Colorado River Flow and Biological Productivity in the Northern Gulf of California, Mexico

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ABSTRACT. A review of published research indicates that the Northern Gulf of California is, historically and currently, one of the most biologically productive marine regions on Earth. This high productivity is driven by a unique mix of factors, including: coastal upwelling, wind-driven mixing, extreme tidal mixing and turbulence, thermohaline circulation that moves intermediate waters into the mixed layer, coastal-trapped waves, regular sediment resuspension, and, to a lesser extent, agricultural runoff, released nutrients from erosion of ancient Colorado River Delta

sediments, and perhaps input from decomposing tidal-flat plant debris. It has been suggested that decreased Colorado River flow, due to anthropogenic water impoundments and diversions, has had a negative impact on the health of the Northern Gulf of California ecosystem, particularly by reducing primary productivity and/or stock production of finfish and shellfish. However, there is no evidence that surface flow from the Colorado River is now, nor has ever been an important driver of primary productivity in the Northern Gulf, and nutrient/chlorophyll studies show no relationship to Colorado River flow (or, if anything, reduced nutrient/chlorophyll levels occur during high river-flow periods). And, there is very limited and equivocal evidence to support the claim that reduced river flow has significantly impacted secondary productivity in the Northern Gulf. The marine ecosystem of the Northern Gulf remains rich in nutrients, high in biodiversity and productivity, and appears to continue to be healthy, except for the impacts of historical and current fisheries. Human extraction of shrimp, Gulf corvina, totoaba (largely illegally), and other marine resources, remain very high in this region. There also is no evidence that reduced Colorado River flow has negatively impacted the health of the critically endangered vaquita porpoise, and assertions that it has done so deflect attention from the actual cause of decline—bycatch in legal and illegal gillnet fisheries. A review of Colorado River Delta research confirms that, historically and perhaps as long as the river has reached the Gulf of California, there have been long periods of no flow, or greatly reduced flow to the sea. Thus, the ecosystem is historically adapted to broadly fluctuating river flows and elevated salinities. Although commonly used by recent researchers, measurements of Colorado River water crossing the border into Mexico do not provide a reliable proxy for how much water (if any) actually reaches the Upper Gulf because of the complex nature of internal basins and diversions in the region.

Contents

1. INTRODUCTION

The ~60,000 km^2 Northern Gulf of California has long been recognized as a diverse and highly productive ecosystem supporting some of the most important fisheries in Mexico. Despite claims to the contrary, we argue that available evidence does not indicate that the overall level of productivity has diminished significantly due to anthropogenic-driven reduction of freshwater input from the Colorado River.

Ecologists commonly define the Upper Gulf of California as that part of the Northern Gulf north of a line drawn between Puerto Peñasco (Sonora) and San Felipe (Baja California)—corresponding to the Upper Gulf of California and Colorado River Delta Biosphere Reserve (Reserva de la Biósfera del Alto Golfo de California y Delta del Río Colorado) (Brusca et al. 2005, Hendrickx et al. 2005, Brusca 2007, Hendrickx and Brusca 2007, Lluch-Cota et al. 2007; see Figure 1). Oceanographically, it has been suggested that the southern limit of the Upper Gulf can be defined as the region where the vertically well-mixed regime of the water column transitions into stratified conditions; this occurs at ~30-m depth in summer and at ~60-m depth in winter. Or, it may be defined as the latitude of the deeper Wagner Basin (whose overlying waters are stratified year-round). Geographically, these delimitations differ little from one another. In addition to the biosphere reserve designation (which is also part of a UNESCO World Heritage Site that includes about 5% of the area of the Gulf), much of the lower Colorado River Delta is designated a Ramsar Site (Convention on Wetlands of International Importance), an Important Bird Conservation Area (Audubon Society), and a component of the Western Hemispheric Shorebird Reserve Network.

This review is divided into four principal parts. The first part provides an oceanographic overview of the Northern Gulf of California (Midriff Islands northward to the Colorado River Delta), which includes the Upper Gulf region (Figure 1). Hundreds of papers have been published on the oceanography of the Gulf of California, and evidence consistently indicates that primary productivity remains high and has not been significantly affected by changes in Colorado River flow and that it is instead driven primarily by nutrient input and mixing from a variety of other sources.

The next section of this paper critically reviews published work that has made a case for reduction in shrimp, finfish and vaquita (*Phocoena sinus*) population size and production due to diminished Colorado River flow. We find the interpretations and conclusions of that body of work frequently over-extend the actual data and that the underlying assumptions are often questionable. We conclude that there is no, or only equivocal, support for a hypothesis of significantly reduced secondary productivity in the Northern Gulf due to reduced river flow.

The next section provides a brief overview of water flow and distribution across the Colorado River Delta. We agree with many others that much of the Colorado River surface water that historically reached the U.S.-Mexico border was diverted or impounded before ever reaching the Gulf of California, and that many assumptions of surface flow into the Northern Gulf based on measurements below Imperial Dam or at the Southerly International Boundary (SIB) gauging station have probably been far too high. Overall, the marine fauna of the Northern Gulf appears to be highly adapted to a long history of fluctuating (and even absent) Colorado River flows and elevated salinities, at least throughout the Holocene. The final section is a summary of our conclusions and suggestions for future research directions.

2. AN OVERVIEW OF NORTHERN GULF OF CALIFORNIA OCEANOGRAPHY AND PRIMARY PRODUCTIVITY

> "Thus in both inner and outer regions of the Gulf the hydrographical features are conducive to high productivity. These two conditions, upwelling of the outer basin and convection in the inner basin [of the Northern Gulf of California], can fully account for the fertility of the Gulf without the necessity of considering the effect of the Colorado River."
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> J. Y. Gilbert and W. E. Allen (1943), based on the first comprehensive study of productivity in the Upper Gulf of California

The Gulf of California is the only semi-enclosed sea in the Eastern Pacific, and it maintains a high net evaporation rate. Bray (1988) estimated the total annual evaporation for the entire Gulf to be 0.95 m yr^{-1}, Lavín and Organista (1988) estimated the evaporation rate for the Northern Gulf at 0.9 m yr^{-1}, and Lavín et al. (1998) estimated an evaporation rate in the Upper Gulf of 1.1 m yr^{-1}. Annual net evaporation - precipitation - runoff has been estimated at 0.61 m yr^{-1} over the entire Gulf (Beron-Vera and Ripa 2002). Average annual rainfall in the Northern Gulf is only ~68 mm yr^{-1} and is highly variable (Miranda-Reyes et al. 1990). Unlike some other semi-enclosed seas (e.g., Mediterranean Sea, Red Sea) where tidal mixing is not significant, the Gulf gains heat on an annual average, and it has long been recognized as the only evaporative basin in the Pacific Ocean (Roden 1958, 1964, Bray 1988, Lluch et al. 2007, Paden et al. 1991). Because of heat gain and evaporation, salinities in the Gulf have always been higher than in the adjacent Pacific at the same latitude. In coastal wetlands (*esteros*, or negative estuaries) of the shallow Northern Gulf salinities are even higher. Thus the flora and fauna of the Gulf, particularly the Northern Gulf, have long been adapted to life at high salinities.

Surface salinity at the mouth of the Colorado River (around the large tidal mud/sand islands of Montague and Pelícano) averages about 38‰, and increases to the northwest, with a seasonal maximum of ~39‰ in August, and a minimum of ~37‰ in December-March (Álvarez-Borrego and Galindo-Bect 1974, Álvarez-Borrego et al. 1975, Bray and Robles 1991, Lavín et al. 1995, 1998, Lavín and Sánchez 1999, Álvarez-Borrego 2001, Lavín and Marinone 2003). Álvarez-Borrego and Schwartzlose (1979) used March 1973 data to describe a winter convection with high salinity and low temperature water moving close to the bottom from the Upper Gulf southward to near Ángel de la Guarda Island, reaching depths of >200 m and characterized by high dissolved oxygen. Cintra-Buenrostro et al. (2012) used oxygen isotopes in the shells of the clam *Mulinia modesta* (cited as *Mulinia coloradoensis*, a junior synonym) to estimate salinities prior to the construction of dams on the Colorado River and found that it might have ranged from as low as 22-33‰ at the river's mouth (Montague Island) to 30-38‰ 40 km southward down the Baja California coast, suggesting at least a periodic, localized river dilution effect.

Surface waters in the Gulf change in response to seasonal (i.e., monsoonal) and long-term (i.e., El Niño-Southern Oscillation, ENSO) climatic events (Kahru et al. 2004, Lluch-Cota et al. 2007). Predominately northerly winter winds are replaced at the onset of the summer monsoon season (variously called the "Mexican monsoon," "North American monsoon," and "Southwest monsoon") with southerly winds that, in the Northern Gulf, create an along-Gulf flow (Bordoni and Stevens 2006). The winds are modulated by pulses or surges that originate in cyclonic disturbances over the eastern Pacific tropical warm pool off Central America and propagate northward into the Gulf (Bordoni and Stevens 2006). The monsoon climate of the Gulf thus leads to seasonally reversing winds that affect surface circulation and mixing (Thunnell 1998). From July to October, prevailing winds blow from the southeast. During winter/spring (December through May), prevailing winds blow from the northwest along the Gulf's axis, with speeds that can reach 8 to 12 m s^{-1}. These winds produce strong upwelling along the eastern coast of the Gulf, including in the Northern Gulf, and around all of its islands, although occasional shifts to westerlies tend to dampen upwelling along the Sonoran coast (Roden 1964, Álvarez-Borrego and Lara-Lara 1991, Bray and Robles 1991). Winter winds create the strongest upwelling, whereas strong water-column stratification reduces upwelling during the hottest summer months (Santamaría-del-Ángel et al. 1999).

The winter/spring northwesterlies bring cold dry air from the western continental U.S., causing local cooling of the shallow Upper Gulf. During the rest of the year, the shallow regions of the Upper Gulf are warmer than the offshore waters. This sea surface temperature pattern corresponds to the ground-level air temperature pattern. Winter/spring upwelling brings cooler waters to the surface, and this is seen around all of the islands in the Gulf, including in the Northern Gulf where these upwelled waters mix horizontally to lower sea surface temperatures over the region. Year-round strong tidal mixing and turbulence causes an effect similar to constant upwelling around the larger islands in the Gulf (Hidalgo-González et al. 1997, Lluch-Belda et al. 2003). Thus, like many other subtropical coastal regions of the world, the Northern Gulf is highly seasonal, with sea surface temperatures reaching 31°-32° C in August and September, and dropping to 15°-17° C in January and February (Lavín et al. 1998, Ramírez-León et al. 2015). Coastal and shallow onshore temperatures typically exceed these extremes. These more recent temperature observations do not differ from those made in the 1970s (e.g., Thomson and Lehner 1976).

Many of the broad oceanographic features of the Gulf are imposed by the Pacific Ocean (Lavín and Marinone 2003) that the Gulf communicates with through a ~200 km wide and ~2700 m deep entrance. And, much of the general circulation of the Gulf can be modeled as Kelvin-like internal waves of annual period forced by the Pacific (Beier 1997, Ripa 1997). Surface drifter studies have confirmed the presence, for most of the year, of a northward coastal current on the shelf and slope of the mainland side of the Gulf (Lavín et al. 2014). For much of the year the mean speed of this coastal current is ~0.30 m/s. In contrast, on the western side of the Gulf recirculating currents dominate surface circulation due to mesoscale eddies. For three to four weeks, in June-July, the mainland coastal current is enhanced to a mean speed of ~0.60 m/s, with maximum speeds of ~0.80 m/s (Lavín et al. 2014). In the study by Lavín et al. (2014), one drifter moved from the mouth of the Gulf ~1000 km to the delta in this current in just 20 days.

Surface flows in the Midriff Islands Region (Figure 1) are intense, due to large tidal flows through narrow passages and the exchange of water between the northern and southern regions, and consequently this region is distinguished by intense tidal mixing (Argote et al. 1995, Beier 1997, Lluch-Cota and Arias-Aréchiga 2000, Mateos et al. 2006). A deep, cold, branching flow typically moves north in the Midriff Island Region, with one branch flowing toward the Canal de Ballenas-Salsipuedes Channel over the San Lorenzo Sill, and the other flowing over the San Esteban Sill. The latter surrounds Isla Ángel de la Guarda and converges with the other branch in the Canal de Ballenas-Salsipuedes Channel, thus producing a persistent upwelling in the channel (López et al. 2006, 2008, Marinone 2007, 2008). Marinone (2007, 2008) showed that deep inflows at both ends of the channel result in persistent upwelling that creates the coldest sea surface temperatures in the Gulf.

The principal surface circulation of the Northern Gulf consists of a cyclonic (counterclockwise) gyre in the summer (June to September), and a weaker anticyclonic (clockwise) gyre from November to March (Beier 1997, Lavín et al. 1997, Beier and Ripa 1999, Martínez-Diaz-de-León 2001, Palacios Hernández et al. 2002, Carrillo et al. 2002). As a result, Colorado River deltaic sediments are transported to accumulate in deeper waters to the south of the delta, and also to the west where they create a gently sloping coastline north of San Felipe, Baja California. On the Sonoran side of the Northern Gulf, a submarine channel extends to the 200 m-deep Wagner Basin where many deltaic sediments ultimately end up. At a larger scale, the strong winter-spring northwesterlies result in a net transport of surface waters out of the Gulf and into the open Pacific, whereas the generally weaker summer-fall southeasterlies allow Equatorial Pacific surface waters to penetrate into the Gulf all the way to its uppermost reaches (Bray and Robles 1991, Thunnell 1998, Lavín et al. 2014).

The long, narrow shape of the Gulf of California creates a "bathtub effect." The tidal range (amplitude) is very small at the center "nodal point" (near Guaymas), and increases northward and southward from the center, like water sloshing back and forth in an elongate trough. The tidal range is greatest in the narrow, shallow Upper Gulf where water from each tidal flow piles up higher, like in a fjord. The Upper Gulf is thus a highly tidal region, with a maximum tidal range (lowest low to highest high) of approximately 10 m (33 ft) (Matthews 1969, Grijalva-Ortiz 1972, Stock 1976).

The earliest Spanish explorers in the Upper Gulf (e.g., Ulloa, Alarcón, Nuño de Guzmán, Consag, Ugarte) commented on the Gulf's frequent reddish-colored waters which, in the central and southern regions were later shown to be due to large phytoplankton blooms that spoke to its high productivity (Streets 1878, U.S. Hydrographic Office 1887, Sykes 1937). And even though the muddy reddish waters of the Colorado River Delta (the source of the name "Vermillion Sea") visibly mask such blooms, studies have shown that large plankton blooms also occur in the Upper Gulf, and intense outbreaks of dinoflagellates have been recorded there since at least the 1960s (Brinton et al. 1986). Most of the red silt of the Colorado River Delta originated in the Little Colorado and San Juan River tributaries, which are notable for their red silt load that, prior to the construction of Hoover Dam, was carried all the way to the Gulf (Sykes 1937).

Since the first oceanographic research accomplished in the Gulf of California, in the 1920s and 1930s, it has been recognized as one of the most productive marine ecosystems in the world (Gilbert and Allen 1943). In fact, today it is ranked as a Class I "highly productive ecosystem (>300 g C m^{-2} yr^{-1})" based on global SeaWiFS primary productivity estimates, and one of the five marine ecosystems with the highest productivity in the world (Enríquez-Andrade et al. 2005). It is a eutrophic sea with phytoplankton production on the order of >1 g C m^{-2} day^{-1} to >4 g C m^{-2} day^{-1} (Álvarez-Borrego and Lara-Lara 1991, Santamaría-del-Ángel et al. 1994a,b, Gaxiola-Castro et al. 1995, Thunnell 1998).

The high productivity of the Gulf generates 40% to 50% of Mexico's total fisheries production and supports over 50,000 jobs (Cisneros-Mata et al. 1995, 2010, Cinti et al. 2010, Erisman et al. 2011, 2015, Lluch-Belda et al. 2014), the largest producer in the country being the state of Sonora (Lluch-Belda et al. 2014). And the Northern Gulf is the most important region in all of Mexico in terms of fisheries production, where 77% of the inhabitants are involved in fishing activities and thousands of small, artisanal-fishing boats (*pangas*) use gillnets to harvest blue shrimp (*Litopenaeus stylirostris*), Gulf corvina (*Cynoscion othonopterus*), Gulf (or bigeye) croaker (*Micropogonias megalops*), Spanish mackerel (*Scomberomorus concolor*), and smaller volumes of sharks, rays, and shellfish (INEGI 2000, Rodríguez-Quiroz et al. 2010, Erisman et al. 2015). The three finfish species are all spring spawners in the Northern Gulf and fishing targets their spawning season (Erisman et al. 2015). The average, annual, reported fish catch in the Northern Gulf, 2001-2005, was 18,326 metric tons, targeting an estimated 80 primary species (Erisman et al. 2011, Munguía-Vega et al. 2014). However, it is estimated that Mexico's reported fisheries catch is only about half the actual catch, due to unreported numbers (e.g., illegal catch, bycatch, etc.) (Cisneros-Montemayor et al. 2013). As of 2010, the Gulf corvina catch far exceeded all others in weight, but shrimp exceed all others in dollar value (Rodríguez-Quiroz et al. 2010). Virtually all of the Northern Gulf *panga* fishers target Gulf corvina, and 93% of them also target shrimp (Rodríguez-Quiroz et al. 2010).

There have been several attempts to model the ecosystem of the Northern Gulf, mainly using the Ecopath modeling software (Morales-Zárate et al. 2004, Lercari 2006, Lercari et al. 2007, Lercari and Arreguín-Sánchez 2009). These have concluded that reducing fishing pressure would increase fisheries stocks and reduce the risk to endangered species such as totoaba (*Totoaba macdonaldi*) and vaquita porpoise (*Phocoena sinus*). Lercari and Arreguín-Sánchez (2009) built an ecosystem model for the Northern Gulf that suggested a viable fishing strategy to protect totoaba and vaquita required a decrease in the industrial shrimp fleet (35-65%), a decrease in the gillnet fleet (52-57%), and an increase of the artisanal shrimp fishery (63-222%) if appropriate fishing methods were to be employed. Morales- Zárate et al. (2004) compared their Northern Gulf model to five other coastal models in Mexico, suggesting a "higher energy use" in the Northern Gulf ecosystem, and that the region has a "highly dynamic, more complex, and probably a more mature ecosystem" than the others.

Álvarez-Borrego (2001) noted that, "Since the times of early explorers the Gulf of California has been described as an area of high fertility, owing mainly to tidal mixing and upwelling processes." Cummings (1977) reported zooplankton volumes in the Gulf of California exceeded by a factor of two the values reported by Cushing (1969 in Cummings *op. cit.*) for upwelling regions such as Costa Rica or Peru. Although shelf seas are globally a sink for atmospheric CO_2 (Páez-Osuna et al. 2016), productivity is so high in the Gulf of California that Rodriguez-Ibañez et al. (2013) estimated it is likely a net source of carbon, in the form of CO_2, to the atmosphere. Zeitzschel (1969) recorded rates of primary productivity that were two to three times greater in the Northern Gulf than rates in the open Atlantic or open Pacific at similar latitudes. Hernández-Ayón et al. (1993) and Cupul-Magaña (1994), using data since 1989, reported higher nutrient concentrations (NO_2^-, NO_3^-, PO_4^{3-}, SiO_2) in the delta region than reported for most estuarine and non-estuarine marine environments around the world. Prehistorically high primary productivity in the Gulf of California is recorded in biogenic sediments from throughout the Holocene, and productivity rates have remained high for the past 2500 years (Douglas et al. 2007, Staines-Urías et al. 2009).

Increased primary productivity in the Central and Southern Gulf has frequently been shown to be associated with ENSO events, however, this effect is not seen uniformly throughout the Gulf (Santamaría-del-Ángel et al. 1994b, Thunnell 1998, Kahru et al. 2004). It appears that the ENSO signal can be masked in the Central and Northern Gulf by strong tidal mixing and upwelling (Álvarez-Borrego and Lara-Lara 1991, Santamaría-del-Ángel et al. 1994a, Herrera-Cervantes et al. 2010, Páez-Osuna et al. 2016).

Numerous studies in the Gulf have examined primary productivity in the Northern and Upper Gulf, and *all* have shown the region to be highly productive for as far back as published records exist and continuing into the present (e.g., Allen 1923, 1937, 1938; Gilbert and Allen 1943; Zeitzschel 1969; Cummings 1977; Hernández-Ayón et al. (1993); Cupul-Magaña (1994); Millán-Núñez et al 1999; Lluch-Cota and Arias-Aréchiga 2000; Pérez-Arvizu et al. 2013; Rodriguez-Ibañez et al. 2013). Zeitzschel (1969) noted that productivity in the Gulf is comparable to such areas as the Bay of Bengal and the upwelling areas off North Africa and the western coast of the Baja California Peninsula.

The shallow waters of the Northern Gulf are constantly churned by extreme tides, strong winds, and upwellings to create the most productive region in the entire Gulf. In the Northern Gulf, tidal mixing and turbulence occur year round, advecting nutrients into the mixed layer and generating high productivity (Douglas et al. 2007). Surface nutrient concentrations in the Northern Gulf may be as high as 1.0 μM PO_4, 4.0 μM NO_3, and 18 μM H_4SiO_4 (Álvarez-Borrego et al. 1978). Chlorophyll concentration and phytoplankton productivity peak in March and April, and decline to their minima in August and September (Álvarez-Borrego et al. 1978, Hernández-Ayón et al. 1993). The most abundant phytoplankton of the Northern Gulf are diatoms (*Thallassiosira*, *Nitzschia*, *Coscinodiscus*, *Thallassionema*) and dinoflagellates (*Gymnodinium*, *Prorocentrum*) (Millán-Núñez et al. 1999). The main mechanisms and sources of fertilization in the Northern Gulf are: water exchange with the open Pacific (most influx from the Pacific is nutrient-rich deeper waters), upwelling along coastlines and around islands, mixing by tidal currents and turbulence, thermohaline circulation that moves intermediate waters into the mixed layer, coastal-trapped waves, input of anthropogenically derived nitrates and silicates from farming on the Colorado River Delta, and erosion of ancient Colorado River sediments (Cupul-Magaña 1994, Argote et al. 1995, Lavín et al. 1995, Gaxiola-Castro et al. 1999). Decomposition of plant matter from halophytes growing on the vast region of the lower delta (visible in Figure 2 as the brown region below the bright-green agricultural fields of the upper delta) no doubt also contributes to high nutrient levels in the Upper Gulf, although there are no estimates of the magnitude of this contribution.

The Upper Gulf has some of the highest nutrient and chlorophyll-*a* concentrations of any of the world’s seas (e.g., Álvarez-Borrego et al. 1978, Hernández-Ayón et al. 1993), and the Upper Gulf and Midriff Islands region (Islas Ángel de la Guarda and Tiburón, and their associated smaller islands, Figures 1 and 2) consistently show the highest productivity levels of the entire Gulf of California (e.g., Álvarez-Molina et al. 2013, Pérez-Arvizu et al. 2013, Ulate et al. 2016). Cortés-Lara et al. (1999) found chlorophyl maxima in the Midriff Islands region an order of magnitude larger than in surface waters at the mouth of the Gulf. High primary productivity in the Upper Gulf is shown by chlorophyll-*a* concentrations reaching 18.2 mg m^{-3} and averaging 1.8 mg m^{-3} (1997-2007; Pérez-Arvizu et al. 2013). Ulate et al. (2016) showed the Northern Gulf to consistently have higher productivity than the Central or Southern Gulf (annual average 1.7 mg m^{-3}, 1998-2010). As shown by Millán-Núñez et al. (1999) and Morales-Zárate et al. (2004), chlorophyll and primary productivity values in the Upper Gulf indicate that it is an area with high autotrophic productive potential, able to maintain a large food chain where there is no freshwater input. There also appear to be no records of severe hypoxia in the Northern Gulf (Lluch-Cota et al. 2010), which is consistent with the high level of mixing in the region.

In addition to having high nutrient levels and primary productivity, the Gulf is also biologically diverse, harboring about 6000 described animal species, over 2800 of which (including over 130 endemic species) inhabit the Northern Gulf (Brusca et al. 2005, Brusca 2007, 2010, Herrera-Valdivia et al. 2015, Brusca and Hendrickx 2015).

We are not aware of any published work providing evidence that a decrease in Colorado River inflow has reduced primary productivity in the Upper Gulf. One direct way to test this hypothesis is to track productivity and river flow over multiple-year time periods, to see if there is a correlation. At least two studies have done this. Nieto-García (1998) compared nutrient levels in the Upper Gulf during one of the largest known post-dam high-river excess flow periods (spring 1993) and a zero-flow period (spring 1996) and found that NO_3 and PO_4 concentrations were actually lower in the flow year (1993). And, when she compared chlorophyll (from in-situ sampling) between the two periods there were no significant differences (Table 1). A 26-year study (Ramírez-León et al. 2015) of satellite-measured chlorophyll in the Northern Gulf also found no statistical relationship between Colorado River inflow and productivity, and found no increase in productivity during the wettest years. In fact, Ramírez-León et al. (2015) found chlorophyll levels actually dropped in the Northern Gulf during the blockbuster El Niño winters of 1983-1984 and 1997-1998, in comparison to those of 1981-1982 and 1999-2000, respectively, suggesting this drop in primary production could have been due to depressed salinities resulting from higher Colorado River flows during those ENSO years.

Seasonal productivity of the Gulf was documented by Thunnell (1998) using sediment traps in the Guaymas Basin. He found late fall-spring sediment deposits dominated by plankton (biogenic sediments) and summer-early fall sediments dominated by lithogenic material (a mix of eolian transport and river runoff, the former being the main contributor). Measureable river runoff is largely due to the summer monsoon rains, which concentrate on the western flanks of the Sierra Madre Occidental ranges to the east, bringing limited fluvial sedimentation to the Gulf (Douglas et al. 2007). Thunnell (1998) characterized this pattern as a direct response to the seasonally reversing monsoon climate, and Thunnell et al. (1994) noted that the diatom production of the Gulf is one of the highest in the world. In the Central Gulf, diatom skeletons can account for 75% or more of the total flux to the benthos (Thunnell 1998). The summer monsoon rains are the main source of water in northwest Mexico, providing 70% of the annual rainfall and 80% of the surface runoff (Douglas 1995, Anderson et al. 2000, Páez-Osuna et al. 2016). Summer monsoon conditions in the Gulf were probably established at least 6000 years before present (González-Yajimovich et al. 2007).

Currently, with lack of direct Colorado River flow to the Gulf of California (and overall high evaporation rates), the Upper Gulf is the equivalent of an inverse (negative) estuary. Like all inverse estuaries, salinity increases toward the head throughout the year. North of the Midriff Islands the Gulf is shallow (mostly <150 m depth) and well mixed vertically throughout most of the year. As with other inverse estuaries in arid regions of the world, the increasing salinity, and thus density, toward the head leads to pressure gradients, water-mass formation, and sporadic gravity currents in both winter and summer (Lavín et al. 1998). Thus, evaporation and increased salinity throughout the Gulf lead to the formation of dense "Gulf Water" which sinks and flows southward (Bray 1988). Gravity currents tend to occur when the tides and winds are at their weakest. Water is most dense from December to February when the high-salinity water sinks beyond 200-m depth, whereas in summer it reaches depths of only 20-30 m (Carriquiry et al. 2001). The high-salinity water found in winter at the bottom of the Northern Gulf's Wagner Basin comes from the Upper Gulf, including the large Bahía Adair, having reached there by gravity currents. Indirect evidence suggests that the most extensive gravity currents form in October and November, and this is likely when the relatively hypersaline surface waters of the Upper Gulf move into mid-depth layers as the water cools (Bray 1988, Lavín et al. 1998).

Lavín and Sánchez (1999) observed oceanographic conditions in the Upper Gulf during a controlled March-April 1993 river water release to the Colorado River Delta. The delta region and uppermost Gulf switched from a negative (inverse) estuary condition to a positive estuary, with salinity and density decreasing toward the head and dilution detectable up to 70 km seaward from the river's mouth, in the westernmost Upper Gulf. Rodríguez et al. (2001) estimated about the same distance for historical (pre-dam) freshwater penetration based on an oxygen isotope analysis of shells of the clam *Mulinia modesta* (in contrast to Cintra-Buenrostro et al.'s 2012 40-

km estimate). Thus, the dilution effect, when it occurs, extends to about the latitude of San Felipe, a relatively small distance into the Northern Gulf and only about 6% the length of the entire Gulf.

Key studies on Northern Gulf oceanography, since 1974, include: Álvarez-Borrego and Galindo-Bect 1974; Álvarez-Borrego et al. 1975; Álvarez-Borrego and Schwartzlose 1979; Bray 1988; Álvarez-Borrego and Lara-Lara 1991; Lavín et al. 1995, 1997a,b, 1998; Nieto-García (1998), Lavín and Sánchez 1999; Soto-Mardones et al. 1999; Martinez-Diaz-de-León 2001; Álvarez-Borrego 2001, 2002; Álvarez and Jones 2002; Carrillo et al. 2002; Palacios-Hernández et al. 2002; Lluch-Cota et al. 2007; and Ramírez-León et al. 2015.

3. COLORADO RIVER FLOW AND FISHERIES PRODUCTIVITY IN THE NORTHERN GULF

> “The problems related to depletion of fish stocks and endangered species (such as the totoaba and the vaquita) in this area are the result of inadequate fisheries management, not the lack of freshwater or nutrient input.” D. L. Alles, 2011

3.1 Introduction

Prior to construction of Hoover (Boulder) Dam, large runoffs of Colorado River water frequently (but episodically) discharged into the Upper Gulf of California. The largest river flows were associated with snowmelts and rains in the Upper Colorado River Basin and occurred May to August, peaking in June (Sykes 1937, Harding et al. 1995, Pontius 1997, Lavín and Sánchez 1999, Dettman et al. 2004, Pérez-Arvizu et al. 2009). Today, however, due to excessive damming and diversion of the Colorado River (beginning with Hoover Dam) almost none of the river flow reaches the Gulf of California except in extremely wet years (e.g., El Niño years). The filling of Lake Mead (which Hoover Dam impounds) continued into the 1940s. Reduced water flows across the U.S.-Mexico border occurred sporadically after Lake Mead filled until construction of Glen Canyon Dam and the filling of Lake Powell, which lasted from 1963 to 1981, during which time practically no water flowed to the Gulf of California. After that, from 1983 to 1988, and in 1993 and 1997-2000, excess water releases into Mexico, through the Morelos Diversion Dam (located in the Mexican border town of Algodones, Baja California) occurred due to flood-flow conditions and release protocols. However, there are no published data on how much of the "excess water" actually reached the Gulf of California. Unpublished surface salinity data from the Upper Gulf, from E. A. Aragón Noriega for June 2000 (pers. comm., Oct. 2016), showed daily mean salinities of ~38‰ – 40‰, implying no river water was reaching the Upper Gulf, even though this was a year of "excess flow" as recorded at the SIB.

The 1980s and 1990s were two of the wettest decades on record in the U.S. Southwest. Cohen et al. (2001) calculated that from 1992 to 1998 a mean of 18.6×10^9 m^3 yr^{-1} Colorado River surface water crossed the border into Mexico, recognizing 1993, 1997 and 1998 as "flood years." However, even in the wet years of the 1980s and 1990s, with increased border releases, much of the surface water entering Mexico did not reach the Gulf of California, but was diverted by a broad variety of canals, drainages, and sinks in the Mexicali Valley where most of it was used for agriculture or lost to evaporation.

The American Southwest has been warming and drying for decades, and at an accelerating pace (Diffenbaugh and Giorgi 2012, Hayhoe et al. 2004, CLIMAS 2012). Analysis of the recent 60-year continuous U.S. Weather Service data for Tucson (Arizona) shows that average annual precipitation has been on the decline since 1991 and has been below the 60-year average since 1997 (Brusca et al. 2013). Overall, since at least 1960, the most consistent source of water to the lower Colorado River Delta of Mexico has been agricultural and wastewater drainage, which has provided ~40% of the total inflows to the Colorado River-Río Hardy mainstem complex in non-flood years (Cohen et al. 2001, Orozco-Durán et al. 2015). Cohen et al. (2001) noted that, since 1960, agricultural drainage and returns from irrigation canals have provided greater discharge (310×10^6 m^3 yr^{-1}) than median discharge from the mainstem of the Colorado River (180×10^6 m^3 yr^{-1}) (based on International Boundary and Water Commission [IBWC] data).

During non-flood years, most of the Colorado River channel south of the border is dry all the way to its junction with the delta's 24 km-long Río Hardy, at which point it usually regains surface water due to a combination of agricultural and wastewater drainage from the Río Hardy (and upstream inflow of seawater during high spring tides). The Río Hardy joins the mainstem of the Colorado River about 65 km north of the mouth of the river (near the tourist camp of *La Mosqueda*), creating a small, brackish, largely perennial flow to the sea (INEGI Maps, Mexicali and San Felipe quadrangles, 1993). During high amplitude spring tides (the large rise and fall of the tide at or close to the new and full moons), Gulf waters can often penetrate the river's channel almost to this junction. Thus, Glenn and Nagler (2007) considered the juncture of the Hardy and Colorado mainstem to be the beginning of the intertidal zone of the Upper Gulf. In contrast, Cohen et al. (2001) considered the final 19 km of the Colorado River to be the beginning of the intertidal zone. The latter is the more accurate 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. And, since the turn of this century, spring tides have rarely penetrated beyond ~25 miles up the river channel due to a large sand bar in the riverbed (see Section 4).

The Colorado River watershed has been in drought condition since 2000, and very little surface water (beyond the annual base allocation to Mexico) has crossed the international border (U.S. Department of the Interior 2013a,b). Climate models predict that the Southwest will continue to warm and dry over the coming decades, reducing the prospect of Colorado River surface water reaching the Gulf of California for the foreseeable future (Christensen et al. 2004, Hayhoe et al. 2004, CLIMAS 2012, Diffenbaugh and Giorgi 2012, U.S. Department of Interior 2013a). Brito-Castillo et al. (2003) estimated past winter stream flows into the Central and Southern Gulf as far back as 1712, extrapolating that low winter stream flows to the Gulf could be predicted for at least the next two decades.

There has been very little written regarding possible effects of climate change in the Gulf of California, and nothing on the effects of climate change on primary or secondary productivity in the Northern Gulf (Páez-Osuna et al. 2016). Notably climate-sensitive species, such as mangroves and hermatypic corals do not occur in the Northern Gulf. Lluch-Cota et al. (2010) modeled the physical and ecological components of the Gulf at three time scales (ENSO, decadal to interdecadal, and long-term trends). They found no significant sustained long-term trend in recent decades for any of the three time series considered. Instead, variability seemed to be fully dominated by the interaction of ENSO and the Pacific Decadal Oscillation. Morzaria-Luna et al.

(2013) assessed vulnerability of fishing communities in the Northern Gulf, attempting to estimate possible effects of anthropogenic threats and climate change, but their study presented no new ecological data related to these threats. Morzaria-Luna et al. (2014) discussed possible impacts of climate warming on coastal lagoons in the Upper Gulf, but their paper, while interesting, was purely speculative, presented no actual data, and concluded with a list of recommended monitoring suggestions. So little has been written on potential effects of climate change in the Gulf of California that even the GIWA (Global International Waters Assessment) Gulf of California assessment chose not to discuss the subject, stating "Due to the lack of data and references, the concern [about climate change] was omitted" (Arias et al 2004).

Climate-change-driven sea level rise will be one of the most important outcomes of global warming. Ruiz-Fernández et al. (2016) estimated sea level rise in the Southern Gulf (using sediment accretion rates in cores from Estero de Urias Lagoon, near Mazatlán) over the past 100 years. They documented increasing rates of sea level rise, from a minimum of 0.73 ±0.03 mm yr^{-1} at the beginning of the 20th century, to 3.87 ±0.12 mm yr^{-1} during the period 1990-2012. Their estimated trend between 1950 and 1970 was comparable to tide gauge records at Mazatlán. It has been projected that by the end of the 21st century global mean sea level will be 0.26 m to 0.98 m higher than today, with a rate of rise during the last 20 years of 8 to 16 mm yr^{-1} (IPPC 2013). Based on time series from tide gauges and from satellite altimetry, Páez-Osuna et al. (2016) estimated sea level rise in the Northern Gulf, from 1993 to 2015, to be 2.0 ±0.4 mm per year, which results in a projection of 0.17 ±0.03 m rise by the end of the 21st century. This rate of rise is greater than that estimated for the Central and Southern Gulf (it is four times the rate of the Southern Gulf). The faster rise in the Northern Gulf is attributed largely to greater thermal expansion of the shallow, warm seas in the region. Continued sea level rise at the head of the Gulf will lead to marine transgression across the lower delta. Low-lying areas will obviously be taken back by the sea first, including Laguna Salada, the Colorado and Hardy River channels, and topographic lows along the Cerro Prieto Fault Line (e.g., Ciénegas Santa Clara and El Doctor).

Mexico's annual 10% share of the Colorado River is delivered to the Morelos Dam at the U.S.-Mexico border. Although the river's mainstem channel continues 150 km to the sea, the river's entire flow is typically diverted at this dam, which is not a storage facility but a diversion and switching station, feeding a complex maze of irrigation canals on the delta. The quality of water entering Mexico from the U.S. was not a serious issue until the early 1960s. But throughout the 1950s, rapid population and agricultural growth in the Southwest fueled ever-increasing demands for Lower Colorado River Basin water. Excess water became scarce and Arizona began pumping saline agricultural waters (from the Wellton-Mohawk Irrigation District) back into the Colorado River, increasing salinity and introducing agricultural byproducts. In November 1961, Mexico formally protested that the salty water it was receiving was not suitable for agricultural use, and thus the U.S. was in violation of the 1944 U.S.-Mexico Treaty on the Utilization of Waters of the Colorado and Tijuana Rivers and of the Rio Grande (the "water treaty"), which had committed 1.5 million acre-feet (1.85×10^9 m^3) of the Colorado River's annual flow to Mexico. In fact, the salinity had climbed from 800 ppm (800 mg/l) to nearly 1500 ppm (1500 mg/l). It took more than 10 years for a proposed solution to this problem to be formally accepted.

In 1973, an agreement was signed (Minute 242 of the water treaty) specifying that the U.S. would meet standards of average water quality by building a desalination plant near Yuma, Arizona, to process the water from the Wellton-Mohawk diversion. The agreement stated that the mean annual salinity of the water delivered to Mexico at the Northerly International Boundary would not exceed 115 ppm (~115 mg/l) greater than the salinity of the river upstream at Imperial Dam (which, in non-flood years, is around 784 ppm). In the meantime, while the plant was being constructed, the U.S. built the Main Outlet Drain Extension (MODE) canal, a bypass canal to carry the salinized Wellton-Mohawk drainage to Mexico's Ciénega de Santa Clara wetland in the southeastern section of the lower Colorado River Delta. The MODE canal began delivering wastewater to the ciénega in 1977, and the wetland grew from ~200 ha (2 km^2) to ~10,000 ha (100 km^2) (Nelson et al. 2013a). Situated in one of the depressions formed by the Cerro Prieto Fault, the ciénega is now the largest wetland on the delta and has had a relatively stable mean input flow of 4.74 m^3 s^{-1} since the MODE canal began operating (Greenberg and Schlatter 2012, Mexicano et al. 2013, Carrillo-Guerrero et al. 2013, Hinojosa-Huerta et al. 2013a,b, Gómez-Sapiens et al. 2013, Glenn et al. 2013a,b). This bypass, and selective pumping of the Wellton-Mohawk wells and drainage, led to a slight reduction in salinity of Mexico's water allotment to 1245 ppm (still well above the 1973 Minute 242 agreement). The desalination plant was finally completed and has had several test runs, but high operational costs and brine disposal issues have so far kept it from going into full operation. In 2007, Nagler et al. reported the salinity of the Colorado River at the international border to be nearly 1000 ppm (inadvertently reported as 1000 "ppt" in Nagler et al. 2007, Nagler, pers. comm.), also above the Minute 242 agreement. As expected, agriculture drainage returns further increase salinity of the river water south of the border, and Valdés-Casillas et al. (1998) found that at the confluence of the Colorado's mainstem with the Río Hardy it ranged from 1810 ppm to 560 ppm, the latter during a 1997 flood event.

It has been estimated that the Colorado River might have delivered an annual average of 16-18 × 10^9 m^3 (565-636 billion ft^3) of fresh water to the lower delta before dams on the river were built (Harding et al. 1995 estimated that pre-dam annual river discharge ranged between 8 × 10^9 and 30.8 × 10^9 m^3 yr^1). And, an estimated 50 to 500 million metric tons of sediment might have been delivered annually to the delta, although the amounts of 135, 160 and 180 million tons are most commonly cited (van Andel and Shor 1964, Milliman and Meade 1983, Minckley 1991, Morrison et al. 1996, Carriquiry and Sánchez 1999, Alles 2011). Montaño (2003), Montaño and Carbajal (2008), and Hernández-Azcúnaga et al. (2014) estimated that the river contributed more than 50% of the total sediment brought to the Northern Gulf, the remainder resulting from wave erosion of the low cliffs and alluvial shores along the coastline of Sonora beginning about five million years ago, when the Colorado River and Upper Gulf probably first encountered one another. Despite the decrease in Colorado River flow into the Northern Gulf, Baba et al. (1991) found no change in the mass accumulation rate of sediments, noting that these are supplied from other sources and from resuspension of ancient deltaic sediments of the Colorado River Delta.

Today, the Colorado River Delta is no longer receiving riverine sediments and instead is being slowly eroded by tides and currents. The main source of suspended sediments in the Northern Gulf today is thus from erosion or resuspension of ancient delta deposits (Carriquiry 1993, Carriquiry and Sánchez 1999, Carriquiry et al. 2001, 2011, Álvarez and Jones 2002, Alles 2011). Most of the seafloor of the Northern Gulf is carpeted with nonconsolidated deposits that originated from the delta, with the finer sediments occurring mainly on its western side and the coarser sediments on its eastern (Sonoran) side (Carriquiry and Sánchez 1999, Carriquiry et al. 2001, Hernández-Azcúnaga et al. 2014). During spring tides, when tidal currents are strong, the resulting turbulence in the water column resuspends and scatters these sediments to such an extent that they become visible to satellite imagery, especially in the uppermost Gulf and Bahías Adair and San Jorge on the northwest coast of Sonora (Lepley et al. 1975, Carabajal et al. 1997, Souza et al. 2004, Hernández-Azcúnaga et al. 2014).

Beginning with the Colorado River Compact of 1922, and followed by the water treaty of 1944 and its pursuant acts, amendments, and agreements, seven western U.S. states and Mexico have been allocated the delivery of a total annual water volume that exceeds typical flows in the Colorado River. A total of 9.3×10^9 m^3 (7.5×10^6 acre-feet, 3.2×10^{11} ft^3) is allotted to the Upper Basin states (Colorado, Wyoming, Utah, New Mexico) and the same amount to the Lower Basin states (California, Arizona, Nevada). The 1944 water treaty guarantees Mexico 1.85×10^9 m^3 (6.53×10^{10} ft^3) of water per year. In both Arizona and California, about 60% of the allotment of Colorado River water is diverted for agriculture. Current U.S. agricultural water prices for Colorado River water range from \$16 to \$32 per acre-foot, whereas municipal prices range from \$300 to more than \$880 per acre-foot. A brief reflection on these statistics illuminates the myriad conflicts that revolve around water usage and conservation in the American Southwest today.

It is clear that the quantity and quality of Colorado River water reaching the Northern Gulf of California has diminished, and it is perhaps not surprising that several researchers have questioned the effects of this on the ecosystem health and productivity of the Gulf (see below). It is well established that return of some measure of Colorado River surface flow to south of the border is desperately needed for the delta's riparian wetlands (e.g., Glenn et al. 1992, 1995, 2001, 2008, 2013a,b, Luecke et al. 1999, Stromberg and Chew 2002, Glenn and Nagler 2007, Zamora and Flessa 2009, Zamora et al. 2013). The main source of water currently supporting those wetlands is the underlying aquifer, which today derives mainly from underflows from irrigated fields in the U.S. and Mexico. However, surface flows are required to reduce soil salt levels and germinate new cohorts of native trees (Hinojosa-Huerta et al. 2013b).

The loss of riparian wetlands across the upper delta is well documented; it is an urgent crisis that needs to be addressed by cooperative measures between Mexico and the U.S. The 2000 Minute 306, 2010 Minutes 316 and 317, and 2012 Minutes 318 and 319 amendments to the U.S.-Mexico Water Treaty, which culminated in a one-time release of a pulse flow (105,392 acre-feet; 130×10^6 m^3) into the delta between March 23 and May 18, 2014, were important steps in that direction (Pitt et al. 2000, Wheeler et al. 2007, Glenn et al. 2013a,b, Flessa et al. 2013, IBWC 2014, Witze 2014, Hodson 2014). However, it should be noted that those protocols are not meant to deliver surface water to the Gulf of California, but only along the riparian corridor of the upper delta (about 98% of the 2014 pulse-water release was absorbed into the water table over the first 60 km from its release at Morelos Dam; IBWC 2014, Zeilinski 2014, NASA 2015). The delta's riparian corridor should not be confused with the marine-dominated lower tidal delta (the intertidal zone) and the Upper Gulf of California, which is the subject of this review. Daesslé et al. (2016) assessed the sources and sinks of nutrients and carbon along the course of the Colorado River on the delta during the 2014 water pulse. They were unable to find evidence for nutrient input into the Upper Gulf from the river flow. In fact, dissolved inorganic nitrogen/nitrates were depleted quickly in the riverbed below Morelos Dam, suggesting a denitrification process and/or significant uptake of nitrogen by riparian and wetland vegetation as the water moved downstream.

Several researchers have suggested that reductions of freshwater surface flow from the Colorado River have negatively impacted biological productivity in the Upper Gulf—including production of wild shrimp (blue shrimp, *Litopenaeus stylirostris*, 65% to 90% of the total shrimp catch in the Northern Gulf, and brown shrimp, *Farfantepenaeus californiensis*), the endemic sciaenid fishes, totoaba (*Totoaba macdonaldi*) and Gulf corvina (*Cynoscion othonopterus*), and the critically endangered endemic vaquita porpoise (*Phocoena sinus*). The published, empirical studies arguing for this hypothesis are reviewed below. Most of the published ecological work in this regard has relied on measurements of Colorado River surface flow at Morelos Dam (at the Southerly International Border, SIB) as a proxy for how much freshwater surface flow was thought to actually enter the Upper Gulf—almost certainly an erroneous assumption (see Cohen et al. 2001, All, 2006 and 2007, All and Yool 2008, and Section 4 below).

The principal published studies arguing that decreased finfish and shellfish productivity in the Upper Gulf might be due to decreased Colorado River flow are: Galindo-Bect et al. (2000), Aragón-Noriega and Calderón-Aguilera (2000), Aragón-Noriega and García-Juárez (2002), and Pérez-Arvizu et al. (2009) for penaeid shrimp; Lercari and Chávez (2007) and Rowell et al. (2008a,b) for totoaba; Rowell et al. (2005) for Gulf corvina; and Kowalewski et al. (2000) and Cintra-Buenrostro et al. (2012) for the clam *Mulinia modesta* (also see http://www.geo.arizona.edu/ceam/Hecold/hecolcd.htm). These studies are reviewed below.

3.2 Penaeid Shrimp

Penaeid shrimp are fished in the Gulf of California by two methods, industrial bottom trawlers (that have a very large bycatch, e.g., Pérez-Mellado and Findley 1985) and artisanal boats (*pangas*) that use small gillnets and have a small bycatch. In the Northern Gulf, over the past three decades, the number of shrimp trawlers has decreased while the number of artisanal boats has steadily increased (Rodríguez-Quiroz et al. 2009). In the Northern Gulf today, industrial trawlers work out of San Felipe and Puerto Peñasco; artisanal shrimp fishers work out of those ports as well as El Golfo de Santa Clara.

Four studies have suggested a correlation between Colorado River flow across the U.S.-Mexico border and shrimp production in the Upper Gulf. Galindo-Bect et al. (2000) examined the industrial shrimp catch from trawlers operating out of San Felipe. Aragón-Noriega and Calderón-Aguilera (2000) and Aragón-Noriega and García-Juárez (2002) sampled blue shrimp postlarvae in the San Felipe area from 1993 to 1997 (the latter study also analyzed commercial catch data from San Felipe and El Golfo de Santa Clara during 1995-1998). Pérez-Arvizu et al. (2009) examined the artisanal shrimp catch out of El Golfo de Santa Clara. All four studies used measurements of Colorado River surface flow taken at the Southerly International Boundary (SIB) gauging station on the U.S.-Mexico border as a proxy for presumed flow reaching the Gulf. (Cohen, 2005, noted that the SIB flow gauge is highly inaccurate and has >15% error rate.) None of these studies measured actual river flow into the Gulf, nor did they report salinities in their study areas during the research time periods—critical variables needed to support the validity of their correlation analyses. Thus, there is no way of knowing how much Colorado River water, if any, was actually reaching the Gulf in the years included in these analyses, or if the sampled shrimp populations were actually exposed to fresh or brackish water. However, owing to the field research of Lavín and Sánchez (1999) we do know that in 1993 a large excess river water release reached the Upper Gulf (but it did not enhance primary productivity; see discussion of Nieto-García [1998] below). We also know that some surface freshwater reached the Upper Gulf in 1984 and 1997, but we do not know how much (Nelson et al. 2013a,b; Figure 3a).

The study by Galindo-Bect et al. (2000) used industrial shrimp trawler catch (landing) data from San Felipe and the number of licensed trawlers working out of that port from 1982 to 1996. They calculated catch-per-unit-effort (CPUE) by dividing reported overall shrimp catch by the number of San Felipe trawlers licensed each year. They did not account for small boat, artisanal shrimp catch and its steady growth over their study period. They did not provide data on actual fishing (trawling) times, boat efforts, size frequency of the vessels, or locations of actual fishing activities. They did not account for the fact that fishers (both industrial and artisanal) from Puerto Peñasco and El Golfo de Santa Clara were also fishing for shrimp in the same areas (Upper Gulf Biosphere Reserve), and that these efforts changed from year to year. They did not consider probable multiple shrimp spawning events during the fishing season. All of these factors contribute in complex but unknown ways to the annual variation in shrimp catch reported for San Felipe.

Their overall annual shrimp catch data showed a statistical correlation to river flow at the SIB station, both for the same year and for flow during the previous year. However, CPUE showed no significant correlation to river flow, or to number of trawlers, nor to total catch. Galindo-Bect et al. (2000) concluded that the higher overall catches recorded in “flood years” during their study period might be due to brackish water improving the survival of early life stages of shrimp and that decreases in river discharges might have adversely affected shrimp production. While their correlation of border-water flows to overall catch by the San Felipe shrimp boat fleet is intriguing, there are several reasons to question their conclusions.

First, commercial shrimp trawlers in the Northern Gulf are highly variable in their fishing efforts. Some fish only one or two nights at a time, others will stay at sea for weeks. Some trawler owners (*patrones*) keep their boats at sea as much as possible during the season; others allow their boats to remain in port for long periods of time. Boat and gear repairs, ability to fuel and provision the boat, and health of the crew also create highly variable fishing efforts among the boats. And because a shrimp boat is licensed in San Felipe does not mean it is always fishing in that region, perhaps not even in the Upper Gulf; it only means that the boat must return to San Felipe to offload and sell its catch. By using only the number of boats licensed to operate out of San Felipe, it is likely that Galindo-Bect et al. (2000) did not capture the true CPUE of the fishing fleet. And, the lack of correlations between CPUE and river flow, and CPUE to trawler number or total catch, argue that their method of estimating CPUE could easily have been inaccurate. Increased overall annual shrimp catch could have simply been the result of increased fishing effort and not increased freshwater inflow to the Upper Gulf. In fact, Rodríguez-Quiroz et al. (2010) showed that increased shrimp catch in the Upper Gulf from 1995-1997 was directly correlated to increased fishing effort, and most fishers believe that increased flow in the river argues favorably for potential catch and may therefore expend more effort fishing during wet years. Both overall catch and catch-per-unit-effort for shrimp in the Northern Gulf have fluctuated widely historically, and consistently since the year 2000, even with virtually no river water reaching the Northern Gulf (Rodríguez-Quiroz et al. 2009).

Accurate catch data for shrimp are notoriously difficult to acquire, and “production data” based on shrimp landings often do not represent actual “catch data” because shrimpers commonly do not offload or sell the smaller-sized shrimp (called *pacotilla*) to the processing plants, or the plants do not accurately classify them. Accurate estimates of catch (by weight or size) should be made on-board the trawlers themselves, where the modal length of shrimp caught may be 15-20 mm shorter than what is found in the processing plants (López-Martínez et al. 2003). Throughout the Gulf of California, interannual variations in shrimp catches are known to vary broadly. For example, from 1950 to 1995, commercial trawler annual catch by the Guaymas fleet varied from a low of ~3000 metric tons to a high of ~7600 metric tons (López-Martínez et al. 2003), roughly tracking fishing effort. In addition, the prolonged ENSO event of 1991 to 1994 (during the period of the Galindo-Bect et al. 2000 study) led to winter sea surface temperatures in the Gulf that were 2°–3° C warmer than the previous two years due to increased northward transport of tropical surface waters and a concomitant decrease in the strength of the California Current (Bernal 1981, Thunnell 1998), and the effect of these warmer waters on shrimp production is unknown.

Another reason to question the Galindo-Bect et al. (2000) conclusion is their use of Colorado River water crossing the border as a proxy for water reaching the Upper Gulf. All (2006, 2007) pointed out that water measurements at the SIB gauging station, near the U.S.-Mexico border, do not reflect water actually reaching the Upper Gulf, and there probably have been no substantial Colorado River surface flows into the Upper Gulf since the 1960s (except for a few of the unusually wet years during the periods of 1980-1988, 1993, and 1997-1999). Cohen and Henges-Jeck (2001) and Cohen et al. (2001) came to the same conclusion in a very carefully calculated mass-balance assessment of surface water on the delta for the years 1992-1998. In fact, it is likely that there has been little substantial flow into the Gulf, except in the largest flood years, since the mid-1930s, beginning with the construction of Hoover and, subsequently, Glenn Canyon Dams. Subsequent to the filling of Lake Powell (behind Glenn Canyon Dam) during the early 1980s, limited and infrequent water flows reached the delta, and some riparian vegetation re-established (Stromberg 2001, Zamora et al. 2001). Although excess flow releases across the border were recorded in 1980-1981, 1983, 1988, and 1993, little river water could have reached the sea from 1980 to mid-1984 due to the presence of a large sand bar blocking the lower river channel, which created up-channel floods on the delta (Nelson 2007, 2013a; Figure 3a). And most of the Colorado River Basin has been in a drought condition since at least 2000, and no Colorado River surface water has reached the Upper Gulf since then (IBWC 2014).

All (2006) stated, "…large influxes of freshwater from the Colorado River rarely reach the Gulf. Thus, other factors, such as overfishing in the shrimp habitat are responsible for the boom and bust cycles in the region's fishing industry." All (2006) argued that the water Galindo-Bect et al. (2000) had assumed flowed to the sea was actually impounded upstream by various diversions in Mexico, including the huge evaporative basin of Laguna Salada (which is at least 11 m below sea level at its lowest point), and most of it never reached the Gulf (see comments on Laguna Salada in Section 4 below). The view that Laguna Salada, and other low basins, have historically captured much or most of the water from the Colorado River Delta during flood years is corroborated by Sykes (1937), Luecke et al. (1999), Cohen and Henges-Jeck (2001), and Cohen et al. (2001), and is revealed in satellite imagery (e.g., Figure 3a). This may help explain why Galindo-Bect et al. (2000) found no correlation between river flow and catch-per-unit-effort during their study period. However, in at least one of the years of the Galindo-Bect (2000) study, 1993, substantial Colorado River flow did reach the Gulf (Lavín and Sánchez 1999, Nelson et al. 2013a,b).

Other than the detailed historic research by Godfrey Sykes from 1890 to 1935 (Sykes 1937; see below), no long-term or sustained records of Colorado River flow south of the border are available, so we have no way to reconstruct the actual history of that flow into the Gulf, other than indirectly, as All (2006) did. A flow gauging station once existed on the river channel south of the border, at El Marítimo, but it was destroyed by the 1983-84 El Niño floods, and Cohen et al. (2001) judged data from that station to be inaccurate anyway for multiple reasons anyway.

Glenn et al. (2007) published a rebuttal to the All (2006) paper, and All (2007) responded to it. All’s response was thorough, but perhaps the most important point he addressed was the claim in the Glenn et al. (2007) rebuttal that Laguna Salada was simply too small to account for the capture of the volume of water crossing the border, and, therefore, the excess must have reached the Upper Gulf. But Glenn et al. (2007), based on an unpublished, undated, online report by Compeán-Jiménez et al. (ca. 1981), used a surface area of only ~400 km^2 (40,700 ha) for Laguna Salada, which is far too small. Further, the Glenn et al. (2007) rebuttal to All’s (2006) paper calculated the “evaporative capacity” of Laguna Salada based on a surface size of just 220 km^2, suggesting that (in 1993) the lake would have lost 0.3×10^9 m^3 of water to evaporation (7% of the 1993 flow). However, based on a review of multiple sources of information, All’s estimate for Laguna Salada’s area of 1000 km^2 appears fundamentally accurate (see Section 4, below). Further complicating the story is Nelson’s (2003a) estimate that flow into Laguna Salada might have ceased around 1986, which would suggest that the first 4 or 5 years of the Galindo-Bect (2000) study was during a period when the river could flow into Laguna Salada, while an unknown number of the remaining 10 years might have been a period when the river flow did not divert into the laguna. However, Cohen et al. (2001) found standing water in Laguna Salada in the years 1993, 1997 and 1998 (using LANDSAT satellite imagery). And, Valdés-Casillas et al. (1998) reported Laguna Salada holding water in 1997.

In the second study examining the relationship of Colorado River flow to shrimp productivity, Aragón-Noriega and Calderón-Aguilera (2000) took shallow-water samples of blue shrimp postlarvae in the San Felipe area for 5 years, 1993-1997. Two of those years had excess Colorado River flow past the SIB (1993, 1997); the other three did not. They reported a weak, but positive correlation between SIB release flow and postlarval abundance, which was highest in the two flood years, 1993 and 1997. They suggested that this observation could indicate a preference by postlarvae for lower salinity water or, because shrimp use this same area as a nursery every year even when there is no freshwater flow, a preference for the "taste" of the river water (e.g., Mair et al. 1982). However, they did not report salinity values in their survey area for any of the years of their study.

Aragón-Noriega and García-Juárez (2002) reanalyzed those blue shrimp postlarvae data from the San Felipe area (1993 to 1997), plus they obtained commercial catch data for the ports of San Felipe and El Golfo de Santa Clara from 1995 to 1998. Only artisanal (*panga*) catch data were used, thus the shrimp catches were from areas near those two ports. They also used Colorado River flow data based on SIB release flow. Although they claimed to have taken salinity from the San Felipe area during their postlarvae sampling (the same sampling as the Aragón-Noriega and Calderón-Aguilera 2000 study), no salinity data were reported in their paper and none have been recoverable by Aragón-Noriega (pers. comm., October 2016). Thus, there is no way of knowing how much, if any, Morelos Dam release water reached the Gulf of California during their study period. The largest postlarval abundances found were in 1993 (43.6 larvae/m^3) when river flow at SIB exceeded 300 m^3 s^{-1}, and 1997 (47.7 larvae/m^3) when that flow barely exceeded 100 m^3 s^{-1}. Thus the 1993 flow was nearly three times the volume of the 1997 flow, yet 1997 showed higher postlarval abundance. This suggests no clear relationship between river flow (at Morelos Dam) and postlarval abundance in the Upper Gulf. The highest average catch-per-unit-effort (kilograms shrimp per fishing day) was in 1997 and 1998 (21.5 kilograms shrimp per fishing day in both cases), but 1997 had a river flow of only 116 m^3 s^{-1}, whereas 1998 had a river flow of 208 m^3 s^{-1}. This suggests that there is no clear relationship between river flow and catch. Their statistical support for a relationship between catch and SIB river flow over the 5 years of the study was very low. Aragón-Noriega and García-Juárez (2002) concluded that their data suggest there is a "threshold" at which river flow enhanced reproduction in blue shrimp in the Upper Gulf, and speculated that threshold to be 100 m^3s^{-1}. However, their data set is too limited to lend strong support for such a hypothesis, and their reliance on border water release and not river water actually reaching the Gulf, as well as the absence of salinity data for the Upper Gulf during their sampling period, renders this conclusion circumspect.

The Aragón-Noriega and Calderón-Aguilera (2000) and the Aragón-Noriega and García-Juárez (2002) papers used the same postlarvae sampling data (Aragón-Noriega, pers. comm., October 2016). However, this is not mentioned in either paper and neither paper cites the other. Furthermore, different conclusions were reached in the two papers, and neither study had strong statistical support. The data set analyzed for postlarval abundance, in both cases, comprised only 5 data points (total catch for each of 5 years), as they did not analyze monthly postlarvae abundance samples independently, but rather combined April through November, even though river flow would likely not have peaked until June, thus reducing the ability to identify a cause-effect relationship between flow and larval abundance.

Pérez-Arvizu et al. (2009) undertook a study similar to that of Galindo-Bect et al. (2000), but instead of using data gleaned from commercial shrimp trawlers from San Felipe they used artisanal (*panga*) catch data from El Golfo de Santa Clara (1995-2002) to estimate total catch and CPUE, the latter calculated on the basis of shrimp kg/day/*panga*. Artisanal fishers do not travel far from their home port and the Pérez-Arvizu et al. (2009) catch data are probably a more accurate estimate of regional catch than were the data used by Galindo-Bect et al. (2000). As with other studies, they used the SIB flow measurements as proxy for river flow entering the

Upper Gulf, although they acknowledged that the amount of water that actually reached the Gulf was unknown. During their study period, 97% of the catch from artisanal fishing consisted of blue shrimp. They also counted shrimp postlarvae in plankton samples (1993-1997) from the San Felipe and El Golfo de Santa Clara areas.

Pérez-Arvizu et al. (2009) concluded that "total catch apparently has a linear relationship with river outflow" and when flow increased there was an increase in shrimp catch during the following season, except for 2002 when CPUE increased but SIB flow did not. However, examination of their Figures 5 and 6 do not support this claim. For example, in addition to the 2002 anomaly (when flow was very low but CPUE high), river flow increased in 1997 and again in 1998, and while CPUE increased in 1997 it did not in 1998. In 1999 river flow decreased, but CPUE remained the same (at the 1998 level), and in 1996 there was no excess flow at all but in 1997 shrimp catches went up and CPUE was the highest in their dataset. Total catch showed similar anomalies in the pattern of flow versus catch (e.g., 1992 had almost no flow, but shrimp catch increased greatly in 1993). They found the highest postlarvae abundance during years when the average river outflow exceeded 80 m^3s^{-1}, and the lowest abundance when the river flow was below this level. However, the relationship between postlarvae abundance and flow was not linear. For example, the flow in 1993 exceeded 300 m^3s^{-1}, yet abundance was the same as in 1997 when the flow barely exceeded 80 m^3s^{-1}. They concluded that a limit of 100 m^3s^{-1} may be necessary to promote shrimp breeding conditions, and that this might be accomplished by an "increase in habitat volume" (although what this means is not explained).

It is well known that the highly productive wild-catch shrimp fishery, extending southward from the Upper Gulf along the coast of Sonora (the Northern and Central Gulf regions), does <u>not</u> rely on freshwater river inputs and true (positive, hyposaline) estuaries. No stage of shrimp development in this area requires brackish water. In this region, shrimp postlarvae migrate into hypersaline lagoons (*lagunas*), negative estuaries (*esteros*), or simply coastal shallows; they generally leave these shallows as juveniles and migrate to offshore waters. In the Colorado River Delta region, shrimp use coastal shallows as nursery areas to pass through their postlarva-juvenile stages (Castillo-Moreno 1999, Aragón-Noriega and Calderón-Aguilera 2001, Ramírez-Rojo and Aragón-Noriega 2006). In a thorough study of shrimp larvae/postlarvae in the Upper Gulf, Galindo-Bect et al. (2010) described spawning areas along the coast of Sonora (notably off Punta Borrascoso and in Bahía Adair), and nursery areas near the towns of El Golfo de Santa Clara and San Felipe. Aragón-Noriega et al. (1999) also found the Borrascoso-Adair corridor to be the most important spawning site for blue shrimp. Many commercially important fishes spawn there as well, including spotted sand bass (*Paralabrax maculatofasciatus*), bronzestriped grunt (*Orthopristis reddingi*), amarillo snapper (*Lutjanus argentiventris*), Gulf grouper or baya (*Mycteroperca jordani*), Cortez halibut (*Paralichthys aestuarius*), striped and white mullets (*Mugil cephalus, M. curema*), Gulf coney (*Hyporthodus acanthistius*), and totoaba (*Totoaba macdonaldi*) (Hastings and Findley 2007, Turk-Boyer et al. 2014).

There has been no appreciable perennial fresh water entering the Gulf from rivers in central-northern Sonora and Baja California (aside from the Colorado River) since the late Pleistocene, so Northern and Central Gulf of California shrimp are well adapted to using hypersaline lagoons, esteros, and coastal shallows as nursery areas (López 1968, García-Borbón et al. 1996, Leal-Gaxiola et al. 2001, Romero-Sedano et al. 2004, Ramírez-Rojo and Aragón-Noriega 2006).

Like blue shrimp, brown (=yellowleg) shrimp in the Gulf also do not require coastal lagoons to complete their life cycle and they can be found in breeding condition in both the open sea and in high-salinity esteros throughout the Gulf (Ramírez-Rojo and Aragón-Noriega 2006, Valenzuela-Quiñónez et al. 2006, Manzano-Sarabia et al. 2007). Morales-Bojórquez et al. (2013) showed that the life cycle of brown shrimp can be entirely completed in either hypersaline lagoons or in the open marine environment over the continental shelf. In hypersaline Laguna (Bahía) Agiabampo, on the Sonora-Sinaloa border, brown shrimp breeding peaks in summer, when water temperatures and salinities are at their maxima (Romero-Sedano et al. 2004, Valenzuela-Quiñónez et al 2006). Valenzuela-Quiñónez et al. (2006) found no evidence of an offshore migration from Laguna Agiabampo when mature brown shrimp reached spawning length, and also showed that the species can complete its full life cycle in this hypersaline lagoon system. Salinity in the Northern Gulf's esteros is always high, and in summer it commonly exceeds 40‰. Penaeid shrimp in the Northern and Central Gulf are clearly adapted to high salinities. These and other studies (Snyder-Conn and Brusca 1977, Leal-Gaxiola et al 2001, Calderón-Aguilera et al. 2003, Romero-Sedano et al. 2004, Valenzuela-Quiñónez et al 2006) have also shown that both blue shrimp and brown shrimp breed throughout the year (in both Sinaloa and Sonora), usually with two seasonal peaks.

The orthodox life-cycle model of penaeid shrimp envisions them requiring fresh or brackish-water "nurseries" as they grow from postlarvae to juveniles. However, this model, developed in the 1970s, was based on areas other than the Gulf of California, and it is now well known that Northern and Central Gulf of California shrimp do not follow this model and do not require (and perhaps do not prefer) brackish water habitats for their nurseries. As Romero-Sedano et al. (2004) noted, "In arid lagoons with permanent connection to the sea and negative estuarine circulation, penaeid shrimp develop a particular life cycle that differs from that accepted for the general shrimp ecology." Leal-Gaxiola et al. (2001) came to the same conclusion, their studies showing that brown shrimp in the Gulf do not depend on coastal lagoons and may not enter them at all during their early life history stages. In contrast, shrimp in the Southern Gulf do use brackish lagoons as nurseries when they are available, although the relationship of salinity gradients to their onshore migration is not strong (e.g., Mair 1980, Mair et al. 1982, Félix-Ortiz et al. 2014).

3.3 Sciaenid Fishes

Totoaba and Gulf corvina, both endemic to the Gulf of California, belong to the family Sciaenidae—the corvinas, drums and croakers—many of which are high-level predatory fishes. Several species are aggregate spawners, making them highly susceptible to overfishing (Erisman et al. 2010). Totoaba is the largest of more than 290 described species of sciaenids (Huddleston and Takeuchi 1980, Hastings et al. 2014). It ranges from the Colorado River Delta to the mouth of the Río Fuerte (Sinaloa) and at least to Bahía Concepción (Baja California Sur) (Findley 2010, Valenzuela-Quiñonez et al. 2011, 2014, 2015, 2016). Totoaba spawns in the Upper Gulf from late winter to early spring. Juveniles spend 2-3 years in the Upper Gulf before migrating south in the fall. Both adults and subadults appear to spend summers in the cool, rich waters of the Midriff Islands region before moving on southward in the fall. In winter they migrate northward again. While adults migrate into the Upper Gulf for spawning, juveniles tend to linger in the Midriff Islands region (Jordan and Evermann 1898, Berdegué 1955, Cisneros-Mata et al. 1995, Valenzuela-Quiñonez et al. 2014, 2015). Sport and artisanal fishers still take totoaba from its southern range localities, though not commonly.

A commercial totoaba fishery started in the late 1920s, relying on take in the Upper Gulf during the species' spawning period. It was the first important commercial fishery in the Gulf and was the impetus for establishing fish camps that later evolved into the Upper Gulf towns of San Felipe and El Golfo de Santa Clara (Bahre et al. 2000, Hastings and Findley 2007). Before the 1930s, the totoaba fishery was almost solely directed to the export of their dried swim bladders (=gas bladders, *buche*) to China (Chute 1928, 1930). From 1935 to 1945, totoaba fishing expanded to become one of the most important sport and commercial fisheries in the Gulf, with total annual commercial landings, from a 4-month fishing season, peaking at 2300 metric tons (Rosales-Juárez and Ramírez-González 1987, Márquez-Farías and Rosales-Juárez 2013). The commercial fishery reached its maximum yield in the early 1940s, and between then and 1975 the species was thought to be greatly depleted due to overfishing (Márquez-Farías and Rosales-Juárez 2013, CITES 2015) although actual population size estimates did not exist. Commercial catch in 1975 was down to 52 tons (Valenzuela-Quiñoz et al. 2014). A complete moratorium (*veda permanente*) on totoaba fishing was enacted by the Mexican government in 1975, in 1976 the species was listed in Appendix II of CITES, and in 1979 it was added to the U.S. list of endangered species (Barrera-Guevara 1990, CITES 2015). Today, totoaba is nominally protected by Mexico's NOM-ECOL-059-94 and ranked as endangered (Findley 2010, Valenzuela-Quiñonez et al 2015).

Totoaba catch began to decline after the building of Hoover Dam, and an inference was thus made that the reduction of freshwater inflow from the Colorado River was perhaps damaging the population (Flanagan and Hendrickson 1976, Cisneros-Mata et al. 1995). However, the decline was also coincident with a large increase in fishing pressure in the Northern Gulf, mainly by dynamiting and extensive gill-netting of aggregating adults and subadults (Bahre et al. 2000), and also bycatch of juveniles by the shrimp trawling industry. These factors confounded any strong conclusions regarding the underlying cause(s) of the decline (Barrera-Guevara 1990, Cisneros-Mata et al. 1995, García-Caudillo et al. 2000). Although exceptionally fecund, this species has low natural productivity and very low survival to maturity (Márquez-Farías and Rosales-Juárez 2013). It cannot withstand heavy fishing pressure. Márquez-Farías and Rosales-Juárez (2013) demonstrated that the rate of population rebound for totoaba is low, confirming its low resilience to overfishing.

Today, the major cause of mortality of totoaba is shrimp trawler bycatch and the gillnet fisheries of the Northern Gulf (García-Caudillo et al. 2000, Márquez-Farías and Rosales-Juárez 2013). Barrera-Guevara (1990) estimated that an astonishing 92% of young-of-the-year totoaba were killed in the commercial shrimp trawl fishery—perhaps enough to have kept the population suppressed in and of itself during the late 20th century. Totoaba continues to be taken illegally, mainly for its swim bladder, also known as “belly” or “fish maw.” The bladders are sold (overwhelmingly for the Chinese market) and the meat, if saved, may be distributed locally and sold as “*curvina*,” “*cabaicucho*” or even “*cabrilla*.” Although the CITES website (accessed May 2015) claims totoaba bladders wholesale for up to $120/kg, fisheries biologists working in the Upper Gulf have informed us that the bladders were wholesaling for up to $8000/kg in 2015, creating a multi-million dollar illegal fishing industry (in July 2016, the bladders were retailing for up to $60,000/kg in China). Illegal take of totoaba is a highly economically motivated activity in the Upper Gulf, putting enormous pressure on the species (as well as the endangered vaquita porpoise, a common bycatch in gillnets set for totoaba). There is no current, reliable estimate of the population size of totoaba (Valenzuela-Quiñonez et al. 2015, 2016). However, the size of the illegal take today, the sporadic sportfishing take throughout the Gulf, and contemporary research all indicate this species is not “virtually extinct” as claimed by Pitt (2001).

Population recovery of totoaba has been inferred based on historical size-range structure, mortality rates, genetic diversity, and distribution (Rosales-Juárez and Ramírez-González 1987, Román-Rodríguez and Hammann 1997, Valenzuela-Quiñonez et al. 2014, 2015, 2016). In 2014, a proposal was submitted to the Mexican government to allow totoaba fishing to re-enter the sport fishery (see García-De León et al. 2010, Valenzuela-Quiñonez et al. 2011, 2014; García-De León 2013), and Valenzuela-Quiñonez et al. (2014, 2015) suggested that the endangered status of the species should be re-evaluated given our growing understanding of the species. Valenzuela-Quiñonez et al. (2014, 2016) showed that no measurable reduction in genetic diversity (based on analysis of DNA microsatellite loci and mitochondrial DNA markers) was experienced by totoaba in the 20th century, that their genetic diversity is high and comparable to that of related non-threatened sciaenid fish species, and that they are probably panmictic. The endangered listing of this species was not based on estimates of population size (which were unknown then, and remain unknown today), but rather on the size of the fisheries take and its decrease during the early 1970s. However, by the 1980s research was beginning to show that totoaba might not be as diminished as originally thought, and in 2014 and 2015 Valenzuela-Quiñonez et al. showed that the present-day totoaba population structure indicates the species is not overexploited, that it has maintained (or possibly even expanded) its known historical distributional range, that its stock size structure has been stable for several decades, and that gillnet bycatch and the recent surge in poaching (for swim bladders) in the Northern Gulf is the main threat to the species. Furthermore, Valdez-Muñoz et al. (2010) and Valenzuela-Quiñonez et al. (2011, 2014, 2015) showed that this species is not hyposaline-estuarine-dependent as previously thought, and thus not dependent on Colorado River flow to the Upper Gulf. Valenzuela-Quiñonez et al. (2014, 2015) concluded that future conservation measures for totoaba must focus on elimination of illegal fishing and bycatch.

Rowell et al. (2008a) used oxygen isotope ($\delta^{18}O$) analyses of pre- and post-dam totoaba otoliths (ear bones) to infer that young fish lived in reduced salinity waters in the Upper Gulf before the construction of dams began on the river. The pre-dam otoliths were prehistoric (~1000–5000 ybp), recovered from aboriginally deposited shell middens on Northern Gulf shores. This is what would be expected because, to the best of our knowledge, totoaba have always spawned in that region and continue to do so today, whether or not the Colorado River reaches the sea and regardless of local salinity conditions. However, there were scant data in Rowell et al. (2008a) to support their assumption that survivorship of young was greater in low salinity waters, or to support their conclusion that "successful restoration of totoaba will likely require a seasonally appropriate influx of Colorado River water to the Colorado River estuary."

Rowell et al. (2008b) compared totoaba otolith growth rings for the first three years of growth in pre- and post-dam fish. The five pre-dam, prehistoric (~1000–5000 ybp) otoliths they examined were recovered from aboriginally deposited shell middens on Northern Gulf shores. Their $\delta^{18}O$ data showed that ~1000–5000 ybp juvenile totoaba used the delta region whether it was brackish or not. Again, this is what would be expected, and totoaba continue to use these same waters today, regardless of river flow or salinity. They also found pre/post-dam otolith growth rate differences only in the first year of growth, not in years 2 or 3. Thus, their extrapolations of overall growth rate and age of maturity are based on estimated faster otolith growth only in young-of-the-year totoaba. Today, totoaba become sexually mature at ages 5 to 7 years and a length of around 1300 mm (Cisneros-Mata et al. 1995, Román-Rodríguez and

Hammann 1997). Rowell et al. (2008b) used a conversion formula (from Román-Rodríguez and Hammann 1997) to scale from otolith size to body size. On this basis, they concluded that, based on today's size-at-sexual-maturity (between ages 5 and 7), pre-dam fish may have reached sexual maturity 3-5 years earlier than post-dam fish, or at an age of 1 to 4 years. This finding is consistent with predictions of life history theory (Stearns 1992) and empirical data on other fishes (e.g., Morita and Morita 2002) that, in general, slow-growing individuals should initiate maturation at an older age and at a smaller size than fast-growing individuals. However, as acknowledged by Rowell et al. (2008b), this is complicated by the prediction that increased mortality of adults (clearly experienced by post-dam totoaba) selects instead for earlier maturation. Because growth rates and mortality rates interact in a complicated manner to affect the age and size at maturity, it remains unclear what the effects of decreased growth rate in the first year of life might have on adult productivity of totoaba. More importantly, even though totoaba growth rates and age at maturity may have changed in recent decades, this does not demonstrate a direct link to putative productivity/stock decline associated with decreased Colorado River flows.

Flanagan and Hendrickson (1976) found no significant relationship between totoaba catch and Colorado River flow and concluded that overfishing was the primary factor in depleting the stock—and the historical catch data provided by Lercari and Chávez (2007) support that view. (The claim by Lercari and Chávez 2007 that their "results confirm the important role of the Colorado River flow cessation on the decrement of the [totoaba] catch" over-extends the strength of their actual findings; see below).

Cisneros-Mata et al. (1995) and Pedrín-Osuna et al. (2001) also strongly suggested that poaching of adults and bycatch of juveniles by the shrimp fishery contribute to low abundance of the totoaba stock. Cisneros-Mata et al. (1995), following Barrera-Guevara (1990), indicated that in the mid-1980s an estimated 120,000 totoaba juveniles died each year as bycatch in shrimp trawl nets, and 6,200 adults (average weight 26 kg) due to poaching. Lercari and Chávez (2007) also concluded that their multiple regression analyses showed catch to be correlated with two independent variables—Pacific Decadal Oscillation Index and Colorado River flow—suggesting these two factors explained up to 70% of the catch variability. However, Lercari and Chávez (2007) examined only abiotic variables and did not include fishing effort, even though the number of boats fishing for totoaba increased greatly from 1942 to 1965. Their source and measurement of river flow data also are unclear, and no evidence was given that they measured actual freshwater flow into the Upper Gulf. The Lercari and Chávez (2007) analysis, and otolith data suggesting that young-of-the-year totoaba may grow faster when lower salinity environments are available to them (Rowell et al. 2008b), are tantalizing hints that river flow to the delta might be beneficial to totoaba growth. However, no data show that river flow is necessary to the life history of this species or that it would increase its population numbers. And there is no published evidence that we are aware of showing a correlation between salinity and the distribution of larval or juvenile totoaba. In fact, Valdez-Muñoz et al. (2010) sampled totoaba juveniles in Upper Gulf and Delta waters with salinities between 35.3‰ and 39.5‰ and reported that captures of juveniles and salinity had no significant correlation. Even the CITES listing for totoaba notes that the negative impacts on this species by reduction of Colorado River flow is questionable (CITES 2015).

The Gulf corvina (*Cynoscion othonopterus*) currently comprises the most important finfish fishery in the Northern Gulf, indeed, in the entire Gulf (Rodríguez-Quiroz et al. 2010). Most gillnet fishers in the region target both corvina and shrimp and alter their efforts seasonally and in relation to market demands (Aragón-Noriega 2014). Rowell et al. (2005) used $\delta^{18}O$ isotope analyses to estimate spawning habitat salinity for Gulf corvina during Colorado River flow and non-flow years, concluding that "successful restoration of the Gulf corvina fishery in the Upper Gulf requires influx of Colorado River water to nursery grounds in the river's estuary." This assumption has since proven decidedly incorrect. Despite an absence of significant influxes of Colorado River surface water to the Gulf of California since the turn of this century, the Gulf corvina fishery has become the largest finfish fishery in the Gulf. Reported annual landings range from 2,200 to 5,900 tons per year over the past decade (Paredes et al. 2010, Rodríguez-Quiroz et al. 2010), with a staggering number of 1.5-1.8 million fish harvested over the 21-25 days of fishing during the annual spawning aggregation (Erisman et al. 2010, 2012). Today, Gulf corvina fishing brings in about U.S. $20 million annually to fishing communities in the Northern Gulf (CIRVA 2016). Reported catches of this species have never been higher than in the most recent decade, although it is estimated to be overfished (Ruelas-Peña et al. 2013).

The principal finding of Rowell et al. (2005) was that when there is freshwater flow into the Upper Gulf, decreasing salinity, Gulf corvina record these brackish-water years in their growing otoliths. This is what would be expected for a species that aggregate-spawns in the Upper Gulf, where changes in river flow can result in a fluctuating salinity environment. However, they found "nursery ground" $\delta^{18}O$ signatures for the otoliths they examined corresponding to salinites ranging from 26 to 38‰—thus the young fish were living in the area when river flow was present and when it was completely absent. Rowell et al. (2005) did not offer data to show that freshwater pulses lead to enhanced recruitment or increased survival. This species aggregate-spawns/breeds annually and is clearly highly successful regardless of whether or not there is any freshwater inflow from the Colorado River. The increased catch of Gulf corvina that Rowell et al. (2005) noted for 1996 could have simply been due to increased fishing effort, rather than increased production becoming evident three years after a 1993 river water release. In fact, for the El Golfo de Santa Clara port, the annual catch grew from 3.2 tons to 1,278 tons between 1993 and 1996 as fishing efforts expanded, and since then it has been as high 5,900 tons (CONAPESCA 2010, Gherard et al. 2013).

The peak Colorado River flows that once entered the Upper Gulf occurred subsequent to the snowmelt in the Rocky Mountains, from May to July (Sykes 1937, Harding et al. 1995, Pontius 1997, Lavín and Sánchez 1999, Pitt 2001). The Gulf corvina spawning/breeding aggregations (and associated fishing effort) take place from late February to late May (Erisman et al. 2012, 2015; Sadovy and Erisman 2010). Thus it seems likely that the environmental stimulus for the spawning aggregations is not a decrease in salinity in the Northern Gulf due to Colorado River inflow, but some other factor, such as rising temperatures of Gulf waters in the spring. Warming seawater temperatures are known to be a spawning cue for totoaba (Cisneros-Mata et al. 1995) and Gulf bairdiella (*Bairdiella icistia*) in the Gulf (R. C. May 1975), as well as other sciaenids elsewhere in the world (e.g., Vizziano et al. 2002, Aalbers 2008). It is also notable that Gulf corvina and totoaba aggregate and spawn during the period of most rapid rise in primary (phytoplankton) productivity in the Upper Gulf (March-April), thus it is possible that there is a productivity cue affecting spawning time.

Legal (and illegal) Gulf corvina fishing targets the spawning period for this species and harvests thousands of tons annually. Because the Upper Gulf is the only known spawning site, this species is highly vulnerable to overfishing and potential collapse (Erisman et al. 2012). The history of collapses in fisheries elsewhere in the world that have targeted the spawning migrations of large-bodied sciaenids is well known (Sadovy and Cheung 2003; Erisman et al. 2012). Illegal fishing (poaching) remains a serious concern in the Northern Gulf, where an estimated 86-90% of Gulf corvina catch and 62% of the total fisheries catch takes place in marine protected areas (Erisman et al. 2012, Rodríguez-Quiroz et al. 2012). Concerns exist that the stock is becoming overexploited and susceptible to collapse due to overfishing (Musick et al. 2000, Rodríguez-Quiroz et al. 2010, Erisman et al. 2010, Ruelas-Peña et al. 2013). Intense fishing of spawning aggregations has led to Gulf corvina being one of the few fish species in Mexico that is regulated by an official management plan (DOF 2007).

Gulf corvina (and totoaba) have been around for many thousands, probably hundreds of thousands, if not millions of years (Huddelston and Takeuchi 2007), and they have survived in the Gulf throughout all of the naturally occurring northward and westward diversions of the lower Colorado River, such as when ancient Lake Cahuilla and all its predecessor lakes in the Salton Basin received and impounded the total river flow, thus keeping it from reaching the Gulf for many years each time. Ancient Lake Cahuilla was actually a chronological sequence of four or more lakes, the last of which was in existence when the Spaniards first arrived in the Pimería Alta (Waters 1983). Although the land-locked lake had apparently completely evaporated by the time the first Spanish explorers reached that region (there is no record of it in the writings of Díaz and Alarcón who passed nearby in 1540, or Oñate who explored the region in 1604), a map by John Rocque (ca. 1762) in the archives of the British Museum clearly shows the Colorado River flowing into an inland lake north of the Colorado River Delta that had no outlet to the sea (Warren 1979). Wilke (1978) documented a series of four lakes extending back over 2000 years, and evidence suggests that other lakes in the Salton Basin intermittently received the entire Colorado River flow before that time, probably throughout the Holocene (Sykes 1914, Wilke

1978, Waters 1983, Laylander 2005). Evidence of a long history of standing surface waters in the Salton Basin/Trough includes travertine deposits (precipitated calcium carbonate) up to 76-cm thick along old beachlines of the lake(s).

The lowest point on the Colorado River Delta's northern crest is about 10 m above mean sea level, and the Salton Basin (Cahuilla Basin) is ~84 m below mean sea level, meaning that the flow of the Colorado River can be directed either northward into the Salton Basin or southward toward the Gulf of California (Carpelan 1961). In fact, two old distributaries of the lower Colorado River carry irrigation drainage water northward from Mexico to the Salton Sea today, the New River and the Alamo River. The lacustrine basin lies in the Salton Trough, which includes the Coachella and Imperial Valleys of southeastern California, and the western half of the Mexicali Valley and the Colorado River Delta in Mexico. The Salton Basin is now partly occupied by what remains of the Salton Sea, a man-made partial recreation of Lake Cahuilla caused by an accidental, anthropogenic diversion of the Colorado River in 1905-1907 (during the summer of 1906, the entire volume of the Colorado River flowed northward from Mexico in the Alamo and New Rivers into the Salton Basin) (Sykes 1937).

Although the Salton Sea is currently the largest inland body of water in California, it is much smaller than ancient Lake Cahuilla and its predecessors because the man-made river diversion lasted less than two years. Lake Cahuilla filled, on each of its most recent four occurrences, to a maximum depth of ~95 m and covered an area of ~5700 km^2 (Waters 1983, Laylander 2005). Wilke (1978) estimated that Lake Cahuilla could fill to an elevation of about 12 m above sea level in 12-20 years, after which the lake would overflow southward toward the Gulf by way of the delta's Río Hardy channel. Sykes (1937) estimated that the Colorado River naturally altered its flow northwestward to enter the Salton Basin at least six times during the

19th century (in 1840 [probably when the New River was formed], 1842, 1852, 1859, 1867 and 1891). As early as 1851, San Diego newspapers were reporting northward flows of the Colorado River from Mexico into the Salton Basin via the New River (Sykes 1937). Other, shallower depressions on the delta have also temporarily impounded Colorado River water, stopping or reducing its passage to the sea, such as Volcano Lake (e.g., during the years 1909 to 1923) and Pescadero Basin (e.g., during the years 1923 to 1929), both of which are geologic/topographic lows along the Cerro Prieto Fault line (Sykes 1937).

The first survey of the Salton Basin was made in 1853 by a party led by Lt. R. S. Williamson, exploring for westward railroad routes south of the Sierra Nevada. W. P. Blake, the geologist of the party, was the first to document that the Salton Basin was below sea level. Much later, he revisited the region after the Salton Sea formed, referring to it as the residual of a more extensive ancient lake that he named Lake Cahuilla. Both Blake (1914) and Sykes (1914) interpreted what they called the Cahuilla Basin (after the local Indian tribe) as an ancient cut-off arm of the Sea of Cortez. Hubbs and Miller (1948), who unnecessarily renamed Lake Cahuilla as Lake LeConte (after a naturalist who worked in the region in the 1850s), estimated that the lake lasted for centuries.

Gulf corvina and totoaba were thus historically exposed to, and are clearly adapted to, long periods of no Colorado River flow to the Gulf at all, and they can successfully spawn and grow across a wide range of salinities, as has been shown for penaeid shrimp in the Northern and Central Gulf. Another Gulf sciaenid fish, *Bairdiella icistia*, has also been shown to grow and spawn successfully in salinities ranging from 15‰ to 40‰ (May 1975). These and a wide array of other species common in the Northern Gulf are clearly adapted to high, and highly variable salinity regimes. For example, Reynolds and Thomson (1974) and Reynolds et al. (1976)

showed that the Gulf grunion (*Leuresthes sardina*), found most abundantly in the Northern Gulf, has an incipient upper lethal salinity of 58‰ to 68‰, with juveniles preferring salinities of 45-54‰, indicative of its adaptation to the elevated salinities of the region.

More compelling evidence supports the idea that, rather than reduced primary productivity effects (ostensibly from reduced river flow) on their early life histories, the boom-and-bust cycles of Gulf commercially-exploited sciaenid fishes are due to fishing trends and overfishing. Like many other exploited fishes, their vulnerability to capture is exacerbated by their behavior of forming large, predictable spawning aggregations at restricted locations (Erisman et al. 2010; Sadovy and Erisman 2010). Most workers have considered unregulated/unenforced fishing to be the primary threat to stock numbers of these and other exploited fishes (Cisneros-Mata et al. 1995, Román-Rodríguez 1990, 1998, 2000; Musick et al. 2000; Sadovy and Cheung 2003, Rodríguez-Quiroz et al. 2010; Erisman et al. 2012, Chao et al., Valenzuela-Quiñonez et al. 2015, IUCN online).

Aragón-Noriega et al. (2009) analyzed historical fishing data for another sciaenid, the Gulf (or bigeye) croaker (*Micropogonias megalops*), in the Upper Gulf. Like other threatened, large Gulf of California sciaenids (e.g., totoaba; Gulf corvina; white seabass or *cabaicucho*, *Atractoscion nobilis*), this species is concentrated (and fished) in the Upper Gulf. The commercial fishery for Gulf croaker began developing around 1991, after a collapse of the regional shrimp fishery due to extreme overfishing by industrial trawlers. By 2009, Gulf croaker was one of the five most important fisheries in the Upper Gulf. As with earlier-established fisheries for totoaba and Gulf corvina, Gulf croaker is taken primarily during its reproductive period (March to August) when the fish become even more concentrated. Aragón-Noriega et al. (2009) found direct correlations between overfishing and catch ("production"), and between legally enacted catch reductions and fishery recovery. Interestingly, they did not find a significant correlation between boat numbers and capture levels, perhaps due to differences in individual fishing (boat) efforts. This appears similar to the results of Galindo-Bect et al. (2000) when they attempted to estimate shrimp catch-per-unit-effort based solely on the San Felipe licensed shrimp fleet catches.

Sánchez-Velasco et al. (2011) sampled fish larvae from summer plankton tows in the Upper Gulf and used a Bray-Curtis Index to define main larval fish habitats (based on species composition). Dissolved oxygen levels were high throughout the study area, and the mean proportion of fish larvae in relation to total abundance of zooplankton was more than 50%, exceeding all other observations of larval fish abundance in zooplankton samples from throughout the entire Gulf. A total of 99 fish "species" (taxa) were recorded, the most abundant being anchovies (*Anchoa* spp.), threadfin herrings (*Opisthonema* spp.), and Sciaenidae (croakers and corvinas). Overall larval abundance was very high, with a mean of 1253 fish larvae per 5-m stratum of the water column. The authors concluded that "the Upper Gulf of California remains an important fish spawning zone and nursery area," and that "the species richness and larval abundance recorded in this study are very high in relation to the fish larvae records for the Northern Gulf of California for the same month." Sánchez-Velasco et al. (2011) found that larval fish habitats with the lowest larval diversity occurred in the most saline environments, leading them to suggest that increased salinity in the Upper Gulf, caused by cutbacks in Colorado River inflow, might have reduced the areal size of lower salinity habitats (i.e., the "preferred larval habitat") for some fishes. But, there are no records or data for fish larvae in this region prior to damming of the river. Although the Sánchez-Velasco et al. (2011) study is revealing in many ways, it does not provide data to unambiguously show that the Upper Gulf ecosystem has been damaged, or that it currently has reduced fish diversity or production due to reduced Colorado River inflow. It is worth noting, also, that the possible roles of river plumes in marine fish recruitment in general is very unclear although numerous hypotheses exist (Grimes and Kingsford 1996).

As with penaeid shrimp, totoaba and Gulf corvina have been living and reproducing in the Gulf of California with little freshwater inflow to their spawning/nursery habitats since the mid-1930s, and episodic flow before that. Fishing pressure and bycatch are thus far-and-away the greatest threats to these two fish species; perhaps the only threats.

3.4 The “Delta Clam”

The *Mulinia* clam story in the Upper Gulf is intriguing. Kowalewski et al. (2000) and Rodríguez et al. (2001a,b) studied old shells of this small bivalve (which they called *Mulinia coloradoensis*) that they reasoned had eroded from deltaic deposits and accumulated in cherniers (shelly beach ridges) on beaches in the Upper Gulf. Kowalewski et al. (2000) estimated that pre-dam densities of this clam were 25-50 individuals m^{-2}, and that $\sim 5 \times 10^{12}$ shells were produced in the area “during the last millennium.” They argued that this clam was endemic to the delta region and has experienced a dramatic decrease in abundance due to loss of productivity in the Upper Gulf resulting from decreased Colorado River input and “decrease in nutrients once supplied by the river” (also see http://www.geo.arizona.edu/ceam/Hecold/hecolcd.htm).

However, the extremely high nutrient levels and primary productivity of the Upper Gulf have been well documented since oceanographers first began studying the region decades ago (see Section 2 above). Cintra-Buenrostro et al. (2012) later reasoned that nutrient depletion from reduced river flow was probably not responsible for the reduction in population size of the *Mulinia* population on the delta, instead postulating that salinity might be important and suggesting that the clam might need brackish water to survive well. As noted by Rodriguez et al. (2001a), the alleged "endemic delta clam" *Mulinia coloradoensis* Dall, 1894 is actually a junior synonym of *M. modesta* Dall, 1894, a synonymy made by Grant and Gale in 1931. Thus this species is not endemic to, nor restricted to the Upper Gulf of California, and it has been reported from habitats ranging from brackish to fully marine salinities. The synonymy is well known and included in the standard compendiums of tropical West American molluscs, including Keen (1971), who mistakenly gave priority to the name "*coloradoensis,*" Coan and Valentich-Scott's (2012) monograph of tropical eastern Pacific bivalves, and the online Macrofauna Golfo Invertebrate Database (http://www.desertmuseum.org/center/seaofcortez/database.php). Coan and Valentich-Scott (2012) re-examined the type material to re-verify the synonymy (Paul Valentich-Scott, pers. comm. 2016) (Figure 4). The type locality of this species is Guaymas (Sonora) and the National Museum of Natural History (Smithsonian Institution) has both type material and other (more recently collected) specimens from that location. The Santa Barbara Museum of Natural History houses specimens from the coast of Baja California (from north of San Felipe southward to Bahía de los Ángeles, across from Isla Ángel de la Guarda) and Sonora (El Golfo de Santa Clara to Bahía Adair). However, despite these data and taxonomic realignments, Smith et al. (2016) continued to consider this clam to be endemic to the Colorado River Delta and use the junior synonym name *Mulinia coloradoensis*.

The genus *Mulinia* is not considered to be freshwater-dependent, and *Mulinia modesta* appears to be eurytopic based on its broad distribution (e.g., Guaymas, Bahía de los Ángeles, Bahía Adair). Although it appears to be tolerant of a wide range of salinities, there is no evidence that it needs brackish or fresh water for any stage in its life history. Although there has not been a direct test of the hypothesis of reduced salinity improving growth rates in *M. modesta*, such a study was done for two other clams from the Colorado River Delta area (*Chione cortezi* and *Chionista fluctifraga*) and just the opposite was found—both species were shown to have increased growth rates during post-dam years, presumably without the adverse influence of reduced salinities due to higher river discharge (Schöne et al. 2003). (Coan and Valentich-Scott [2012] considered *C. cortezi* to be a junior synonym of *C. fluctifraga*.)

Mulinia modesta is a filter-feeding clam and depth, wave exposure, and sedimentation processes are likely important to its occurrence. Loss of river inflow in the post-dam era has switched the delta region's sediment flow from longitudinal/long-basinal to cross-basinal, and sediment dispersal now is mainly controlled by oceanic forcing (instead of fluvial processes) dominated by the cyclonic gyre of the Northern Gulf (Carriquiry et al. 2001, Álvarez and Jones 2002). This has created a different sedimentary regime in the Upper Gulf, which may have caused localized decrease in abundance of *M. modesta*. Sediment mobilization and bedforms in the Northern Gulf are strongly controlled by tidal dynamics (Hernández-Azcúnaga et al. 2014).

3.5 Vaquita

The vaquita (*Phocoena sinus*), a small porpoise found only in the northernmost Gulf of California, is the world's most critically endangered marine mammal (Arellano Peralta et al. 2011, Arellano Peralta and Medrano González 2013, Rojas-Bracho and Reeves 2013, CIRVA 2016). It is listed as endangered by the U.S., Mexico, and CITES. The entire population lives within a 2000-4000 km^2 area centered near Roca Consag, about 40 km east of San Felipe, Baja

California (Rojas-Bracho et al. 2006), giving it the most restricted range of any marine cetacean species. The vaquita is believed to be a relict population of an ancestral species most closely related to two southern hemisphere species (the spectacled porpoise, *P. dioptrica*, and Burmeister's porpoise, *P. spinipinnis*) that crossed the equator during a period of Pleistocene cooling (Norris and McFarland 1958, Vidal et al. 1999, Munguía-Vega et al. 2007). Genetic analyses have corroborated this interpretation and have estimated that vaquitas were likely never very abundant (Rosel et al. 1995, Taylor and Rojas-Bracho 1999, Munguía-Vega et al. 2007). Coincident with the species' discovery and its description 1958 (Norris and McFarland 1958), came the realization that vaquitas frequently become entangled and drowned in gillnets and shrimp trawls (Norris and Prescott 1961). The primary cause of vaquita mortality today is well known to be incidental capture (bycatch) in shrimp and finfish gillnets that also incidentally or illegally take totoaba, and the fate of vaquita today is directly tied to the illegal totoaba fishery (Villa-Ramírez 1976, Brownell 1982, Hohn et al. 1996, Vidal et al. 1999, Rojas-Bracho and Taylor 1999, D'Agrosa et al. 2000, Rojas-Bracho et al. 2006, Jaramillo-Legorreta et al. 2007, Rojas-Bracho and Reeves 2013).

International marine mammal scientific organizations agree that deaths in gillnets entirely explain the decline in vaquita numbers (International Whaling Commission [IWC] 1991a, b, c, 1995, 1996, International Union for Conservation of Nature and Natural Resources [IUCN] Red List, International Committee for the Recovery of the Vaquita [CIRVA] 2014, 2015, 2016, Rojas-Bracho et al. 2008). However, allegations in the past have argued that at least some of the decline is due to declining productivity resulting from reduced Colorado River flow into the Upper Gulf (e.g., Villa-Ramírez 1993, Fleisher 1994, 1996). The hypothesis entertained largely by the fisheries sector, as stated by Ramírez-León et al. (2015), is that the vaquita population has declined because the lack of Colorado River flow has reduced nutrient input to the Northern Gulf, and thus its primary productivity, causing the ecosystem to collapse. Galindo-Bect (2012) and Galindo-Bect et al. (2013) argued that although the mortality of the vaquita is mainly due to bycatch, the damming of the Colorado River has caused declines in other species (shrimp and totoaba) and that something similar may be happening to vaquita. However, Ramírez-León et al. (2015), and many other studies (see Section 2, above) found no evidence that nutrient concentrations or primary productivity has decreased and concluded that nutrient-related issues are not risk factors for the vaquita. There also is no evidence for decline in vaquita prey species that might have been caused by reductions in river flow, nor any evidence that pollutants (specifically chlorinated hydrocarbon pesticides), that in the past could have been carried to the Northern Gulf of California by Colorado River water, pose a risk (Calambokidis 1988, Vidal et al. 1999, Rojas-Bracho and Taylor 1999, Rojas-Bracho et al. 2006).

Rosel and Rojas-Bracho (1999) sequenced a portion of the mitochondrial DNA control region (a portion of the 5’ end of the hyper-variable control region of the mtDNA molecule) from 43 individual vaquita. Every animal had identical sequences. The complete lack of polymorphism in the control region is unique among cetaceans that have been studied, and it strongly suggests that vaquita experienced a bottleneck or founder event, likely at the species’ inception, followed by a small long-term population size. Thus the low mtDNA genetic variability they observed was likely a historical feature of the species, rather than the result of recent diminishment of population size. Taylor and Rojas-Bracho (1999) also found no support for the low genetic diversity having resulted from the recent decline in abundance, also concluding that the lack of heterozygosity is the result of a historical bottleneck or founder effect. Both papers noted that no evidence of inbreeding depression has been observed, and that lack of variability in the control region does not necessarily translate into low overall levels of heterozygosity in the nuclear genome. Hohn et al. (1996) and Rosel and Rojas-Bracho (1999) concluded that if incidental mortality of the species could be eliminated, the species could exhibit positive population growth.

Munguía-Vega et al. (2007) investigated genetic sequence variation at two major histocompatibility complex (Mhc) class II loci in vaquita (*Phocoena sinus*) and its putative closest relative, the Burmeister's porpoise (*P. spinipinnis*). Mhc class II genes encode cell-surface glycoproteins that bind and present antigens from extracellular pathogens (e.g., bacteria) to T helper cells, and they are an essential part of the immune response of vertebrates (Klein 1986). They found one putative functional allele fixed at the locus DQB, and two presumed functional alleles at the locus DRB (differing by a single nonsynonymous nucleotide substitution). Identical trans-specific DQB1 and DRB1 alleles were identified between vaquita and Burmeister's porpoise, supporting a sister-group relationship. Fixation of one allele, due to genetic drift, commonly occurs at the DQA or DQB loci in small-range (e.g., island) endemic mammals. Analysis of the data suggested to Munguía-Vega et al. (2007) that the low levels of Mhc class II variation seen in vaquita are not the result of the recent population decline in this species, but of long-term small population size over at least 2000-10,000 years. Taylor and Rojas-Bracho (1999), Munguía-Vega et al. (2007), and others have previously suggested that vaquita have probably never had an abundant or widespread population. Ortega-Ortiz (1993), Torre-Cosio (1995), and Munguía-Vega et al. (2007) note that a high frequency of non-deleterious anatomical malformations among vaquita supports the likelihood of fixed alleles. However, there is no evidence that the observed anatomical anomalies cause impairment to the survival or reproduction of individuals, or whether this condition was present in the ancestral form (or a trait fixed through genetic drift). Low levels of genetic variation at Mhc genes in other species have led to concern about a low adaptive potential and high susceptibility of the population to novel infections disease. However, to date there have been no reports of infectious disease in vaquita, and its parasite load is not unusually high or uncommon (Vidal et al. 1999). The NOAA Vaquita Fact Sheet (NOAA 2016) also states that low genetic diversity does not appear to be a threat to the survival of vaquita.

Rojas-Bracho and Taylor (1999) undertook a detailed analysis of risk factors for vaquita. They concluded there is no evidence that Upper Gulf productivity has declined due to reduced Colorado River flow, vaquita food is not limited and no diminishment of vaquita prey species has been documented, pollutant levels in the region are too low to be a risk to vaquita, and reduced fitness from inbreeding (i.e., inbreeding depression) is not evident. They further note that the single serious risk to this species is mortality resulting from fisheries bycatch.

Thus, it appears that the threats facing vaquita have changed little since its discovery more than 50 years ago. Due to the species' low abundance, low reproductive potential, and limited geographic range in a region where fishing is the sole source of income for most people, the vaquita is highly vulnerable to fishing pressure (Rojas-Bracho et al. 2006). In 2015, the Mexican government implemented a near-complete ban on the use of gillnets and long-lines for two years in the area where vaquita are most abundant. However, with an estimated fewer than 60 individuals left (CIRVA 2016, Vidal 2016), it remains to be seen if this last-ditch effort will succeed in saving the vaquita from extinction (Aragón-Noriega et al. 2010). The most recent analysis by the International Committee for Recovery of the Vaquita (CIRVA 2016) states that, today, essentially all vaquita deaths are caused by the increase in illegal gillnet fishing for totoaba swim bladders.

3.6 Fisheries Productivity in the Northern Gulf—Reprise

In considering the above, we conclude that there is no support for the hypothesis of decreased Colorado River flow reducing primary productivity in the Northern Gulf of California, and there is only weak to unsubstantiated support for the idea that river flow reduction has historically been responsible for decreased productivity of shrimp, totoaba, or Gulf corvina. And, there is no evidence whatsoever that reduced river flow is even partly responsible for the reduction in vaquita numbers. Any potential loss of nutrients from reduced Colorado River flow is compensated for by agricultural runoff, halophyte decomposition, erosion of the deltaic sediments (which release nutrients that have accumulated there for thousands of years), and, most importantly, by the daily influx of nutrients moving in from the open Pacific and upwelling in the highly mixed waters of the Northern Gulf. Alles (2011) and others have concluded, the depletion of commercially exploited fish stocks and the collapse of the vaquita population are the result of inadequate fisheries management, not the lack of freshwater or nutrient supply from the Colorado River. Ainsworth et al. (2012a,b) modeled the Northern Gulf under different fisheries scenarios and concluded that if full compliance with current fisheries regulations could be achieved, vaquita and totoaba populations would experience significant population increases, although at a cost to the fishing community of about 30% of its annual revenue.

Bobadilla et al. (2011) undertook a thorough review of the history of environmental policy in the Upper Gulf, describing the evolution of various federal decrees in the area. They note how chaotic the situation has become with so many conflicting laws and declarations, and that this is possibly because the decrees have tried not to interfere with shrimp fishing in the region. They note that some other possible reasons management tools for totoaba and vaquita have proven to be ineffective are: there has been no consistency between the goals of fisheries and conservation sectors, the decrees are not clear on how they will achieve success, the fishers have not been sufficiently or appropriately informed about the harm done by their work practices and they only respond to their own needs and interests, and there is not enough honest inspection and surveillance so illegal and improper practices occur. Regarding totoaba, they note that protection has been ineffective mainly because the laws have focused on protection of adults without regard to juveniles. Bobadilla et al. (2011) point out that "…..the 1993 decree that banned totoaba fishing nets to protect the vaquita leads us to inquire: why after 18 years since 'the boom' period that a total ban on totoaba fishing was enacted (a decree in 1975) it was not implemented and the nets used to catch them were still being used? This is another example that in Mexico the laws have often been a dead letter, and there is a strong need for effective law enforcement."

Interannual variations in fishery takes are most likely due to changes in fishing pressure and natural cycles. In 2010, over 2000 *panga*s were fishing in the Upper Gulf, mainly out of the three fishing ports of San Felipe, El Golfo de Santa Clara, and Puerto Peñasco. Rodríguez-Quiroz et al. (2010) showed that 62% of the artisanal fishing from these three ports takes place in the Upper Gulf of California and Colorado River Delta Biosphere Reserve (including the Vaquita Refuge area). The growth of artisanal fishing in the Upper Gulf has been huge over the past two decades, with the number of *pangas* increasing from 635 to 1269 from 1995 to 1997, and to 2017 by 2003—over 40% of the entire Gulf of California *panga* "fleet" is now operating in the Upper Gulf. Most of these fishers use gillnets that incidentally capture vaquita and totoaba. By 2007, the number of pangas fishing in the Upper Gulf of California far exceeded that recommended when the Biosphere Reserve was declared (DOF 2005). It is expected that the small-boat fishery will continue to grow as Mexican authorities reduce the size of the industrial fleet (Rodríguez-Quiroz et al. 2009).

The hypothesis that increasing freshwater flow from the Colorado River to the Gulf of California might improve productivity in the Upper Gulf is interesting, but as yet there seems to be no strong or unequivocal data in support of this idea, and multi-year studies have shown no correlation between river flow and nutrients or productivity (e.g., Nieto-García 1998, Ramírez-León et al. 2015). In fact, there is some evidence that nutrient concentrations and primary productivity actually drop during periods of high freshwater flow into the Upper Gulf (Nieto-García 1998, Ramírez-León et al. 2015; Table 1). There is also some evidence that clams (bivalve molluscs) in the Northern Gulf grow more slowly in lowered salinities (Schöne et al. 2003). As early as 1943, Gilbert and Allen (reporting on 1939 and 1940 Gulf research cruises of Scripps Institution of Oceanography) noted that the internal hydrographical features of the region "can fully account for the fertility of the Gulf without the necessity of considering the effect of the Colorado River."

Yet, seemingly exaggerated claims of environmental degradation in the Upper Gulf marine environment due to reduced Colorado River flow are common in the review literature (e.g., Kellogg 2004, Arias et al. 2004, Glenn and Nagler 2007, Calderón-Aguilera and Flessa 2009, Zamora et al. 2013, Glenn et al. 2013a, Kostogiannis 2015). Glenn et al. (2013a) even went so far as to suggest that "delta restoration" to "restore fisheries in the Upper Gulf of California" may be an impossibly ambitious goal. This is not to say that increased freshwater flow to the Upper Gulf might not change things—it might increase production of some species and reduce production of others in the ecosystem. However, we lack data to specifically address that question, and there is very little in the way of solid evidence that increased river flow to the Gulf would improve the health of an already healthy marine ecosystem that suffers primarily from fisheries issues. Thus, we disagree with Glenn and Nagler's (2007, page 361) claim that, "The biggest need for the intertidal and marine zone is more [fresh] water." We would argue that the biggest need is improved fisheries management/enforcement.

4. THE COLORADO RIVER DELTA – A HIGHLY VARIABLE ENVIRONMENT

The Colorado River Delta (that area with alluvium deposits from the Colorado River) covers an area of 8,612 km^2 (3,325 mi^2), situated between 31° 03' and 33° 45' N latitude. The Colorado River is unique among the major delta-forming rivers of the world in that it has alternately discharged its waters into the sea and into land-locked basins.

The Mexican portion of the Colorado River Delta was first mapped by Derby in 1851 (Derby 1852), by Ives in 1858 (Ives 1861), and most famously by Sykes in 1907 and again in 1937, although today a variety of satellite-based images allow for accurate GIS mapping of the region (Figure 2). The most comprehensive and detailed description of the delta ever published was probably that of Godfrey Sykes (1937) for the American Geographical Society, although many present-day workers have overlooked that important volume. Sykes's description was based on 45 years of surveys in the delta, often accompanied by botanist-explorer D. T. MacDougal. His 193-page narrative, with abundant statistics, maps and photographs, provides an accurate history of Colorado River flow across the delta and the changing physiographic history of the region from 1890 to 1935 (including a blow-by-blow account of the accidental formation of the Salton Sea). By making detailed comparisons of notes and maps of the delta from previous explorers, beginning with Francisco de Ulloa in 1539, and continuing through the explorations of Joseph C. Ives, logs of steamships that once connected the Gulf to Yuma (Arizona), and border projects by the Imperial Land Company and the U.S. Government, Sykes described the dynamic history of the delta and its river channels as they changed from one decade to the next, and even from one flood event to the next.

Sykes (1937) showed that the undammed Colorado River in the delta changed course frequently, islands and shoals formed and disappeared, and various topographic lows became temporary lakes that impounded the river's flow for years at a time. From 1909 to 1930, Sykes described the river as flowing predominantly to the western side of delta, where it was deflected by the Sierra Cucapá. From there, it could run northward to the Salton Basin (via New River), southward in the Río Hardy channel to either the Laguna Salada Basin or to the sea, or it could pool in one of the large topographic lows just south the U.S.-Mexico border, such as Volcano Lake or Pescadero Basin (east of the Sierra Cucapá). Even when the main channel was on the eastern side of the delta, it could drain directly into Volcano Lake (a topographic low on the Cerro Prieto fault line) via the old Paredones River. When the river flowed northward, it threatened the towns of Calexico/Mexicali or Yuma and, in fact, it flooded those towns on more than one occasion. The two main watercourses that drained the Colorado River toward the Salton Basin were the Alamo River and the New River, whose channels still exist, although today they mainly carry irrigation drainage from croplands. Just after the turn of the 20th century, the U.S. and Mexico began building levees on the Mexican side of the border to protect Yuma and Calexico/Mexicali, the first being the Volcano Lake Levee constructed in 1908, and since then hardly a year passed without the U.S. or Mexico constructing new levees or canals on the delta.

During the 16th and 17th century explorations of Alarcón, Díaz and Kino, the mainstem of the Colorado River also flowed on the western side of the delta, probably occupying the Río Hardy channel. However, by the time of the Derby (1852) and Ives (1858) surveys, the mainstem had moved to the eastern side of the delta, and it may have maintained that position until the great floods of 1890-91, when the river again broke toward the west. During those floods, most of the river's water flowed north into the Salton Basin (Sykes 1937). Beginning in 1901, U.S. land developers opened canals directly from the river to the Imperial Valley to support a fledgling agricultural enterprise, and it was the flood-rupture of these diversions in 1905 that led to the most recent refilling of the Salton Basin (creating the Salton Sea). In more recent (post-dam) times, the river has been channeled again on the eastern side of the delta by an extensive series of dikes and levees. Over the past 75 years, most of the delta has been converted to irrigated agriculture.

Feirstein et al. (2008) estimated the volume of Colorado River deltaic sediments at approximately 41,682 km^3, but Dorsey (2010) calculated it to be 220,000 km^3–340,000 km^3. Most of these sediments lie within the Salton Trough/Basin, a topographic depression that extends over parts of southeastern California, southwestern Arizona, and northwestern Mexico, within the Sonoran Desert (Lippmann et al. 1999, Anderson et al. 2003, Crowell et al. 2013). The trough is a classic graben formation lying on the west side of the San Andreas transform fault system and was formed by active rifting along the landward extension of the East Pacific Rise. This rifting/spreading center thus lies between the Pacific and North American tectonic plates. Cartographers generally recognize the region, from north to south, as the Coachella, Imperial, and Mexicali Valleys, as well as the floodplain of the Colorado River that abuts the Upper Gulf of California. Sediments in the Salton Trough have accumulated atop a Paleozoic basement of limestone, sandstone, conglomerate, and metamorphic rocks (Gastil et al. 1992, Delgado-Granados et al. 1994, Nations and Gauna 1998, Fletcher and Munguía 2000, Johnson et al. 2003, Bialas and Buck 2009). The sediment-basement interface is irregular and occurs at depths from 1.4 to 5.6 km (Anderson et al. 2003, Lovely et al. 2006, Crowell et al. 2013, Pacheco et al. 2006). Historically, large-scale flood events on the Colorado River served to recharge the aquifer of this large contiguous hydrologic basin.

Although the Colorado River Delta includes the Salton Basin, much of the recently published hydrological research focuses only on the southern portion of the basin, from the U.S.-Mexico border south to the Upper Gulf of California—that part of the delta lying within the Mexicali Valley (e.g., Olmsted et al. 1973, Feirstein et al. 2008). Some recent workers have even constrained the "delta," for working purposes, to the area of the Colorado River between the constructed levees, plus the various wetlands—about 600 km^2 (Luecke et al. 1999, Cohen et al. 2001). The larger of these wetlands today are the Río Hardy and El Doctor wetlands, the Ciénega de Santa Clara, and Ciénega El Indio. The 36 km-stretch of the Colorado River from the Morelos Dam (at the California-Baja California border) to San Luis Río Colorado (at the Arizona-Sonora border) is considered as the uppermost extent of today's remnant Colorado River Delta in Mexico and has been called the limitrophe reach (Cohen et al. 2001, Cohen 2013). Since the 1980s, the Colorado River channel has been bordered by high, engineered levees that prevent surface water from reaching most of the riverbed (and vice versa).

The delta region from the U.S.-Mexico border to the Upper Gulf lies in the Lower Colorado River Valley subdivision of the Sonoran Desert, which is one of the hottest and driest ecologically-defined areas in North America. Zamora-Arroyo et al. (2013) stated that precipitation on the delta averaged about 65 mm yr^{-1}, whereas Cohen et al. (2001) reported it as

54 mm yr^{-1} based on IBWC data for the years 1992-1998. Thompson (1968) and Ezcurra and Rodríguez (1986) reported average annual precipitation across the delta region as 68 mm, with evaporation rates up to 250 cm yr^{-1}. Not only is it the driest part of the Sonoran Desert, it experiences significant spatial variability in precipitation; long-term annual precipitation means from El Centro (California) average around 12.7 mm (1956-1998), from Mexicali (Baja California) average 160 mm (1973-1991), and from Yuma Valley average 11.6 mm (1987-1998) (Feirstein et al. 2008). Felger (2000) reported annual precipitation means of 55.3 mm at San Luis Río Colorado (1927-1967) and 40.2 mm at Riito (1950-1967), based on data from Hastings (1964) and Hastings and Humphrey (1969).

An understanding of the Colorado River Delta's overall water budget has only just begun to come into focus. Across the entire delta (on both sides of the international border), agriculture is the single largest water user, consuming nearly 50% of total river inflow, whereas natural vegetation uses about 10% of the total inflow. Urban water use accounts for about 2% of total regional water consumption, most of this being met with groundwater pumping (Cohen and Henges-Jeck 2001). However, evapotranspiration (from cropland and open-water delivery canals) accounts for the single largest consumptive use of water in the delta, removing nearly half of the total inflows during non-flood years (Cohen and Henges-Jeck 2001). Recharge associated with agriculture is the primary source of recharge to the aquifer today (Cohen and Henges-Jeck 2001). Cohen (2013) used monitoring-well data to plot water table depth along the limitrophe stretch between Morelos Dam and the Southerly International Boundary (SIB). He found that over the past 70 years the water table dropped 12 m near the SIB, and about 3 m near Morelos Dam. Depth and variability of the water table varies greatly along the limitrophe, tending to drop more quickly in response to lack of surface flow the farther downstream the measurements are taken.

Carrillo-Guerrero et al. (2013) calculated a water budget for the delta south of the border that estimated a total surface water input of 2985 million m^3 yr^{-1} combined Colorado River flow past Morelos Dam, plus rainfall (based on data from April 2004 to April 2005). The U.S. has been compliant in meeting its annual water allotment delivery to Mexico of 1.85×10^9 m^3. However, the water delivered is generally of too low quality for urban use and often too high salinity for agricultural use. In non-flood years, about 90% of the Colorado River water entering Mexico is diverted as soon as it crosses the border, at Morelos Dam, into the Canal Reforma and Canal Alamo where it is distributed via approximately 1,662 km of irrigation canals to border-region agriculture (Cohen and Henges-Jeck 2001, Cohen 2005, Feirstein et al. 2008, Carrillo-Guerrero et al. 2013).

In addition to water from the Colorado River allotment, over 700 federal and private wells in the Mexicali Valley pump subterranean water for urban and agricultural use. During non-flood years, water from wells pumping the Mexicali-San Luis Río Colorado aquifer is used to meet agricultural demands and reduce salinity levels of the water entering from the U.S. The Mexicali agricultural valley (Federal Irrigation District 014-Río Colorado) has over 200,000 ha of irrigated fields (Nagler et al. 2007, Carrillo-Guerrrero et al. 2013). The main crops are wheat, alfalfa, and cotton that, together, occupy 74% of the cultivated area and use 71% of the water available in the district (Carrillo-Guerrero et al. 2013). At least a quarter of the water delivered for agricultural use is lost from the irrigation canals alone, due to evaporation and ground seepage (Carrillo-Guerrero et al. 2013, based on CONAGUA estimates). Alfalfa is the region’s most water-intensive crop, with a very high evapotranspiration rate (Erie et al. 1982, Jensen 1995).

Carrillo-Guerrero et al. (2013) estimated evapotranspiration rates from agricultural fields and freshwater/marsh wetlands in the region. They concluded that in non-flood years about 90% of the water diverted into agriculture fields in the Mexicali Valley is lost due to evapotranspiration alone (about 1.9×10^9 m^3 yr^{-1}, based on data for the 12-month period April 2004-April 2005). This is roughly the same amount of water guaranteed by the U.S.-Mexico Colorado River water treaty, and thus the amount of surface water that typically crosses into Mexico during non-flood years. However, the calculations of Carrillo-Guerrero et al. (2013) do not include water lost by way of crop and other vegetation biomass production, nor loss of water to the system by pumping it entirely out of the Mexicali Valley (e.g., water supplies to Tecate, Tijuana, etc.).

Carrillo-Guerrero et al. (2013) note that seepage losses from irrigation canals contribute to formation of a high, non-saline aquifer that supports trees along the Colorado River's riparian corridor because subsurface seepage losses drain toward the river channel as underflow. And they estimate that about 10% of the inflows to the Mexicali Valley end up being used by "natural ecosystems" (e.g., riparian habitats on the delta). Also, the half-dozen or so riparian (fresh and brackish water) marshes of the Colorado River Delta are maintained almost entirely by agricultural return flows from Mexico and the U.S. For example, in the west, the Río Hardy marshes are sustained by brackish agricultural flows from the Mexicali Valley Irrigation District that discharge into the Río Hardy channel. In the east, Ciénega de Santa Clara, the largest brackish marsh in the Sonoran Desert, is sustained primarily by brackish water pumped from the Wellton-Mohawk Irrigation and Drainage District in the U.S. and sent for disposal in Mexico via the Main Outlet Drain Extension (MODE) canal, which supplies 95% of the ciénega's water, with most of the remainder being supplied by the Riito-Santa Clara drain that transports surface irrigation runoff from the agricultural fields of the San Luis Río Colorado Valley in Sonora (Mexicano et al. 2013, García-Hernández et al. 2013a).

Orozco-Durán et al. (2015) also used Mexican National Water Commission (CONAGUA) data to assess water balance across the delta. Those data estimated that 755×10^6 m^3 of ground water (including rain infiltration) moves across the border annually from the Lower Colorado River Basin (CONAGUA 2006, 2007, 2010; Orozco-Durán et al. 2015; W. Daesslé, pers. comm. 2015). Combined with the Carrillo-Guerrero et al. (2013) estimates of surface water (Colorado River + rainfall, see above), this yields a total freshwater influx to the delta of about 3.74×10^9 m^3 yr^{-1}. In the Mexicali Valley Basin, wells pump groundwater to the surface for use in urban centers as far away as Tecate and Tijuana, and for agricultural and industrial use. Water used outside the delta area (e.g., Tijuana and Tecate) is lost to the regional system and removed from the delta's water budget, as is water lost by evapotranspiration and in agricultural and wetland biomass production. Water used within the basin is partly recycled as it sinks back down to the water table from unlined agricultural and industrial canals, wastewater discharge, septic systems, etc. The amount of water that is removed from the system, by being exported outside the Mexicali Valley, by agricultural biomass production, and by evapotranspiration is very high. The National Water Commission estimated that less than 35×10^6 m^3 yr^{-1} (4.6%) finds its way to the Upper Gulf, through a mix of subterranean and surface flow, the latter mainly being via the Río Hardy drainage and Ciénega de Santa Clara seepage. To put this estimate in context, this is about 2% of the 1.85×10^9 m^3 (1.5 million acre-feet) of river water annually allotted to Mexico by the water treaty. (To further put this in context, California alone uses 4.0-5.5 million acre-feet of water annually just to grow alfalfa [University of California 2016].)

The delta's aquifer is known to have high storage capacity and subterranean water moves very slowly toward the Gulf. However, the 35×10^6 m^3 yr^{-1} estimate may be too high, as some of this estimated discharge probably does not actually reach the marine environment, but is captured and impounded in freshwater artesian springs (*pozas*) along the southernmost Cerro Prieto fault, such as El Doctor wetlands near the town of El Golfo de Santa Clara, and the numerous *pozas* of coastal Bahía Adair, where it supports small refugial Colorado River Delta riparian wetland habitats.

Zamora et al. (2013) estimated that, today, less than 1% of the Colorado River's water reaches the Gulf, noting that the river's relict lowermost channel is plugged by sediment that accumulates during flood tides. Ebb tidal flows are not strong enough to keep the channel open, and weak-flowing (or no) river water cannot maintain it. During spring tide cycles, when no channel blockage was present, tidal flows could reach about 65 km upriver from Montague Island near the river's mouth due to the slight topographic gradient (about 16 cm/km) (Thompson 1968, Payne et al. 1992, Nelson et al. 2013a,b). However, without adequate river flow these penetrating tidal currents result in bedload transport from the Gulf into the lower channel which builds an obstructive, recurring tidal sand bar across the river bed about 25-30 km upstream from Montague Island (about half-way to the junction of the Río Hardy). The sand bar apparently develops when river flow is greatly reduced or absent, and is re-opened only when sporadic high-river flows occur. Anecdotal reports of a sand bar obstruction in the lower river channel appeared as early as the late 1950s (Kira 2000), but the first official report was in 1972, when Mexico's Secretaría de Agricultura y Recursos Hidráulicos (SARH) reported it 23 km above Montague Island (U.S. Army Corps of Engineers 1982). The sand bar was noted in LANDSAT satellite images by Nelson et al. (2013a,b) as early as 1972, and by Zamora et al. (2013) beginning after the year 2000, and by 2009 Zamora et al. (2013) estimated the up-channel tidal flow topped the sand bar only 12 days per year. Nelson et al. (2012a) also recorded the presence of the sand bar in 2011 using pressure-based logger data in the river channel.

Zamora et al. (2013) reasoned that the sand bar began accumulating after Glen Canyon Dam began operations in 1964, which is likely when tidal processes became dominant over fluvial processes in the lowermost river channel. During some of the unusually wet years of the 1980s and 1990s, when excess river flows were delivered to Mexico, the sand bar was apparently, at least periodically, scoured open. Payne et al. (1992) reported that the sand bar was washed away by the large 1984-1988 floodwater releases down the channel of the Colorado River. All (2006) argued that most of this discharge ended up in Laguna Salada where it was lost to evaporation, with little of it reaching the Gulf. On-site observations of the river mouth by S. M. Nelson showed that at least some fresh water reached the sea in 1984, 1993, and 1997 (Nelson et al. 2013a,b), but the actual amount is unknown. Analysis of LANDSAT satellite images from late 1979 through 1985 indicated that the sand bar impounded flood waters during the unusually wet years of the early 1980s, resulting in flooding that connected the river channel to the Ciénega de Santa Clara at least twice (Nelson et al. 2013a). Nelson (2007) noted that the presence of the sand bar resulted in back-flooding of most of the delta during the late 1983-early 1984 El Niño (see Figure 3a), but by November 1984 the floods had finally opened a channel through the sand bar to allow the remaining (unevaporated) water to reach the sea. Connectivity between the river and Ciénega de Santa Clara ended when the river cut a new channel through the sand bar in late 1984 (Nelson et al. 2013b). Flood releases during the 1990s kept the river channel open, but a new tidal sand bar formed after 2000, when river flow again fell (Nelson et al. 2013b, Zamora et al. 2013). Nelson et al. (2013a) noted the sand bar could be seen re-forming itself in 2006 LANDSAT images, at approximately the same location as the pre-1983 bar, and by 2008 it was high enough to cross over in a two-wheel drive vehicle during neap tide periods. However, Zamora et al. (2013) felt that spring tidal bores might have been able to top the sand bar several times a year even since 2000.

The groundwater flow and surface seepage that does reach the Upper Gulf has the potential to contribute some dissolved nitrates and silicates to the sea. However, most nitrates in surface and ground waters in the Mexicali Valley are derived from agriculture drains and sewage waste, and these might enter the Gulf primarily by surface seepage via the Ciénega de Santa Clara wetland. Their potential average annual contribution (via the ciénega) has been estimated at 59,400 kg N-NO_3 (Orozco-Durán et al. 2015). Running southeast from Ciénega de Santa Clara is the so-called Santa Clara Slough—a roughly 26,000-ha basin subject to periodic inundation from the Northern Gulf’s high-amplitude spring tides, which historically reached the margin of the ciénega several times each year (Nelson et al. 2013a). The slough receives brackish water inflow from the ciénega, especially during winter months when delivery of agricultural wastewater increases and evapotranspiration decreases (Glenn et al. 2013a,b, Greenberg and Schlatter 2012). During summer months, wastewater inflow to the ciénega is reduced and evapotranspiration rates reach their highest levels of the year, thus little or no water passes through to the slough (Greenberg and Schlatter 2012, Glenn et al. 2013a,b). And, throughout the year, water exits the slough primarily through evaporation (Glenn et al. 2013a,b, Nelson et al. 2013a).

Silicates reaching the Upper Gulf, mostly in surface flow/seepage, are probably the result of ground water associated with geothermal sources in the region, and these may be a nutrient source for the large diatom populations of the Northern Gulf (which require silica to make their shells). Silica-rich brines from the delta's Cerro Prieto geothermal power station, for example, have an average value of 69.2 mg L^{-1} Si-SiO_2 (Orozco-Durán et al. 2015). Phosphates, however, are mostly transformed into a particle phase and precipitated out in sediments before reaching the Gulf, a process occurring at every dam the Colorado River encounters as phosphorous becomes trapped in reservoir sediments (Stevens et al. 1995, Stromberg and Chew 2002).

Agricultural return-flows to the Colorado River channel in Mexico also carry high levels of fertilizers and insecticides. For example, during the 1990-91 crop cycle, at least 70,000 tons of fertilizers and 400,000 liters of insecticides were used in the Mexicali Valley (Daesslé et al. 2009, based on DGE 1993). This has increased the organic and inorganic compounds in the upper delta region (visible in Figure 2 as the bright green of agricultural fields), including mercury, copper, arsenic, DDT, DDE, and DDD, in both surface and ground waters (García-Hernández et al. 2013b, Lugo-Ibarra et al. 2011, Daesslé et al. 2009).

Laguna Salada Basin (also known as Laguna Macuata, in the Pattie Basin, in the early 20th century) is situated in a fault depression between the massive Sierra de Juárez (of Baja California) on the west, and the 90 km-long Sierra Cucapá-Sierra El Mayor range on the east, the latter being fault-bounded ranges reaching ~1000 m in elevation (Figure 2). Laguna Salada Basin is a tectonically active pull-apart basin (described by some geologists as a western subbasin of the Mexicali Valley), a graben (or half-graben) formed by the Laguna Salada Fault on the east (part of the Pacific-North American Plate boundary system, and a probable southern continuation of the Elsinore Fault in southern California), and the Sierra Juárez Fault on the west

(Mueller and Rockwell 1995, Martín-Barajas et al. 2001, Fletcher and Spelz 2009, Alles 2011, Nelson et al. 2012). Hot artesian springs were reported from the western slopes of the Sierra Cucapá by Sykes (1937) and also appeared on his 1907 map of the region. The location of the Laguna Salada Fault itself is easily recognized by surface features, such as fault scarps, faulted alluvial fans, and freshly exposed bedrock. Visible, young alluvial deposits were probably displaced during the large regional earthquakes of 1892, 2008 and 2010, and the basin itself is filled 4-6 km deep with alluvial deposits (Martín-Barajas et al. 2001).

Like the Salton Basin, the Laguna Salada Basin has land surface elevations that lie below sea level, and the basin is lower in elevation than the Río Hardy channel at the southern tip of the Sierra El Mayor (Sykes 1937). In April 2016, we measured a low point in the upper part of the basin (~32°32'N, 115°42'W) using a hand-held GPS altimeter (calibrated 14 hours prior at sea level) at 11 m below mean sea level. Laguna Salada is a closed freshwater sink and evaporative basin, as is the Salton Sea. The northern boundary of the laguna is today effectively set by the high berm that supports Mexico's Federal Highway No. 2, which runs east-west through a pass in the northernmost Sierra Cucapá.

Compeán-Jimenez et al. (ca. 1981) estimated that Laguna Salada had the potential to lose 13,968 m^3 of water per hectare annually through evaporation, but this is probably a significant under-estimation given that they calculated the surface area at only 400 km^2 (less than half the potential areal coverage when the laguna is filled) and with a volume of just 730,106 m^3 (also probably a significant under-estimate).

The great depth of alluvial deposits in Laguna Salada clearly indicates that it has served as a flood-drainage basin for the Colorado River for millennia, and historically, during flood years, water also drained from the mainstem of the Colorado River (below the confluence with the Río Hardy) into the laguna, by way of the topographic low between the southern tip of the Sierra Cucapá-Sierra El Mayor range, and the northern tip (*El Promontorio*) of the Sierra de las Pintas (Sykes 1937, Mueller and Rockwell 1995, Cohen and Henges-Jeck 2001). Sykes (1937) described flood flows filling Laguna Salada numerous times during his field studies, between 1910 and 1932. In the late 19th century it supported a valuable subsistence fishery for the indigenous Cucapá People (when it was called Laguna Maquata). However, construction of Hoover and Glen Canyon Dams cut off the lake's freshwater inflow (the Colorado River) and that fishery was destroyed as the lake dried. Laguna Salada had a resurgence in the late 1970s and early 1980s, during flood years, but those surface waters quickly evaporated (Álvarez de Williams 2007, Brusca 2007). Nelson et al. (2013a) suggested that flow into Laguna Salada may have largely ceased in 1986. However, large precipitation events in the Southwest could lead to it refilling in the future.

The size of the laguna is highly variable, ranging from completely dry to nearly 1000 km^2 in area of surface water. The Laguna Salada Basin itself exceeds 90 km in length, paralleling the western flanks of the Sierra Cucapá-Sierra El Mayor range (Figures 2 and 3; also see Figure 1.1 in Cohen and Henges-Jeck 2001 and the 1937 Sykes' map). Compeán-Jiménez et al. (ca. 1981) cited the laguna as approximately 400 km^2. However, All (2006) reported it at ~1000 km^2, various Arizona Geological Society maps show it at just over 1000 km^2, Mueller and Rockwell's (1995) map shows it at ~800 km^2, Mexico's official INEGI map (Instituto Nacional de Estadística, Geografía e Informática, 1993) shows it at over 800 km^2, Sykes (1937) measured the basin at 1,280 km^2, and the cartography of the American Automobile Association map depicts it at around 950 km^2. GIS maps of the delta show the "bathtub ring" area of Laguna Salada to be 990 km^2 in size, which is the same as the LANDSAT image of the filled laguna in 1984 (Figure

3a), although the total amount of flood water trapped on the delta in June 1984 was approximately 2500 km^2. The high-water line of Laguna Salada is also easily recognized in Google Earth satellite images, and the calculated size of this area (using a polygon algorithm provided in Google Earth) is just under 1000 km^2. The entryway to the basin, which can be breached by heavy river flows (especially when combined with high spring tidal flows up the river channel), is south of the Sierra Cucapá-Sierra El Mayor range, as shown in Cohen and Henges-Jeck (2001, p. 3), Sykes (1937), Mexico's INEGI maps, and satellite imagery (Figure 3). The prominent "thumb" at the southern end of the Laguna Salada Basin, demarcated by the northern point, or *Promontorio*, of the Sierra de las Pintas, is evident in Sykes's 1937 map and in satellite images (Figure 3).

Using NASA images over a span of nearly two decades, All (2007) showed the extreme ebbs and flows of water into Laguna Salada and that during the 1980s flood years (at least the first half of the decade) about 1000 km^2 were inundated. In fact, what matters is not the amount of water in the basin at any given time (such as the Compeán-Jiménez et al. "snapshot in time"), but the capacity of the basin itself, which is approximately 1000 km^2.

Laguna Salada can also form as a small lake during summer monsoon rains, but it is often completely dry. However, even when Laguna Salada appears "dry" it commonly is not, because of its high capacity to store interstitial water in the deep, silty, alluvial sediments extending beneath its surface, and this water bank can be covered by a 2.5 to 7.5-cm-thick cap of crystalized salt. As with All (2007) and Álvarez de Williams (2007), we have had our 4-wheel-drive vehicles stuck more than once attempting to drive across what appeared to be a dry lake bed that actually had a thick layer of water-saturated mud just below the crystallized salt surface.

Evidence of Laguna Salada flooding also comes from records of the brackish-water barnacle *Amphibalanus subalbidus* (formerly *Balanus subalbidus*). This West Atlantic-native barnacle can live in nearly freshwater salinities (Poirrier and Patridge 1979) and seems to have found its way into the Colorado River Delta in the wet years of the 1980s. In 1989, A. Boetzius found specimens of *A. subalbidus* in a dry portion of Laguna Salada Basin, and, in the same year, barnacle specialist R. Van Syoc found living specimens in a flooded part of the laguna (Van Syoc 1992). In 1989 Álvarez de Williams (2007) found dead shells in Laguna Salada, in 1990 Van Syoc found dead shells in the Río Hardy, and in 1991 R. Brusca found dead shells in a dry peripheral area of Laguna Salada; the latter specimens had been growing in profusion at a height of 1.5 m on dead shrubs in the westernmost part of the basin (Brusca 2007). In 2002, barnacle specialist W. Newman found living *A. subalbidus* on the delta again, but this time in agriculture canals at New River and Colonia Zacatecas, suggesting that there had been an exchange of water between there and Laguna Salada, possibly during the huge 1983-1984 flood that inundated the delta (Newman, pers. comm.). *Amphibalanus subalbidus* is native to the Gulf of Mexico and has never been reported from the Gulf of California (or anywhere else in the East Pacific) in modern times. This barnacle is well known from estuarine habitats in the Gulf of Mexico (Poirrier and Partridge 1979). Van Syoc (1992) concluded that the modern-day *A. subalbidus* is the same species as the fossil barnacle, *Balanus canabus* Zullo and Buising, 1989, described from the Bouse Formation of the lower Colorado River area of Arizona and California, and Van Syoc (1992) relegated the latter species to a junior synonym of *A. subalbidus*. This last discovery suggests that this now-West Atlantic species once lived in the Colorado River Delta, but then went locally extinct, only to be reintroduced in recent times. Dead specimens of *A. subalbidus* can be found embedded in the sediments throughout the laguna today (Figure 5).

The topographical gradient of the Colorado River in the lower delta region is so slight (about 16 cm/km; Thompson 1968) that the river loses its firm channel and becomes a meandering network of small streams, oxbows, sloughs, and backwaters. The expanse of the delta between the southern end of the Laguna Salada Basin (on the west) and the Ciénega de Santa Clara wetland (on the east) is low-lying mudflat that can become inundated by brackish water during now-rare flood events of the Colorado River, and much of it can also become saturated with seawater during the highest spring tides in the Upper Gulf. Today, this lowermost delta region is fundamentally marine in nature, not riparian. Much of it is vegetatively dominated by the endemic marine grass *Distichlis palmeri* (Felger 2000). In fact, the final 19 km of the Colorado River has been viewed as part of the Upper Gulf's intertidal zone (Cohen et al. 2001). Because flood flows down the Colorado River channel in this lowermost delta region are not naturally well channelized, water thinly spreads out over the entire area.

Responding to a long history of flooding on the delta (and loss of homes and agricultural land), the Mexican government channelized much of the region, diverting most of the lowermost delta water flow directly into the Laguna Salada Basin. In 1974, a 3 m-deep canal was constructed to move floodwaters from the Colorado River and lowermost delta (Irrigation District No. 14) into the basin. The government also excavated the Canal Alimentador (Feeder Canal), near the Cerro Prieto geothermal power generating plant just east of the Sierra Cucapá, that moved floodwaters from the west-central Mexicali Valley to Laguna Salada. The 1983-84 floods washed out a large, natural earthen berm along the Río Hardy channel, which had acted to keep water in the channel, and thus flowing to the delta wetlands. After this event, however, overflows were diverted into the Laguna Salada Basin via the Laguna Salada Canal.

The 24 km-long Río Hardy (a former channel and now tributary of the Colorado River) collects water from the eastern watershed of the Sierra Cucapá-Sierra El Mayor range, as well as flood, agricultural, and various waste waters from the western Mexicali Valley. With declines in precipitation over the past 25 years, most of the Río Hardy flow is now from agricultural drainage, wastewater of the Cerro Prieto geothermal wells (which began operating in 1973), and wastewater from the Arenitas secondary sewage treatment plant (that flows through the small Las Arenitas wetland, recently created by local conservation groups in collaboration with the state government to help biologically treat the outflow from the plant). The Río Hardy water is thus of poor quality; it is high in total salts and may contain pesticide residues, heavy metals, selenium, and nitrates from fertilizers. During most high-flow events from 1983 to 1985, water apparently flowed from the Río Hardy more or less directly into Laguna Salada. However, Nelson et al. (2013a,b) also documented at least some of the flood flow in the river channel all the way to the Gulf in 1984, 1993 and 1997, so not all of the delta's water was impounded in the laguna.

The government report by Compeán-Jimenez et al. (ca. 1981) found *Tamarix ramosissima* (tamarisk, salt cedar) and *Typha latifolia* (cattail) to be the dominant macrophyte vegetation at Laguna Salada. The study also found 11 species of freshwater fishes and 2 species of crustaceans—none indigenous to the Colorado River south of the U.S.-Mexico border, and all introduced from California and Arizona, probably via the flood flows that crossed the international border. In addition, some marine euryhaline species immigrated into the laguna from the Sea of Cortez—striped mullet (*Mugil cephalus*), machete (*Elops affinis*), small squids, etc. In the past, high spring tides in the Upper Gulf occasionally reached the laguna, periodically introducing marine species of fishes and invertebrates. This largely ended with construction of

Mexico's Federal Highway No. 5, running south to San Felipe. Although the floodwater connection of Laguna Salada to the Sea of Cortez may have largely been closed in the early 1980s, the euryhaline striped mullet was apparently able to spawn and recruit in brackish water and individuals have been sporadically reported from irrigation waters of the Mexicali Valley ever since at least 1967. It has been suggested that the floods of the 1983-84 El Niño might have destroyed most of the diversion canals leading to Laguna Salada, but the extent and impact of this is unclear, as is any channeling that might have been repaired or rebuilt since that event.

The major impact of all these sinks and natural and man-made diversions in the delta, that redirect surface-water flood flows in the Colorado River channel, has been to prevent river water from directly reaching the Gulf of California. As a result, since the mid-1970s only during the flood years of 1978, 1982-1988, 1993, and 1997-1999 is it likely that any significant Colorado River surface water could have reached the Upper Gulf (seepage out of Ciénega de Santa Clara aside). The amount that actually reached the Gulf during those flood years remains a hotly debated topic.

5. CONCLUSIONS AND FUTURE RESEARCH DIRECTIONS

Our review of published research and our personal observations indicate that the Northern Gulf of California is, historically and currently, one of the most biologically productive marine regions on Earth. This high productivity is driven by a unique mix of factors, including: coastal upwelling, wind-driven mixing, extreme tidal mixing and turbulence, thermohaline circulation that moves intermediate waters into the mixed layer, coastal-trapped waves, regular sediment resuspension, and (to a lesser extent) agricultural runoff and perhaps input from decomposing tidal-flat plant debris, and released nutrients from erosion of ancient Colorado River Delta sediments. Suggestions that decreased Colorado River flow due to upstream anthropogenic water impoundments and diversions has had a negative impact on the health of the Northern Gulf of California ecosystem, particularly by reducing primary productivity and/or stock production of finfish and shellfish, appear to be ill-founded. There is no evidence that surface flow from the Colorado River is now, nor has ever been an important driver of primary productivity in the Northern Gulf, and there is only equivocal or disputable evidence to support the claim that reduced river flow has impacted secondary (finfish) production in that region. Two tests of the river flow-productivity hypothesis made by tracking nutrients and phytoplankton production over time periods that included high, low, and zero river inflow, found no correlation. In fact, both studies found that decreased nutrients and primary productivity were associated with high freshwater flows into the Upper Gulf. Aside from impacts of historical and current fisheries activities, the marine ecosystem of the Northern Gulf remains healthy, rich in nutrients, and high in biodiversity and productivity. Primary productivity and human extraction of shrimp, Gulf corvina, totoaba (largely illegally), and other marine resources, remain very high in this region. The ecosystem is historically adapted to widely fluctuating Colorado River flows and elevated salinities. There also is no evidence that reduced Colorado River flow has negatively impacted the health of the critically endangered vaquita porpoise, and assertions that it has done so deflect attention from the actual cause of decline—high levels of bycatch in legal and illegal gillnet fisheries. Climate change models (and actual data trends) suggest there will be even less Colorado River water reaching the Gulf of California in the foreseeable future, and that the delta will be gradually inundated by Upper Gulf waters as sea levels continue to rise. However, productivity should remain high and fisheries can be sustained if they are properly managed.

Future research should focus on the potential effects of climate change on the Northern Gulf ecosystem and, importantly, on the potential rate of marine transgression across the Colorado River Delta as sea levels continue to rise. More information is also needed on the possible negative impact of freshwater inflow from the Colorado River on productivity in the Northern Gulf. Future studies of river-flow impact on the Upper Gulf should include ground-truth surface salinity measurements in the study area, to determine how much, if any, Colorado River water is actually reaching the Upper Gulf.

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FIGURE CAPTIONS

Figure 1. The Gulf of California, showing geographic place names mentioned in the text.

Figure 2. GIS-based map of the Northern Gulf of California and Colorado River Delta. The Laguna Salada Basin covers approximately 990 km^2.

Figure 3. LANDSAT images of the Colorado River Delta, showing Laguna Salada Basin filled (1984) and empty (1990). (A) The 1983-84 El Niño event led to excess water releases into the Colorado River channel through Morelos Dam, filling the Laguna Salada Basin and connecting it to Ciénega de Santa Clara when most of the delta flooded from April to June. This June 1984 composite image of the Colorado River Delta, based on Landsat Thematic Mapper (sensor 5), shows Laguna Salada covering approximately 990 km^2, and a total flooded area of the delta covering 2,500 km^2. Dark blue and black represent standing surface water (data ground-truthed). For scale, the Sierra Cucapá-Sierra El Mayor range is approximately 90 km long. (B) After several years without flooding rains or excess water releases through Morelos Dam, Laguna Salada is reduced to a very small size (1990 image). LANDSAT images courtesy of Alejandro Hinojosa-Corona (CICESE, Ensenada, México).

Figure 4. Type specimens of *Mulinia modesta* (senior synonym of *M. coloradoensis*) from Guaymas, Sonora, Mexico (Smithsonian Institution). Photo courtesy Paul Valentich-Scott (Santa Barbara Natural History Museum, California).

Figure 5. Dried shells of the barnacle *Amphibalanus subalbidus* in situ in Laguna Salada (2016). *A. subalbidus* is an Atlantic species likely introduced to Colorado River Delta brackish-water wetlands in the 1980s.

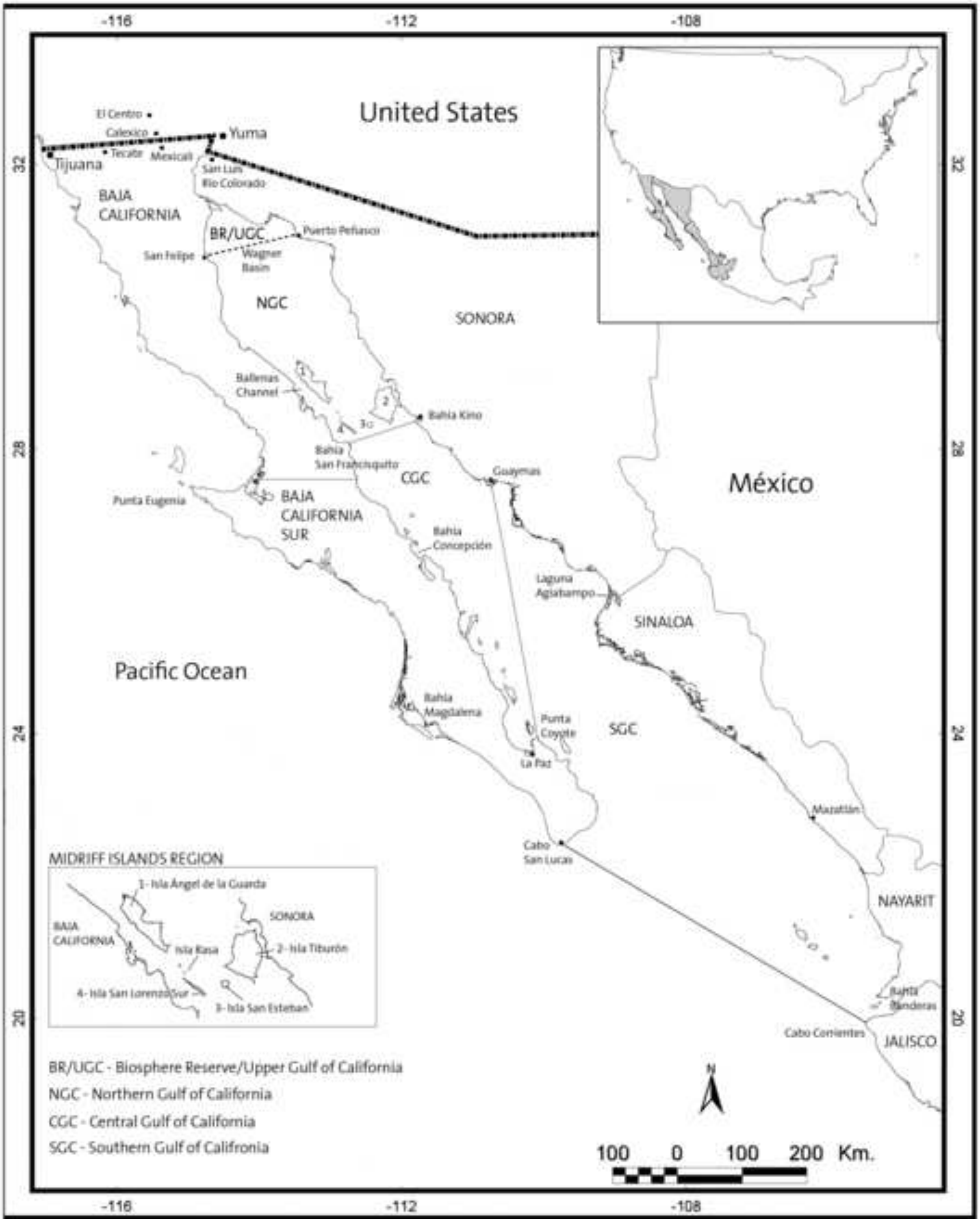
TABLE CAPTION

Table 1. Ranges of surface salinity (S), nutrients (NO_3, PO_4), and chlorophyll *a* (Chl) concentration values in the Upper Gulf. Values are from water samples and CTD measurements. Nutrients are in µM and Chl is in mg m^{-3}. 1993 was a “wet” year, 1973 and 1996 were “dry” Colorado River flow years. Salinity data for March 1973 are from Álvarez-Borrego et al. (1975), and from Lavín and Sánchez (1999) for April 1993. Nutrients and Chl data from April 1993 and April 1996 are from Nieto-García (1998). WUG, Western Upper Gulf. CUG, Central Upper Gulf. EUG, Eastern Upper Gulf.

Table 1. Ranges of surface salinity (S), nutrients (NO_3, PO_4), and chlorophyll *a* (Chl) concentration values in the Upper Gulf. Values are from water samples and CTD measurements. Nutrients are in μM and Chl is in mg m^{-3}. 1993 was a “wet” year, 1973 and 1996 were “dry” Colorado River flow years. Salinity data for March 1973 are from Álvarez-Borrego et al. (1975), data for April 1993 from Lavín and Sánchez (1999), and data for April 1996 from Nieto-García (1998). Nutrients and Chl data from April 1993 and April 1996 are from Nieto-García (1998). WUG, Western Upper Gulf. CUG, Central Upper Gulf. EUG, Eastern Upper Gulf.

	Years	S (‰)	NO_3	PO_4	Chl
WUG	1993 (wet)	32.0 - 35.4	0.1 - 0.3	0.3 – 0.7	0.5 – 1.5
	1973 (dry)	36.2 - 36.4			
	1996 (dry)	36.0 – 37.0	0.5 – 1.0	1.0 – 2.0	0.5 – 1.5
CUG	1993 (wet)	32.2 - 35.4	0.1 – 0.7	0.2 – 0.6	0.5 – 1.5
	1973 (dry)	36.0 - 36.1			
	1996 (dry)	35.8 – 36.4	0.5 – 1.0	1.0 – 2.0	0.5 – 1.5
EUG	1993 (wet)	34.6 - 35.4	0.3 – 0.5	0.6 – 0.7	0.5 – 4.5
	1973 (dry)	35.7 – 36.2			
	1996 (dry)	35.8 – 36.2	0.1 – 0.5	1.0 – 2.0	0.5 – 1.0

Figure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2- Isla Tiburón
4- Isla San Lorenzo Sur
3- Isla San Esteban
BR/UGC - Biosphere Reserve/Upper Gulf of California
NGC - Northern Gulf of California
CGC - Central Gulf of California
SGC - Southern Gulf of Califronia
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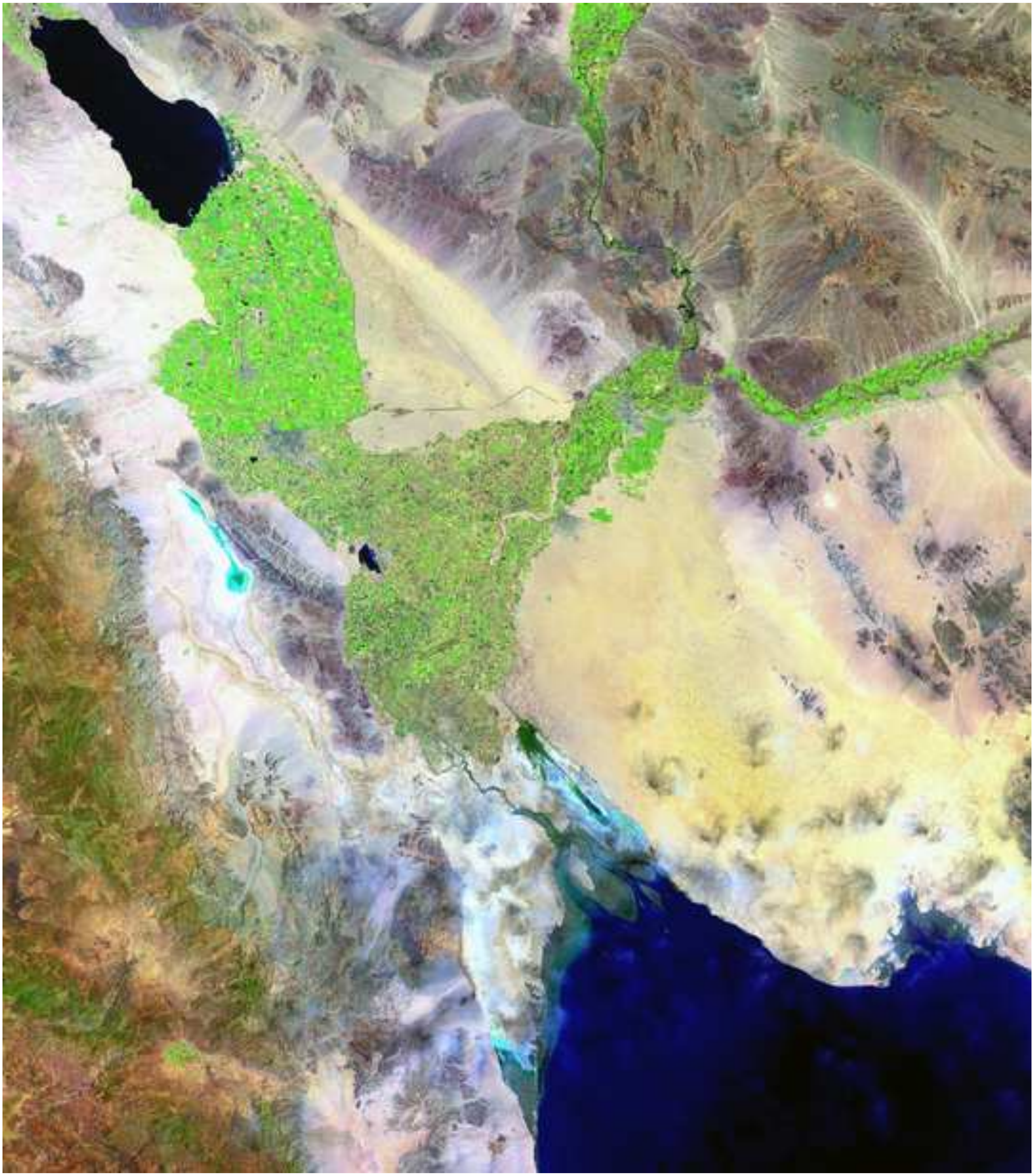

Figure


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