
Effects of Upstream Diversion of Colorado River Water on the Estuarine Bivalve Mollusc *Mulinia coloradoensis*

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Abstract: *The Colorado River of the United States and Mexico is extensively dammed and diverted; only a fraction of its previous flow still reaches its estuary. How has the lack of freshwater inflow affected the estuary's biota? Because no prediversion studies are available for comparison, we examined the composition and geochemistry of subfossil shells dating from before the Colorado's diversion. The bivalve mollusc *Mulinia coloradoensis* was once the most abundant species of clam inhabiting the Colorado Delta. Today, however, only a small population survives near the mouth of the river. The relative abundance of empty shells of this species decreases with increasing distance from the mouth of the Colorado River, indicating that *M. coloradoensis* was dependent on the flow of the river. The $\delta^{18}\text{O}$ values in shells of subfossil *M. coloradoensis* are significantly more negative than $\delta^{18}\text{O}$ values in live-collected shells of *Chione fluctifraga*, the most common bivalve living on the delta today. This indicates that *M. coloradoensis* lived in water lower in salinity than is now typical of the delta. The decline in abundance of *M. coloradoensis* is most likely due to the post-1930 decrease in flow of Colorado River water to its estuary. Paleontological and geochemical analyses of subfossils can provide environmental baselines for communities that existed prior to human alteration of the habitat.*

Efectos de la Desviación de las Aguas del Río Colorado en los Moluscos Estuarinos Bivalvos *Mulinia coloradoensis*

Resumen: *El río Colorado de los Estados Unidos y México esta represado extensivamente y desviado, y solo una fracción de su flujo previo alcanza el estuario. ¿De qué manera ha sido afectada la biota del estuario por esta falta de aporte de agua dulce? Debido a la carencia de estudios previos a la desviación para realizar comparaciones, examinamos la composición y geoquímica de conchas sub-fósiles que datan de fechas anteriores al desvío del río Colorado. El molusco bivalvo *Mulinia coloradoensis* fue alguna vez una de las especies de almejas más abundantes del delta del Colorado. Sin embargo, a la fecha, solo una pequeña población sobrevive cerca de la boca del río. La abundancia relativa de conchas vacías de esta especie disminuye con un incremento de la distancia a la boca del río, indicando que *M. coloradoensis* dependía del flujo del río. Los valores de $\delta^{18}\text{O}$ en conchas de sub-fósiles de *M. coloradoensis* son significativamente más negativos que los valores de $\delta^{18}\text{O}$ de conchas vivas colectadas de *Chione fluctifraga*, el bivalvo más común que habita el delta en la actualidad. Esto indica que *M. coloradoensis* vivió en aguas con salinidades más bajas que la salinidad típica actual del delta. La disminución de la abundancia de *M. coloradoensis* probablemente se debió a la disminución del flujo de agua del río Colorado hacia su estuario antes de 1930. Las técnicas paleontológicas y geoquímicas pueden proveer perfiles de los registros sub-fósiles de comunidades que existieron antes de las alteraciones humanas al hábitat y pueden ser usadas para establecer datos iniciales.*

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Introduction

Long-term studies needed to document ecological change are lacking in most areas, especially in the marine realm (Livingston 1991; Dayton et al. 1998). As a result, conservation biologists are faced with the formidable task of differentiating ecological change due to natural causes from change that has been induced by humans. It is important to establish a natural standard for a community that can be used as a benchmark (Dayton et al. 1998) from which to evaluate ecological change. In many areas, humans have affected the environment for so many years that even historical records, such as old fishery catch logs, do not extend far enough into the past to reveal how natural populations functioned. It is particularly difficult to describe unambiguous baselines for spatially and temporally variable habitats such as estuaries (Abood & Metzger 1996). The paleontological record can often overcome the problem of temporal variability by providing a time-averaged record of the past community. In addition, paleontological studies can aid in establishing the natural range of variation by examining communities of past centuries or millennia—especially those present prior to human habitation. Fur-

thermore, paleoecological techniques can be used to strengthen circumstantial evidence for the effects of human-induced environmental change on biotas.

Estuaries experience frequent environmental change through periodic freshwater influx and from tidal influence, and species living in this environment are often tolerant of broad environmental fluctuations. But compounded perturbations caused by human modifications (Paine et al. 1998), may make estuarine communities some of the most threatened of coastal assemblages (Smith 1997). Estuaries can be affected both by changes in marine conditions such as pollutants or invasive species and by upstream modifications such as dams and river diversions. Dams and diversions can reduce the amount and alter the timing of freshwater influx to deltaic environments (Ward & Stanford 1979). Lack of freshwater inflow to deltaic areas affects the salinity, temperature, sediment influx, and nutrient regimes of estuarine habitats (Livingston 1991). Increased salinity, caused by a lack of freshwater input, has been demonstrated to be a cause of oyster disease and population decline in estuaries (Craig et al. 1989). High dams upstream can also interfere with the life-cycles of other

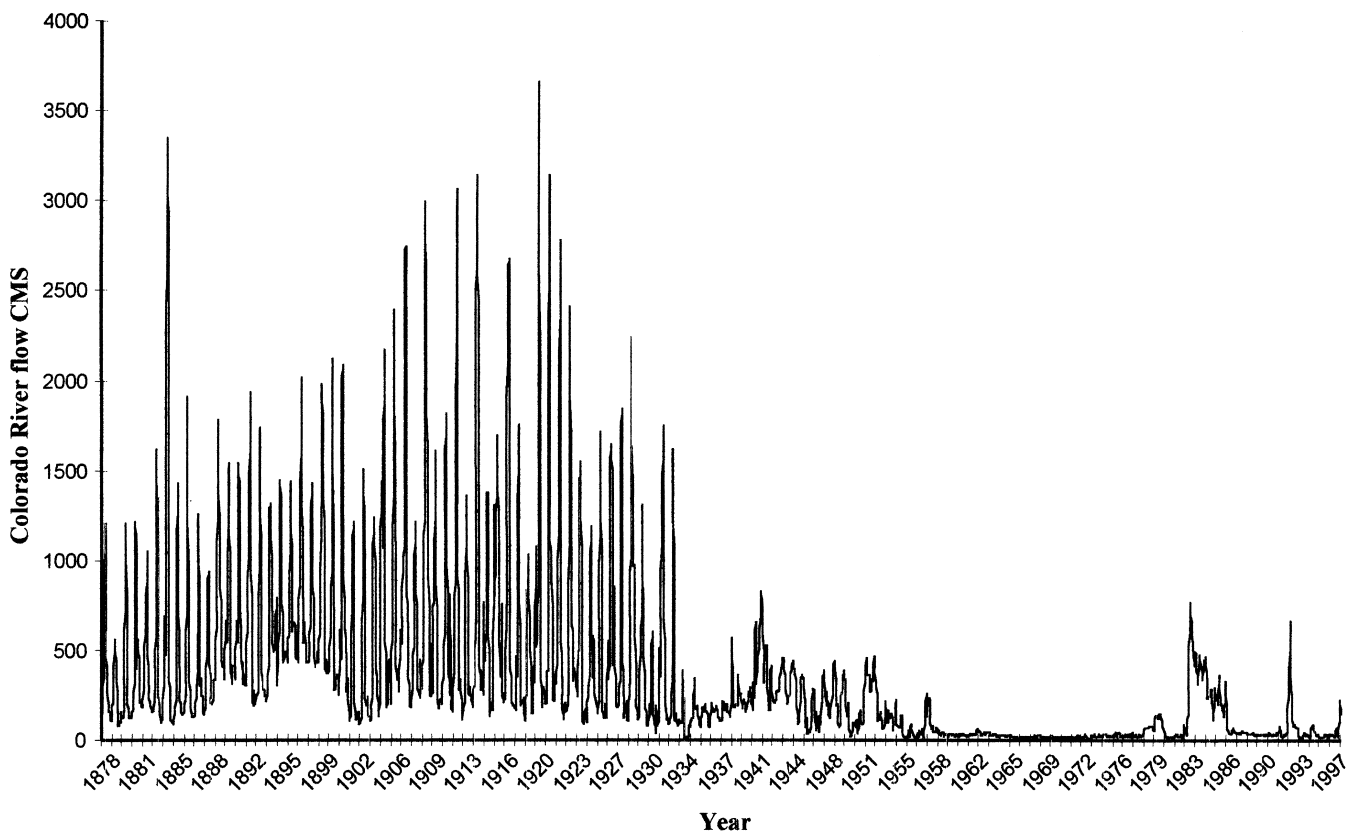


Figure 1. Record of mean monthly Colorado River flow from 1878 through 1998 in cubic meters per second (CMS) (U.S. Bureau of Reclamation, www.yao.lc.usbr.gov).

species that depend on rivers, such as shrimp and fish with obligate amphidromy (Holmquist et al. 1998).

With the completion of Glen Canyon Dam in 1963 and the nearly complete diversion of the Colorado River for human uses, freshwater inflow to the river's estuary in Mexico has diminished greatly (Fig. 1). Before the completion of Hoover Dam in 1935, the river supplied between 16 billion and 18 billion m^3 per year of water (Stockton & Jacoby 1976) to its delta. Today the estuary at the Colorado River Delta receives only 0.7 billion m^3 of river water per year (average of last 5 years; U. S. Bureau of Reclamation, <http://www.yao.lc.usbr.gov>). How has this decrease in river inflow affected estuarine environments and species in Mexico?

Shells of the bivalve mollusc *Mulinia coloradoensis* Dall make up 84–95% of the shells in the beaches of the Colorado River Delta (Kowalewski et al. 1994). The large number of empty valves of this species is in stark contrast to the small number of living specimens present in the same area.

M. coloradoensis was first described by Dall (1894), from the "Head of the Gulf of California in the estuary of the Colorado River," who noted that they were "abundant." Live individuals of this species were last documented by Thompson (1968), despite extensive field work in the area (Kowalewski et al. 1994; Kowalewski 1996). In 1998 we located a small living population at

Isla Montague (Fig. 2) at the mouth of the Colorado River.

The decline in abundance of this species may be due to the greatly diminished flow of Colorado River water to the gulf. Because no faunal surveys were conducted prior to the initial diversions of the Colorado River in about 1905, cause and effect cannot be determined directly. In short, we have no "before" to compare to the present-day "after." This is a common problem in the assessment of the effect of human activities on natural systems.

We used two approaches to reconstruct the estuarine paleoenvironment of *Mulinia coloradoensis* and to address the larger question of the effect of upriver modifications on estuarine species downriver. First, we examined what is known about the biology and ecology of *M. coloradoensis* and analyzed the relative abundance of empty shells of the species at progressively greater distances from the mouth of the Colorado River. Second, we used the isotope geochemistry of subfossil shells to infer paleoenvironmental conditions. We illustrate how paleoecological and isotopic techniques can help uncover the causes of ecological change. In using the shelly remains of once-living animals on the Colorado Delta, we are "putting the dead to work" (Kidwell & Flessa 1995) to show that upstream dams can affect downstream biotas.

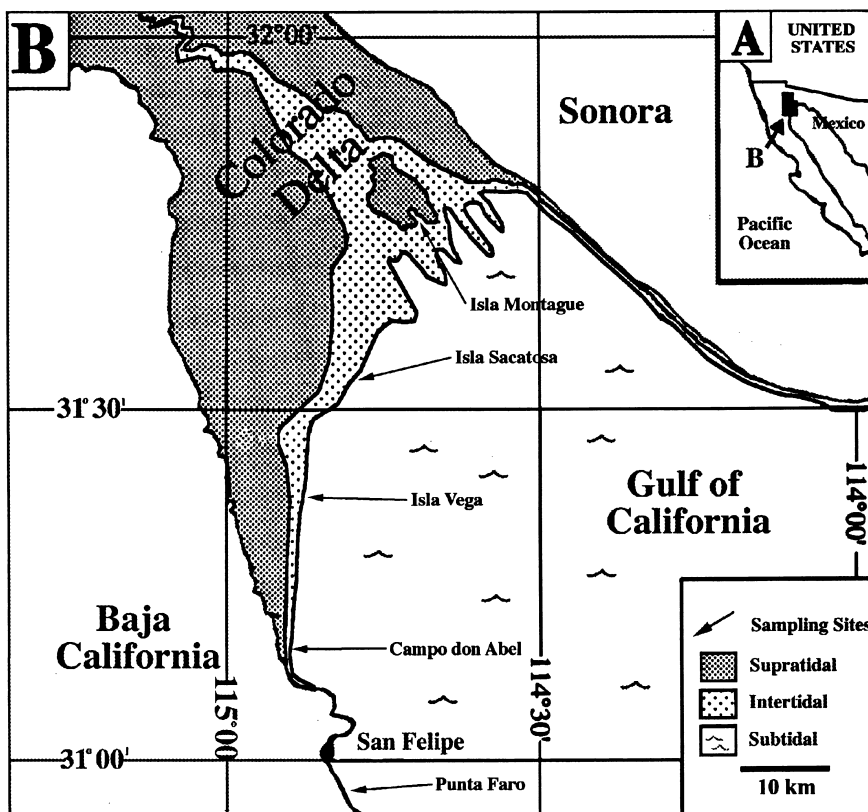


Figure 2. Map of study area: (a) Baja California and Gulf of California and (b) northern Gulf of California, Colorado River Delta, and sample localities.

Study Area

We conducted our field work in the southernmost portion of the Colorado River Delta in Baja California, Mexico (Fig. 2). This is an arid (precipitation, <60 mm per year) and hot (mean air temperature for January 14° C; for July, 34° C) area with an exceptionally large tidal range—up to 10 m in the river's mouth (Thompson 1968; Ezcurra & Rodriguez 1986). Water temperatures reach a monthly mean value of 30° C during the summer and 15° C in the winter (Thomson 1999). Salinity now ranges between 35‰ and 40‰ (Lavín et al. 1998; personal observations).

The delta plain of the lower Colorado Delta consists of a parallel series of shelly beaches called cheniers, separated by mud flats. The delivery of sediment from the Colorado River controls the formation of the cheniers (Thompson 1968). When the influx of sediment from the Colorado River is high, the tidal flats prograde seaward. Low influx of sediment to the gulf causes erosion of the fine-grained material and reworking of coarser sediment, mostly mollusc shells, into chenier ridges. On the Colorado Delta, these cheniers are composed of shells of *M. coloradoensis*.

The cheniers are ordered chronologically, with the most recently formed chenier at the modern shoreline and progressively older cheniers toward land (Kowalewski et al. 1994). The modern cheniers were formed within the last 70 years when construction of dams and other diversions greatly reduced the input of sediment from the river. The oldest cheniers were probably formed at least 1500 years ago by the natural diversion of the Colorado to the Salton Trough (Thompson 1968). We collected specimens from the modern cheniers. Shells from the modern cheniers dated by radiocarbon and amino acid techniques range in age from 215 to 650 radiocarbon years old (Kowalewski et al. 1994, 1998), with, as is conventional, the year 1950 as the present.

Shelly remains reflect, in general, the diversity, composition, and relative abundance of the organisms that produced them; between-habitat transportation of empty shells is rare (reviewed by Kidwell & Flessa 1995). Thus, shelly remains can serve as a useful baseline from which to assess the effects of environmental change.

Mulinia in North America

Mulinia lateralis of the Atlantic coast is the best known species of the genus. All other species of the genus *Mulinia* in North America occur in the Gulf of California and west coast of Mexico and have not been studied extensively.

The limited work on *Mulinia* in the Gulf of California is characterized by some taxonomic uncertainty. Bro-

derip and Sowerby (1829) described the species *Mulinia pallida* from specimens collected at San Blas, Nayarit, Mexico, and Dall (1894) described two species from the Gulf of California: *Mulinia modesta* from specimens collected at Guaymas, Sonora, and *Mulinia coloradoensis* from specimens collected at the “head of the Gulf of California in the estuary of the Colorado River.”

Grant and Gale (1931) concluded that all three species were simply geographic variants of *Mulinia pallida*, but Keen (1971), the leading authority on molluscs of the tropical eastern Pacific, synonymized only *M. modesta* with *M. coloradoensis*. According to Keen, then, there are two species of *Mulinia* along the west coast of Mexico: *M. pallida*, with a range from the “southern part of the Gulf of California to northern Peru,” and *M. coloradoensis*, “restricted to the Gulf of California and west Mexican area.” In distinguishing the two species morphologically, Keen noted that the posterior ridge of *M. pallida* is sharper than in *M. coloradoensis*. The designation of these species as distinct is now accepted practice among students of eastern Pacific molluscs (e.g., Bernard 1983; Gemmell et al. 1987).

Although an extensive analysis of species of *Mulinia* in the Gulf of California is beyond the scope of our project, we conducted a limited morphometric analysis of the two species. Specimens identified as *M. pallida* from localities ranging from Nayarit and Sinaloa to San Felipe, Baja California, were obtained from museum collections. We examined the sharpness of the posterior ridge in 50 specimens of *M. coloradoensis*, from our own collections, and in 50 specimens of *M. pallida*. The posterior ridge in *M. pallida* was significantly sharper than the ridge in *M. coloradoensis* (Fig. 3). These results are consistent with Keen's (1971) characterization of *M. coloradoensis* as a distinct species, and we follow her designations here.

Although there is some basis for considering *M. coloradoensis* and *M. pallida* as distinct species, our analysis is limited by a small sample size and the small number of shell features studied. In addition, the geographic distribution of the two species is poorly known. Additional work is required to determine if *M. coloradoensis* is limited to the Colorado Delta or if it occurs in other parts of the Gulf of California.

Most occurrences of the genus *Mulinia* in North America are associated with the mouths of rivers or low-salinity lagoons, suggesting that species of this genus may prefer these environments. For example, Parker's (1963) survey of invertebrates of the Gulf of California shows that 8 of the 11 occurrences of species of *Mulinia* are in environments of this type.

Although the once great abundance of *M. coloradoensis* at the mouth of the Colorado River has been documented (Dall 1894; Kowalewski et al. 1994), little is known about the biology of this species. *M. coloradoensis* is an infaunal, suspension-feeding bivalve. We found

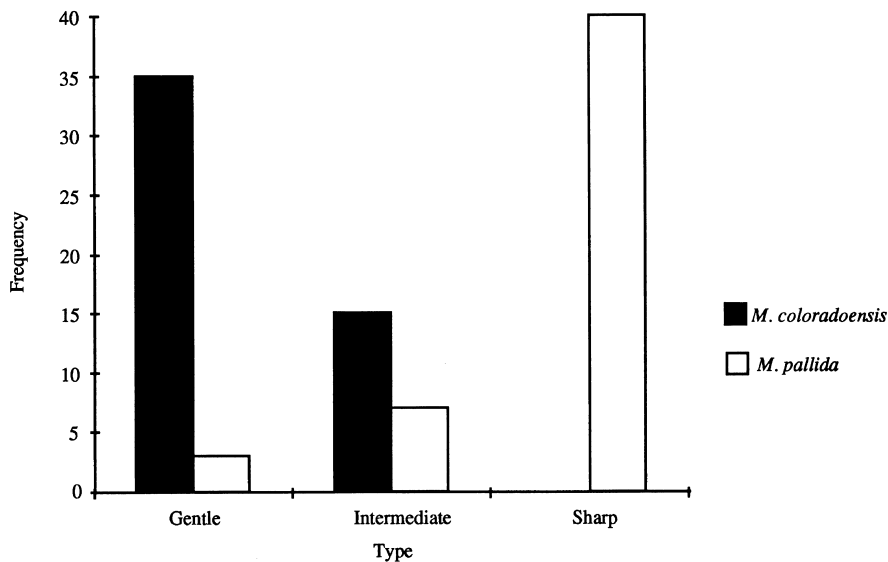


Figure 3. Frequency of posterior ridge type in *Mulinia coloradoensis* and *Mulinia pallida*.

a few living specimens in the low intertidal mud of Isla Montague (Fig. 2) at depths of about 7 cm beneath the sediment surface. Individuals of *M. coloradoensis* grow to lengths of almost 60 mm. Nothing is known about the life history of *M. coloradoensis*. The isotopic profile within a 37-mm shell (Fig. 6a) suggests a life span of about 3 years.

Isotope Paleoecology

Marine and fresh water have different oxygen isotope compositions because fresh water has its ultimate origin in the evaporation of seawater and evaporation strongly favors ^{16}O over ^{18}O . Rain or snow preferentially removes ^{18}O from atmospheric water vapor, leading to even greater depletions of ^{18}O in the freshwaters of continental interiors (Rozanski et al. 1993).

The isotopic composition of water and carbonate is reported as the deviation of the $^{18}\text{O}/^{16}\text{O}$ ratio of the sample from that of a standard (std):

$$\delta^{18}\text{O sample} =$$

$$\left(\frac{(^{18}\text{O}/^{16}\text{O}) \text{ sample} - (^{18}\text{O}/^{16}\text{O}) \text{ std}}{(^{18}\text{O}/^{16}\text{O}) \text{ std}} \right) 1000,$$

where units are per mil (‰) and the standard used is standard mean ocean water for waters or Pee Dee Belemnite for carbonates. In this notation, typical freshwater $\delta^{18}\text{O}$ values range from -3‰ to -20‰ , and seawater $\delta^{18}\text{O}$ is close to 0‰ .

The difference in oxygen isotope composition between fresh and marine water can be used to estimate the contribution of river water to estuaries. More negative $\delta^{18}\text{O}$ values indicate more freshwater entering the

estuary, whereas higher values indicate less freshwater inflow. The isotopic composition of the mixed water thus reflects the relative proportions of river and seawater in estuaries (Dodd & Stanton 1990).

Bivalve molluscs grow by precipitating calcium carbonate (CaCO_3) in accretionary bands along the outer margin of the shell. This accretion of shell material creates a chemical record of local environmental conditions.

The isotopic composition of shell is a function of the $\delta^{18}\text{O}$ of the water in which the individual is living, the ambient temperature, and the amount of evaporation. Changes in the $\delta^{18}\text{O}$ of water are directly recorded in the shell while it is growing. If the local water changes by 1‰ , due to freshwater inflow for example, shell material growing in that water will also change by 1‰ . But small temperature changes have little effect on the shell $\delta^{18}\text{O}$ values. A temperature shift of 4.7°C is needed to change the $\delta^{18}\text{O}$ values by 1‰ (Grossman & Ku 1986).

We estimated the effects of temperature and evaporation on the isotopic composition of shell material by sampling shells of bivalves living in the absence of freshwater influx. We used the $\delta^{18}\text{O}$ variation in bivalves currently living in the delta as an index of the $\delta^{18}\text{O}$ values during times of no Colorado River flow. The $\delta^{18}\text{O}$ values in subfossil shells in the Colorado Delta that are below the minimum values of the typical temperature-driven range in live bivalves reflect the influence of Colorado River water.

Methods

We collected specimens from cheniers at five localities within the northern Gulf of California at various dis-

tances from the mouth of the Colorado River: Isla Montague (at the mouth of the Colorado River), Isla Sacatosa, Isla Vega, Campo don Abel, and Punta Faro (Fig. 2).

We determined how the relative abundance of *M. coloradoensis* shells changes with distance from the mouth of the Colorado River. We counted all the individuals within bulk samples of all shells from each site and calculated the percentage of *M. coloradoensis* shells. The bulk samples consisted of 930 individuals from Isla Montague, 2000 from Isla Sacatosa, 300 from Campo don Abel, and 300 from Punta Faro. Percent values of *M. coloradoensis* for Isla Vega and south of Isla Vega are from Localities 7 and 8 of Kowalewski et al. (1994), where samples sizes were 1384 and 2612, respectively.

For the isotopic analyses, we used shells of live specimens of *Chione fluctifraga* from Isla Sacatosa; subfossil shells of *M. coloradoensis* from Isla Montague, Isla Sacatosa, Isla Vega, and Campo don Abel; and shells of live *M. coloradoensis* from Isla Montague. One live specimen of *M. coloradoensis* was collected in February 1998 during a release of Colorado River water and another was collected in February 1999 during no-flow conditions.

C. fluctifraga is an abundant bivalve that lives in the Colorado River delta today, when little river water reaches the gulf. We used this species to document the primarily temperature-driven seasonal cycle of $\delta^{18}\text{O}$ in the shell in the absence of significant amounts of Colorado River water. Stable isotopes in fossil material have been used to estimate paleotemperatures (e.g., Dodd & Stanton 1975) and to determine paleosalinities (Eisma et al. 1981; Ingram et al. 1996).

We used the isotopic composition of dead *Mulinia* shells to estimate the relative amount of river influx to the delta when the clam was alive. The $\delta^{18}\text{O}$ values within shells of the live-collected *M. coloradoensis* were used to assess the likelihood that "vital effects" could cause differences in the isotopic composition of *M. coloradoensis* and *C. fluctifraga* shells. If the isotopic signals within shells of each species are similar under similar conditions of temperature and salinity, then differences in isotopic composition reflect differences in temperature and/or salinity.

Three valves of live-collected *C. fluctifraga*, 12 valves of subfossil *M. coloradoensis* (three from each site), and 2 valves of live-collected *M. coloradoensis* were sliced into sections approximately 1.0 mm thick from the umbo to the commissure. In each section we drilled holes using a 0.5-mm dental drill. Four to eight holes were drilled in each shell section, and each hole was made within a discrete growth band in the shell.

The resulting powders (<1 mg) from each drill hole were dried under vacuum at 200° C for 1 hour and analyzed with an Autocarb device coupled to a Fisons Prism mass spectrometer. Each sample was placed in a common acid bath at 90° C. All specimens sampled were un-

altered aragonite. All values are reported in the (per mil, ‰) notation relative to the Pee Dee Belemnite (PDB) standard.

Results

Geographic Variation in Abundance of *M. coloradoensis*

Shells of *M. coloradoensis* dominate the cheniers on the Colorado River Delta (Fig. 4). Near the mouth of the river (Isla Montague to Isla Vega) valves of *M. coloradoensis* comprised between 75% and 95% of all the shells. With increasing distance from the mouth of the river, the relative abundance of *M. coloradoensis* shells decreased. Proportions of *M. coloradoensis* shells dropped to 27% at Campo don Abel, and no shells were found at Punta Faro, 75 km south of Isla Montague.

Isotopic Variation

Shells of live-collected *C. fluctifraga* had $\delta^{18}\text{O}$ values that ranged between 0.79‰ and -2.48‰, with a mean of -1.35‰. A typical annual isotopic profile for a live-collected *C. fluctifraga* (Fig. 5) has a range of values between 0.79‰ and -2.5‰. We refer to the range of values found in live-collected *C. fluctifraga* as the typical northern Gulf of California "marine" range of $\delta^{18}\text{O}$ values for our sampling sites. The range measured in our live-collected *C. fluctifraga* from Isla Sacatosa was similar to the modern marine range we have measured in live-collected shells of *C. fluctifraga* from other localities in the northern Gulf of California.

Shells of subfossil *M. coloradoensis* frequently had $\delta^{18}\text{O}$ values much lower than those found within shells of live *C. fluctifraga*. The $\delta^{18}\text{O}$ values for shells of *M. coloradoensis* ranged from 1.0‰ to about -6.0‰, with a mean of -2.0‰ (Fig. 6). A one-way analysis of variance (ANOVA) comparing all $\delta^{18}\text{O}$ values from subfossil *M.*

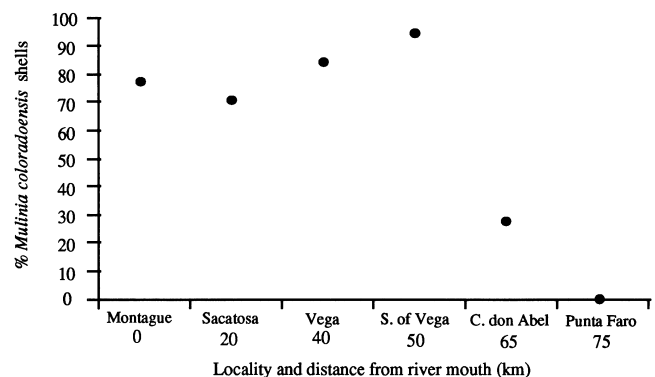


Figure 4. Relative abundance of *Mulinia coloradoensis* shells in beach deposits. Kilometer values are distance from mouth of Colorado River.

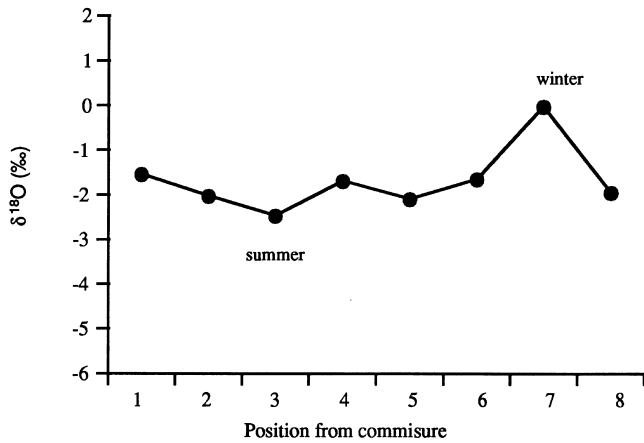


Figure 5. Oxygen isotope profile for a live-collected *Chione fluctifraga* (ST1-A4R) from Isla Sacatosa. Position 1 is sample at growing edge of shell. (Data details available from authors.)

coloradoensis to those from the live-collected *C. fluctifraga* showed that the two species differed significantly in their isotopic values ($F = 4.39$, $p = 0.038$, $n = 106$) (Fig. 7).

The isotopic profile within the February 1999 (no river flow) live-collected specimen of *M. coloradoensis* displayed the typical northern Gulf marine isotopic variation, with a range of values (+0.24‰ to -2.14‰) within that recorded in live-collected shells of *C. fluctifraga* (+0.80‰ to -2.50‰).

Discussion

Geographic Variation in Abundance of *M. coloradoensis*

The overwhelming dominance of *M. coloradoensis* shells at the mouth of the Colorado River and their decline with increasing distance suggests that populations of *M. coloradoensis* are influenced by freshwater inflow. They may have required the lower salinity conditions formerly present at the mouth of the Colorado River. It is also possible that spawning in *M. coloradoensis* is linked to episodes of high influx of freshwater from the Colorado River or that nutrients linked to the freshwater influx may have created a favorable habitat for this species.

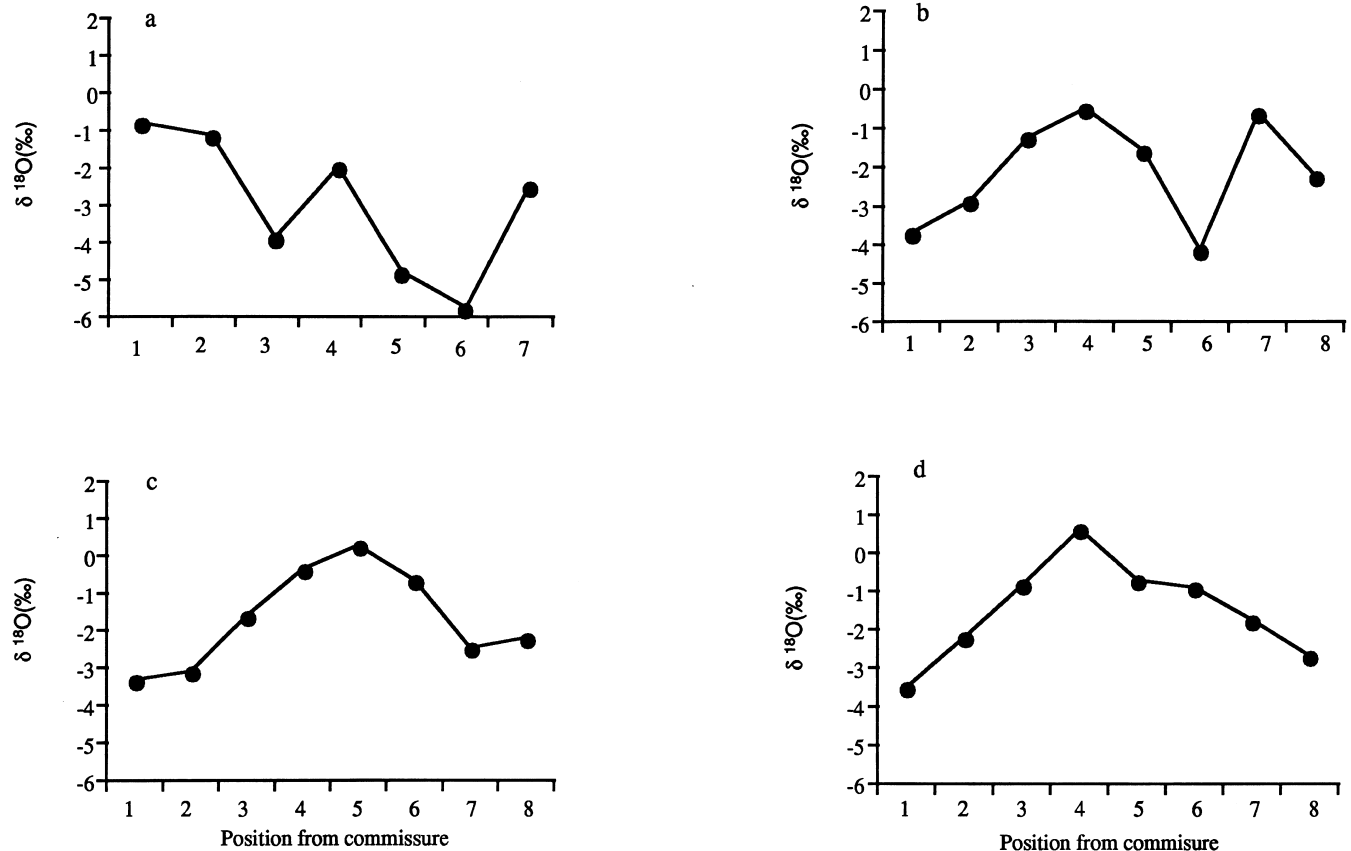


Figure 6. Oxygen isotope profiles for subfossil *Mulinia coloradoensis* shells collected from (a) Isla Montague (IM6-D3L), (b) Isla Sacatosa (ST8-D3L), (c) Isla Vega (IV3-D2L), and (d) Campo don Abel (CD1-D6L). Position 1 is sample at growing edge of shell. (Data details available from authors.)

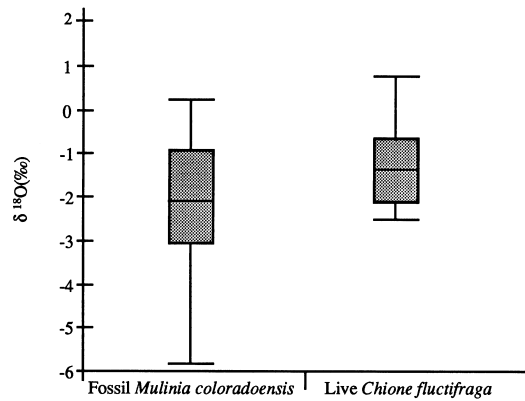


Figure 7. Oxygen isotope values and ranges for fossil *Mulinia coloradoensis* and live-collected *Chione fluctifraga*. Box area equals 25% and 75% quantiles, center line is the mean, lines outside box equal 5% and 95% values. (Data details available from authors.)

Isotopic Variation

THE TEMPERATURE-DRIVEN CYCLE IN *CHIONE FLUCTIFRAGA*

The $\delta^{18}\text{O}$ variation within shells of live-collected *Chione fluctifraga* appears to be driven by the seasonal temperature cycle (Fig. 5). Warm summer temperatures yielded more negative $\delta^{18}\text{O}$ values in shells, and summer growth resulted in a broad minimum value of about -2.0‰ . We attribute the more positive $\delta^{18}\text{O}$ values to cooler winter temperatures. According to Grossman and Ku (1986), a temperature change of 4.7°C results in a 1‰ change in isotopic composition of molluscan aragonite. Thus, the 3.27‰ variation in live *C. fluctifraga* shell $\delta^{18}\text{O}$ is accounted for by the annual temperature variation of approximately 15°C in the northern Gulf of California (Thomson 1999) ($3.27\text{‰} \times 4.7^\circ\text{C} / \text{‰} = 15.4^\circ\text{C}$). Evaporation may have driven the $\delta^{18}\text{O}$ of seawater (and thus shell material) to some of the more positive values. Because Colorado River water did not flow into the Gulf of California when these specimens were alive, the isotopic variation in these shells is due solely to the seasonal variation in water temperature, evaporation, and precipitation. The temperature and evaporation cycles in the northern Gulf of California would generate a similar $\delta^{18}\text{O}$ cycle in *M. coloradoensis* specimens if no river water had reached the Gulf during their lifetimes.

MULINIA COLORADOENSIS

The $\delta^{18}\text{O}$ values in subfossil shells of *M. coloradoensis* below the marine range of variation found in live *C. fluctifraga* reflect the influx of freshwater from the Colorado River. Isotopic variation in *M. coloradoensis* shells resulted from seasonal variation in water temperature, evaporation of seawater, and periods of major freshwa-

ter influx, such as during the arrival of spring snowmelt at the delta. The significant difference between the $\delta^{18}\text{O}$ values found in subfossil *M. coloradoensis* and those found in *C. fluctifraga* shows that these two species of clams grew in different waters.

Both evaporation and temperature can also cause variation in $\delta^{18}\text{O}$ values. Can these explain the low values found in subfossil specimens of *M. coloradoensis*? Because evaporation drives the $\delta^{18}\text{O}$ in water and shell material toward higher values, not lower ones, higher evaporation is not a viable explanation. Lower evaporation would simply drive the values closer to the average ocean value of approximately 0‰ , but not below.

Temperature change is not a likely explanation either. Increased temperatures when the subfossil *M. coloradoensis* was alive would make the $\delta^{18}\text{O}$ values lower than those found today, but the *M. coloradoensis* shells date from 215 to 650 radiocarbon years ago (Kowalewski et al. 1998). This range encompasses the Little Ice Age (A.D. 1300–1910), when global temperatures are estimated to have been about 1.0°C cooler (Porter 1986). Thus, lower temperatures in the recent past are more likely to have occurred than higher ones.

In any event, it would be difficult to generate the low isotopic values seen in subfossil *M. coloradoensis* with an increase in temperature. For temperature change to have caused the low $\delta^{18}\text{O}$ values in shells of subfossil *M. coloradoensis*, temperatures in the Gulf of California would have to have been approximately 20°C higher when those specimens were alive than they are today. A 4.7°C temperature shift changes $\delta^{18}\text{O}$ values by only 1‰ (Grossman & Ku 1986), and low $\delta^{18}\text{O}$ values found in subfossil *M. coloradoensis* (e.g., -6.4‰) are about 4‰ lower than the low values of today (i.e., -2.5‰). This 4‰ difference would require an increase in temperature of approximately 20°C . An increase of this magnitude is climatically and oceanographically unlikely.

The range of values found within the shells of live-collected *M. coloradoensis* did not include the low values found within the shells of subfossil *M. coloradoensis*. The range of values within the shells of the live-collected *M. coloradoensis* was similar to that found within shells of live-collected *C. fluctifraga*. This supports the assumption that both species precipitate their shells in equilibrium with the ambient water and that differences in oxygen isotope fractionation are not a confounding factor in comparisons of these two clams. The range of values in the February 1999 (no river flow) *M. coloradoensis* shell matches those found within the live-collected *C. fluctifraga* shells. The $\delta^{18}\text{O}$ values in the February 1998 (limited river flow) live-collected shell of *M. coloradoensis* were more variable and included values that were slightly lower than in the February 1999 specimen and the *C. fluctifraga* shells. This is most likely due to the effect of a small, controlled release of isotopically negative freshwater from the Colo-

rado River in 1998 (U. S. Bureau of Reclamation, <http://www.yao.lc.usbr.gov>).

Conservation Implications

Paleoecological techniques and biogeochemical analyses offer a way to reconstruct communities and environments as they existed prior to significant human modification. This underutilized approach in conservation biology can overcome the problem of insufficient long-term data in assessing ecological change and can be used to strengthen circumstantial evidence for human-induced environmental effects in the absence of direct historical data. Using these techniques, we have shown that the sharp decrease of Colorado River inflow of freshwater, nutrients, or sediments to the delta region is likely to have caused the major decline in abundance of *M. coloradoensis*. Increased river flow to the delta might allow this species to persist or even recover to former population sizes.

Little other work has been done on the effects of reduced freshwater inflow on the Colorado River estuary and northern Gulf of California. Galindo-Bect et al. (2000) show that higher shrimp catches in the northern gulf are associated with episodes of controlled releases that reach the estuary. Lavín and Sánchez (1999) and Carbajal et al. (1997) consider hydrographic changes, and Carriquiry and Sánchez (1999) discuss some of the sedimentary effects.

The marine and estuarine portions of the Colorado Delta in Mexico are habitats for two known endangered species: the Vaquita, or Gulf of California Harbor Porpoise (*Phocoena sinus*), and the Totoaba fish (*Totoaba macdonaldi*). The decline of these two species has been attributed to overfishing, accidental catches in shrimp nets, and the indirect effects of habitat alteration resulting from the decline in Colorado River flow (Cisneros-Mata et al. 1995; Morales-Abril 1994). Unlike these two vertebrates, *M. coloradoensis* is not harvested for food nor is it affected by the harvesting of other species. The decline in the population of *M. coloradoensis* on the Colorado Delta is best explained as the direct consequence of the decrease in freshwater flow from the Colorado River.

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