potential use by third parties is fundamentally inappropriate in scientific discourse.

We are also concerned about the use of the term “pre-print” by the journal. Brusca’s work is preliminary to nothing as it is not in review (our response is not in review either). We attempt to be thorough in our response here. But we want to keep this to a one-time response to

criticism and we hope that the journal will not encourage attacks on published work by giving them undue status as may be implied by the term “preprint”.

References:

Brusca R. (2018) Lax science can have negative impacts on conservation: A rebuttal to Lau and Jacobs (2017) PeerJ Preprints 6:e26767v1 <https://doi.org/10.7287/peerj.preprints.26767v1>.

Brusca, R.C., 2007. Invertebrate biodiversity in the northern Gulf of California. In: Felger, R.S., Broyles, W. (Eds.), *Dry Borders. Great Natural Reserves of the Sonoran Desert*. University of Utah Press, Salt Lake City, pp. 418–504 (chapter 29).

Brusca, R. C. (1973). *The Handbook to the Common Intertidal Invertebrates of the Gulf of California*. University of Arizona Press.

Campanella, D., Hughes, L. C., Unmack, P. J., Bloom, D. D., Piller, K. R., & Ortí, G. (2015). Multi-locus fossil-calibrated phylogeny of Atheriniformes (Teleostei, Ovalentaria). *Molecular phylogenetics and evolution*, 86, 8-23.

Carpenter, P. P. (1873). *The Mollusks of Western North America Embracing the Second Report Made to the British Association on this Subject, with Other Papers; Reprinted by Permission, with a General Index Philip P. Carpenter* (Vol. 252). Smithsonian institution.

Carriquiry, J. D., Sánchez, A., & Camacho-Ibar, V. F. (2001). Sedimentation in the northern Gulf of California after cessation of the Colorado River discharge. *Sedimentary Geology*, 144(1-2), 37-62.

Cohen, M. J., Henges-Jeck, C., & Castillo-Moreno, G. (2001). A preliminary water balance for the Colorado River delta, 1992–1998. *Journal of Arid Environments*, 49(1), 35-48.

Crabtree, C. Ben. (1989). A New Silverside of the Genus *Colpichthys* (Atheriniformes: Atherinidae) from the Gulf of California, Mexico. *Copeia*, 1989(3), 558–568.
<http://www.jstor.org/stable/1445481>

Crane, J. (1975). *Fiddler crabs of the world*. Princeton. Princeton, New Jersey.

Dietl, G. P., & Smith, J. A. (2017-online 2016 as cited by Brusca). Live-dead analysis reveals long-term response of the estuarine bivalve community to water diversions along the Colorado River. *Ecological Engineering*, 106, 749-756

Dolby, G. A., Hechinger, R., Ellingson, R. A., Findley, L. T., Lorda, J., & Jacobs, D. K. (2016). Sea-level driven glacial-age refugia and post-glacial mixing on subtropical coasts, a palaeohabitat and genetic study. *Proc. R. Soc. B*, 283(1843), 20161571.

Dolby, G. A., Ellingson, R. A., Findley, L. T., & Jacobs, D. K. (2018). How sea level change mediates genetic divergence in coastal species across regions with varying tectonic and sediment processes. *Molecular Ecology*, 27(4), 994-1011.

Ellingson, R. A., Swift, C. C., Findley, L. T., & Jacobs, D. K. (2014). Convergent evolution of ecomorphological adaptations in geographically isolated Bay gobies (Teleostei: Gobionellidae) of the temperate North Pacific. *Molecular phylogenetics and evolution*, 70, 464-477.

Felder DL, Staton JL (1994) Genetic differentiation in trans-Floridian species complexes of *Sesarma* and *Uca* (Decapoda: Brachyura). *J Crustac Biol* 14(2):191–209

Compean Jimenez, G., Baylon Grecco, O., Robles, H., & Aranda, E. Federal Fishery Delegation in Baja California: Preliminary Study of the Fishery in Laguna Salada, Baja California. <http://www.sci.sdsu.edu/salton/PrelStdFisheryLagunaSalada.html>

Glenn, E. P., Mexicano, L., Garcia-Hernandez, J., Nagler, P. L., Gomez-Sapiens, M. M., Tang, D., Lomeli, M.A., Ramirez-Hernandez, J., and Zamora-Arroyo, F. (2013). Evapotranspiration and water balance of an anthropogenic coastal desert wetland: Responses to fire, inflows and salinities. *Ecological engineering*, 59, 176-184.

Lavín, M. F., Castro, R., Beier, E., Cabrera, C., Godínez, V. M., & Amador-Buenrostro, A. (2014). Surface circulation in the Gulf of California in summer from surface drifters and satellite images (2004–2006). *Journal of Geophysical Research: Oceans*, 119(7), 4278-4290.

Lavín, M. F., & Sánchez, S. (1999). On how the Colorado River affected the hydrography of the Upper Gulf of California. *Continental Shelf Research*, 19(12), 1545-1560.

Lau, C. L., & Jacobs, D. K. (2017). Introgression between ecologically distinct species following increased salinity in the Colorado Delta-Worldwide implications for impacted estuary diversity. *PeerJ*, 5, e4056.

Nowak, K. C. (2011). *Stochastic streamflow simulation at interdecadal time scales and implications to water resources management in the Colorado River Basin* (Doctoral dissertation, University of Colorado at Boulder).

Shih, H. T., Ng, P. K., Davie, P. J., Schubart, C. D., Türkay, M., Naderloo, R., Diana, J. & Liu, M. Y. (2016). Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, *sensu lato* and its subgenera. *Raffles Bulletin of Zoology*, 64.

Silva, I. C., Mesquita, N., & Paula, J. (2010). Lack of population structure in the fiddler crab *Uca annulipes* along an East African latitudinal gradient: genetic and morphometric evidence. *Marine Biology*, 157(5), 1113-1126.

Sykes, G. (1937). *The Delta of the Colorado*. Carnegie Institute of Washington.

Swift, C. C., Findley, L. T., Ellingson, R. A., Flessa, K. W., & Jacobs, D. K. (2011). The delta mudsucker, *Gillichthys detrusus*, a valid species (Teleostei: Gobiidae) endemic to the Colorado River delta, northernmost Gulf of California, México. *Copeia*, 2011(1), 93-102.

Wang, J. (2004). Application of the one-migrant-per-generation rule to conservation and management. *Conservation Biology*, 18(2), 332-343.

Waters, M. R. (1983). Late Holocene lacustrine chronology and archaeology of ancient Lake Cahuilla, California. *Quaternary Research*, 19(3), 373-387.

Webster, E. B. (1913). *Report on the Northern District of Lower California: With Special Reference to the Climate, Water Supply, and Agricultural Production, Present and Prospective, of the La Frontera Subdivision of the Northern District, and the Mineral Resources of the Whole of the Northern District*. Press of Frye & Smith. pp 359