

Dead delta's former productivity: Two trillion shells at the mouth of the Colorado River

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ABSTRACT

The diversion of the Colorado River by dams and irrigation projects, started in the 1930s, triggered the collapse of the Colorado delta ecosystem. Paleontological, ecological, geochronological, stable isotope, field, and satellite image data provide estimates of the delta's benthic productivity during the 1 k.y. directly preceding the artificial shutdown of the river. At least 2×10^{12} shells of bivalve mollusks make up the current beaches and islands of the delta. The 125 individual valves dated using ^{14}C -calibrated amino acid racemization indicate that these shells range in age from A.D. 950 to 1950. Seasonal intrashell cycles in $\delta^{18}\text{O}$ values indicate that average-sized bivalves lived at least 3 yr. The most conservative calculation based on these numbers indicates that during the time of natural river flow, an average standing population of $\sim 6 \times 10^9$ bivalve mollusks (population density $\sim 50/\text{m}^2$) thrived on the delta. In contrast, the present abundance of shelly benthic macroinvertebrates is $\sim 94\%$ lower ($3/\text{m}^2$ in 1999–2000). The dramatic decrease in abundance testifies to the severe loss of benthic productivity resulting from diversion of the river's flow and the inadequacy of its partial resumption (1981 to present). An integration of paleontological records with geomorphological, geochemical, and geochronological data can provide quantitative insights into human impact on coastal ecosystems.

Keywords: paleoecology, productivity, estuary, Colorado River, Holocene.

INTRODUCTION

Human efforts to divert and control the major rivers of the world have resulted in the erosional reduction of deltas and the deterioration of their ecosystems (Stanley and Warne, 1993; Leichenko and Wescoat, 1993; Fradkin, 1996). The Colorado River delta (Gulf of California) exemplifies these processes particularly well. Starting in the 1930s, dams and irrigation projects diverted water flow from the Colorado River, which resulted in the dramatic decrease of nutrient and sediment flow into the delta (Thompson, 1968; Fradkin, 1996). The river diversion triggered the collapse of the delta ecosystem, a key stopover for migratory birds and an important nursery for diverse and threatened endemic marine life, including the smallest known marine mammal, the vaquita (a porpoise, now thought to number only a few hundred individuals), and the totoaba (a fish now virtually extinct) (Luecke et al., 1999).

The partial restoration of the river flow by floodwater, sporadic releases from reservoirs, agricultural return flows, and municipal wastewater has led to some revival of the delta in the past 20 yr. The collapse and subsequent partial recovery have been documented to some extent for the riparian vegetation, terrestrial fauna, and migratory birds (Luecke et al., 1999).

Although the contemporary Colorado delta has been intensely researched (Luecke et al., 1999), little is known about the delta ecosystem from the era of natural river flow. Because we lack direct observations from this period, we combine paleontological and geological data to estimate the past and current abundance of the shelly fauna, used as a proxy for the benthic productivity of the estuary. This approach allows us to compare biotic and environmental conditions before and after a major human perturbation.

NUMBER AND AGE OF SHELLS ON THE COLORADO DELTA

The lower Colorado delta is characterized by extensive mud flats and a tidal range that reaches 10 m (Thompson, 1968). Following the shutdown of the river and cutoff of the sediment supply to the delta, tidal currents and waves began to erode the intertidal muds, exhuming mollusk shells and working them into the shoreline into residual beach ridges (Thompson, 1968). The ridges extend continuously along the high-tide line and form numerous intertidal bars and islands. Disarticulated valves of bivalve mollusks constitute more than 99% of all shell material concentrated in the ridges and are dominated by the bivalve *Mulinia coloradoensis* (84%–95%); the bivalve *Chione fluctifraga* (1%–8%) is the only other species that occurs in notable quantities (Kowalewski et al., 1994). Only currently forming ridges are included in this analysis; older generations of ridges that record natural episodes

of the Colorado River diversion (Thompson, 1968; Waters, 1983) and are now partly buried under the supratidal muds are excluded from our calculations.

Calculations based on satellite images, field measurements, and bulk samples indicate that the modern ridges entomb the shells of at least 2×10^{12} dead clams (4×10^{12} disarticulated valves) (Table 1). For numerous reasons (see Table 1), this estimate is highly conservative. In order to interpret the estimate in terms of past productivity we need to know the amount of time during which the shells accumulated. Do the 2×10^{12} shells represent a short interval of high productivity or a long interval of low productivity?

Dating of 125 shells by amino acid racemization analysis (D-alloisoleucine/L-isoleucine, or A/I) calibrated with radiocarbon dating shows that specimens dating from the past 50 yr are absent in the ridges (or too rare to be sampled) (Fig. 1A). Shells from clams alive before 1950 are common and their age-frequency distribution is continuous (for 50 yr bins) back to A.D. 950. Essentially all dated shells (123 of 125; 98%) are from the past 1000 yr (A.D. 950–1950) directly preceding the river shutdown in the 1930s. Given the dating precision of ± 50 yr (Fig. 1B), we cannot show that the youngest shells are exactly from the 1930s, but a decrease in shell frequency in the age class A.D. 1900–1950 is consistent with that interpretation.

That the age distribution is significantly skewed toward younger age classes (Fig. 1A) should not be interpreted as evidence for an increase in benthic productivity in more recent centuries. Such skewness is a common characteristic of dated shells and most likely reflects an exponential decay of older shells destroyed by taphonomic processes (e.g., Flessa and Kowalewski, 1994). The almost monotonic rise in number of shells toward younger age classes suggests that productivity was constant through time; when constant productivity is assumed, shell survival through time shows a statistically significant fit with an exponential curve (Fig. 2). The calculation based on the exponential equation (Fig. 2) suggests that the 2×10^{12} shells represent the surviving $\sim 40\%$ of $\sim 5 \times 10^{12}$ shells that were produced in the delta during the last millennium.

The extreme scarcity of shells older than A.D. 950 does not mean that benthic productivity was

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TABLE 1. COMPUTATION OF THE TOTAL NUMBER OF BIVALVE MOLLUSK SHELLS CONCENTRATED IN THE BEACH RIDGES OF THE LOWER COLORADO DELTA

Estimated parameter	Estimated value
Total area of beach ridges *	$5.96 \times 10^6 \text{ m}^2$ (C.I.: 5.85-6.06)
Average beach ridge thickness †	4 m
Total volume of beach ridges §	$2.4 \times 10^7 \text{ m}^3$
Shell density in beach ridges ‡	$87500/\text{m}^3$
Total number of shells #	2.1×10^{12}

*An estimate based on a high-resolution satellite image processed using 4-point calibration and blob analysis (Blob Tool, HL Image++ Software). The estimate is a mean value for 10 independently calibrated, replicate blob analyses. The 95% confidence interval (C.I.) based on 10^4 -iteration bootstrap analysis. The actual area of the ridges is underestimated because the outer parts of the ridges buried under the intertidal mud layers are ignored.

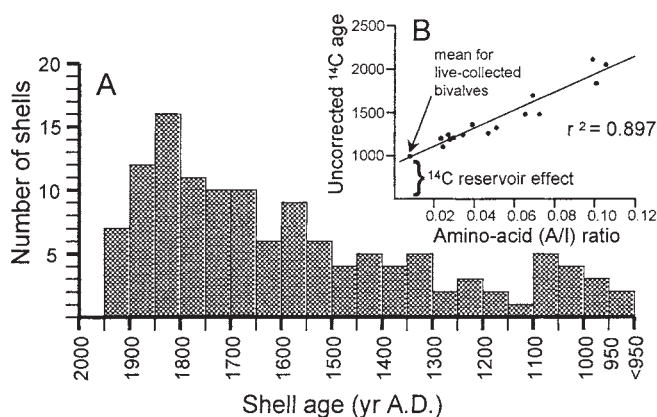
†An average based on two field-measured (November 95) topographic profiles. The two measured ridges include a small, incipient intertidal ridge (2.5 m) and a typical mature shoreline ridge (5.5 m). The estimate underestimates the actual thickness of the ridges because it ignores the parts of the ridges buried below the present-day surface of the mud flat.

§The total volume estimate is restricted to the currently (1930–2000) forming ridges and excludes older generations of ridges formed during prehistoric episodes of natural diversion of the river to the Salton Trough (Thompson, 1968; Kowalewski et al., 1994; Waters, 1983).

‡37 samples (0.004 m^3 each), sieved with a 12.5 mm mesh, yielded ~13000 complete valves (~6500 bivalves) (Kowalewski et al., 1994). Because shell fragments (>12.5 mm) represent >50% of the sieved material by weight, the 37 samples contain bioclastic material from at least 6500 additional bivalve mollusks. Each sample, therefore, contains an average of ~350 bivalves per 0.004 m^3 ($87500/\text{m}^3$).

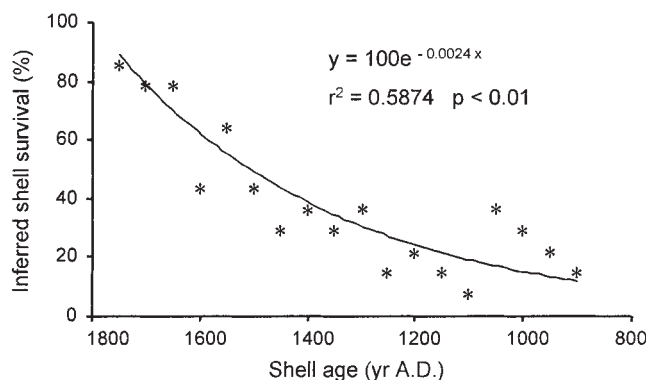
#This estimate ignores gastropods (<1% material) and all shell material smaller than 12.5 mm. In all subsequent computations presented here the estimate is rounded to the nearest trillion to avoid conveying a false sense of precision.

Figure 1. A: Age-frequency distributions of 125 *Chione fluctifraga* shells collected from modern ridges and dated using A/I amino-acid ratios (Kowalewski et al., 1998). Distribution is significantly skewed toward younger ages: skewness (k_3) = 3.92, $p = 0.001$ (p is estimated by k_3 value of sample and 999 random k_3 values generated by drawing samples of 125 observations from symmetrical distributions; two Monte Carlo models based on normal and uniform distributions yielded same estimate of p).



B: A/I racemization rate calibration using ^{14}C -dated shells (see Goodfriend, 1989, for description of method). Radiocarbon reservoir age was estimated from ^{14}C measurements of eight shells of mollusks that were live collected before 1940. Resulting calibration is corrected for reservoir effect (~1 k.y. in northernmost Gulf of California; Goodfriend and Flessa, 1997) and provides dating precision of ~50 yr (Kowalewski et al., 1998).

Figure 2. Exponential decrease in shell frequency in relation to increased shell age. Inferred shell survival is derived from age-frequency distribution of dated shells (Fig. 1A) under assumption that productivity was constant through time. Average number of dated shells (14) for two youngest age classes from before 1930s (A.D. 1800–1850 and A.D. 1850–1900) was used to compute inferred shell survival in older age classes (e.g., survival for A.D. 1750–1800 class = $12/14 = 85.7\%$).



low before the tenth century. The sequential unroofing of the tidal mud may not have exhumed still older shells, and shell-rich horizons are common just centimeters below the present-day sediment surface. In addition, older shells may have been removed during previous erosion events caused by episodes of natural river diversion to the Salton Trough (Thompson, 1968; Waters, 1983). Our estimates of the quantity and age structure of shells focus on the mollusk valves already reworked into the beach ridges.

In summary, dating shows that the 2×10^{12} shells concentrated in the beach ridges originated during the last millennium and represent only a fraction of the clams that lived in the delta during that time interval.

ESTIMATES OF PAST BENTHIC PRODUCTIVITY

Two additional parameters need to be assessed in order to estimate past benthic productivity in the delta: (1) population turnover rate and (2) the size of the area from which shells were derived.

Shells of the dominant clam *Mulinia coloradoensis* average 30 mm in size (mean = 29.4 mm, $n = 2117$, 37 samples; Kowalewski et al., 1994). Stable isotope profiles obtained by microsampling *M. coloradoensis* shells along their growth axes reveal seasonal cycles and demonstrate that the clam requires at least 3 yr of growth to attain 30 mm in length; i.e., a 30 mm shell will typically include three seasonal oxygen isotope cycles (Rodriguez et al., 2001). Thus, no more than 333 generations of clams lived during the past millennium: regardless of spawning frequency, an average-size shell found in the beach ridges must have occupied its quota of the intertidal space for at least 3 yr. A minimum average standing population of 6×10^9 bivalve mollusks ($2 \times 10^{12}/333$) must have existed continuously for the past 1 k.y. to account for the shells now accumulated in the ridges.

The populations from which shells were derived must have been limited to a restricted area. First, mollusk shells rarely undergo substantial postmortem transport (Anderson et al., 1997; Flessa, 1998). Second, the beach ridges are a local product of intertidal reworking, where tides and waves are sufficiently strong and persistent to erode shells of infaunal mollusks and transport them toward the high tide line. Finally, the dominant bivalve *M. coloradoensis* is a brackish-water species limited to shallow environments directly influenced by the river (Rodriguez et al., 2001). Thus, the overwhelming majority of shells were derived from the intertidal zone that extends in front of the beaches for about 60 km along the northeastern coast of Baja California. Field measurements taken at lowest spring tide estimated the width of the intertidal at 650 m in the south, 2200 m in the central part, and 1400 m in the north (Fig. 3, transects 1–4). Generously assuming an average width of 2000 m, the largest

area for shell production that can be postulated is $60 \times 2 \text{ km} = 1.2 \times 10^8 \text{ m}^2$. Given the population turnover of 3 yr and the source area of $1.2 \times 10^8 \text{ m}^2$, the average density of intertidal mollusks during the past millennium (A.D. 950–1950) was ~ 50 individuals per m^2 ($6 \times 10^9 / 1.2 \times 10^8$).

These calculations are likely to underestimate the past benthic productivity. Not only is our initial computation for minimal values highly conservative (Table 1), but it includes an overly optimistic assumption that no shells were destroyed during the past 1 k.y., whereas as much as 60% of the shells may have been lost (see preceding and Fig. 2). Moreover, the estimate ignores substantial quantities of shells still scattered on the surface of the intertidal zone (these mollusks were excluded because of their unknown age structure, but, undoubtedly, many of them lived during the past 1 k.y.) and all material smaller than the mesh size used for sample processing (there are 2×10^{12} shells larger than 12.5 mm; Table 1).

The postulated size and density of the past populations of *M. coloradoensis* are not unreasonable considering that the present-day populations of its Atlantic relative *M. lateralis* reach densities of hundreds to thousands of specimens per square meter of the seafloor (e.g., Walker and Tenore, 1985; Montagna et al., 1993). *M. lateralis* displays an opportunistic (r-selected) population strategy (i.e., high fecundity and high juvenile mortality) and often plays a key role in sustaining diverse marine carnivores, including invertebrates, fish, turtles, shorebirds, and marine mammals (Walker and Tenore, 1985; Williams et al., 1986; Van Dolah et al., 1991; Montagna et al., 1993).

PRESENT-DAY BENTHIC PRODUCTIVITY IN THE DELTA

In contrast to the past benthic productivity, the present-day density of the intertidal macrobenthos is extremely low. Seven intertidal transects, positioned to ensure a broad sampling coverage of the intertidal flats, were conducted in October–December 1999 and February 2000 (Figs. 3 and 4). Sites close to the river mouth yielded density estimates of shelly fauna (Fig. 4) comparable to those obtained for sites located far from the delta, suggesting a lack of any river-related productivity gradient in the modern delta ($p > 0.05$; Wilcoxon test). Such a gradient may have existed in the past, as suggested by changes in the faunal composition of beach ridge materials away from the delta (Rodriguez et al., 2001). Given consistent estimates of density among all transects, average values (Table 2) should provide a reliable estimate of the present-day abundance of macrobenthos. The present-day density of large (>12.5 mm) mollusks (predominately *Chione*) is ~ 3 individuals/ m^2 . This is only 6% of the average density during the past 1 k.y. Moreover, only 12 live specimens ($0.2/\text{m}^2$) of *M. coloradoensis* were found. Even after the addition of all small mollusks and all shelled nonmollusk macrofauna, the current den-

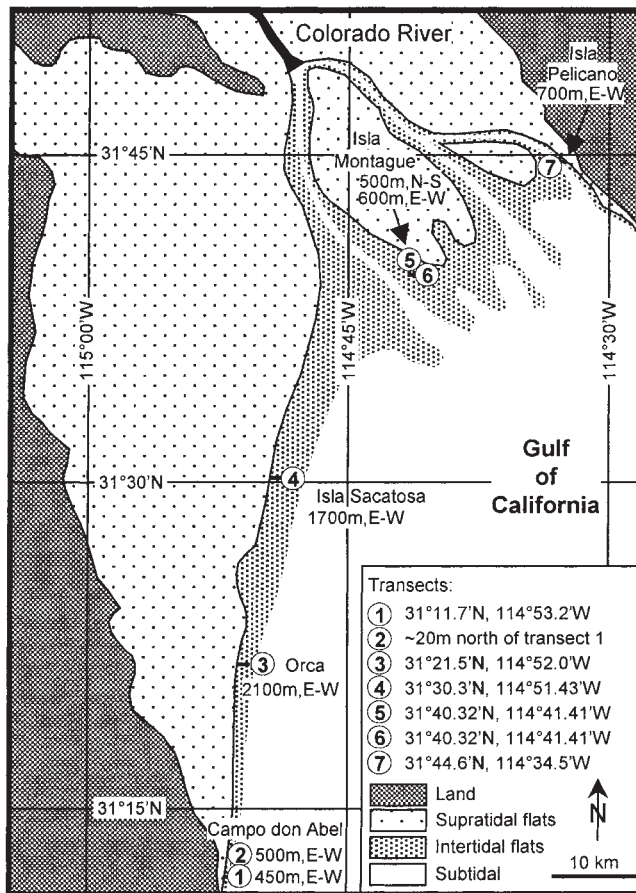


Figure 3. Map of lower Colorado River delta based on high-resolution satellite images, field observations, and previous studies (Thompson, 1968; Kowalewski et al., 1994). Positions of transects used to survey live benthos (see Table 2; Fig. 4) are identified by circled numbers.

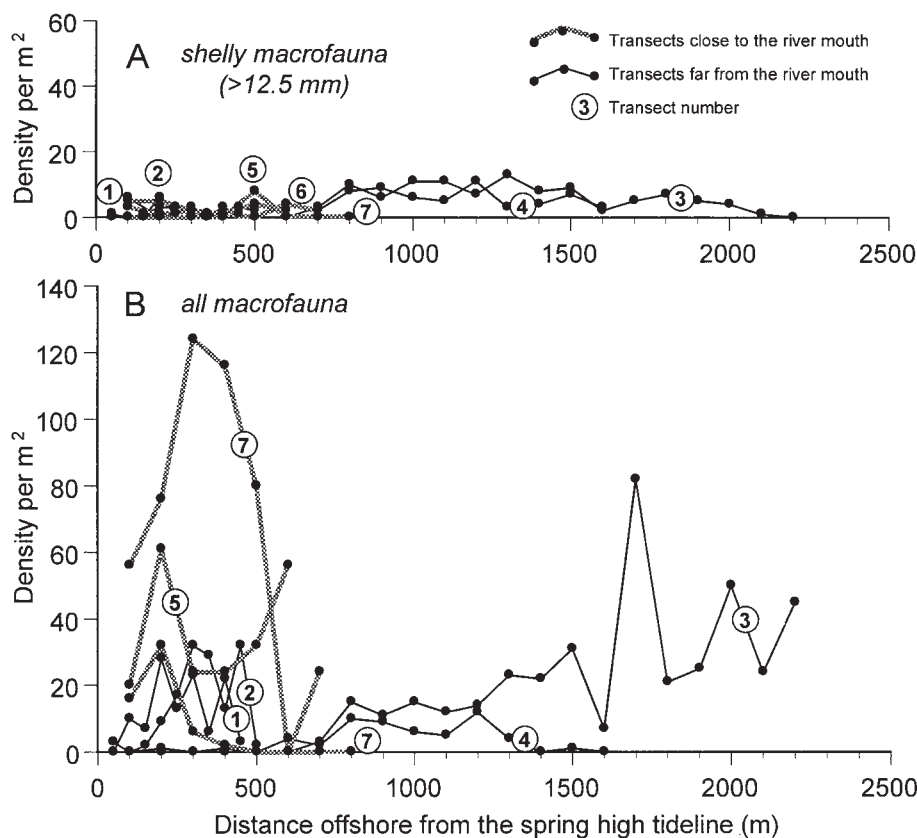


Figure 4. Present (1999–2000) density of benthic macrofauna along seven intertidal transects across macrotidal flats of lower Colorado River delta. A: Large shelly macrofauna (>12.5 mm). B: All macrofauna (>6 mm). See Table 2 for details and Figure 3 for exact locations of transects.

TABLE 2. SURVEY OF LIVE MACROBENTHOS FROM THE INTERTIDAL ZONE OF THE LOWER COLORADO DELTA

Type of Benthos	Number of live individuals*	Density/m ²	Mean density per site	95% Confidence intervals	
				Bootstrap	Parametric
Shelly fauna (shells >12.5 mm)	224	3.1	3.0	2.28–3.78	2.26–3.78
Shelly fauna (shells > 6.0 mm)	923	13.0	13.6	10.18–17.28	9.96–17.19
All fauna (specimens > 6.0 mm)	1169	16.4	18.8	13.67–24.79	13.13–24.59

Note: Estimates based on 258 samples (sampling area 0.25 m² each, 71.25 m² total) collected at 78 sites along 7 transects across the intertidal zone (December 1999: 4 transects; February 2000: 3 transects). Site-level estimates based on four (65 sites), two (12 sites) or one sample per site (1 site). Estimates of 95% confidence intervals based on parametric approach (assuming normality) and balanced bootstrap simulations (5000 iterations each). Bootstrap confidence limits computed using the percentile method (Manly, 1997).

*The density estimates are based on specimens recovered from the top 20 cm of intertidal sediments. Field observations indicate that the live shelly fauna is dominated by shallow burrowers (e.g., *Mulinia* and *Chione*) and epifaunal forms (e.g., *Nassarius*). The only deep-burrower common in the area (*Tagelus*) that may have escaped our sampling efforts is not abundant enough to notably affect the estimates (distinctive burrow openings visible on the sediment surface suggest that the density of *Tagelus* rarely exceeds 1/m²).

sity of the benthos (~18/m²) is still only 36% of the density during the times when the river flowed to the delta (Table 2). Thus, the difference cannot be attributed to a mere shift in the size or type of benthos, but reflects a substantial decrease in benthic productivity.

CONCLUSIONS

The dramatic reduction of fresh water and nutrients is the most likely cause for the dramatic drop in population levels. *M. coloradoensis* has nearly vanished from the delta today: sparse remnant populations are limited to areas near the mouth of the Colorado River (Rodriguez et al., 2001). Shrimp catches and fish diversity correlate with the amount of the river water reaching the delta (Luecke et al., 1999; Galindo-Bect et al., 2000). A notable increase in the levels of selenium and other harmful pollutants associated with the agricultural water waste (Glenn et al., 1996) also may have played a negative role. Although nutrient levels and phytoplankton productivity on the delta today are high (Hernandez-Ayon et al., 1993; Millán-Núñez et al., 1999), they were presumably even higher during times of river input.

Despite the past 20 yr of intermittent river flow, the intertidal macrobenthos has remained decimated compared to the population levels before the time of substantial human-induced river diversion. The recent partial reestablishment of the Colorado River resulted in some revival of riparian habitats and has been proclaimed a hopeful sign for a partial restoration of the delta's ecosystem (Leucke et al., 1999). However, our estimates provide strong evidence against a similar revival of the marine part of the estuary. Paleocological approaches that integrate paleontological, geomorphological, geochemical, and geochronological data can be used for quantitative assessments of human impact on coastal ecosystems.

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