

A CASE STUDY IN CONSERVATION PALEOBIOLOGY:
THE MOLLUSCAN COMMUNITY OF THE COLORADO RIVER ESTUARY

A Dissertation

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Abstract

The Colorado River no longer reaches the Gulf of California in most years due to numerous upstream dams and associated water diversions for consumptive use. The downstream estuary in Mexico has undergone habitat change as a consequence; however, a paucity of pre-impact data has made it challenging to assess the full scope of change. Fortunately, along the shoreline in the estuary there are accumulations of clam and snail shells that predate dam construction and can provide an invaluable perspective on past community dynamics in the molluscan community.

Shell accumulations in the estuary were sampled during 2013 and 2014 at three sites along the north-south salinity gradient that existed prior to upstream water diversions. The living community was sampled during 2014 at the northern-most of these sites, which corresponds to the most estuarine environment from the past. In the following five chapters, a variety of analytical methods are applied to different subsets of the samples to assess change at multiple levels of the ecological hierarchy. Major results from these chapters include: (1) identification of a new predatory snail species in the estuary; (2) evidence suggesting decreases in predator populations in the estuary due to reduction in prey availability; (3) documentation of population decreases in species with preferences for low-salinity conditions and population increases for species with preferences for high-salinity conditions; (4) increases in community evenness and richness in the post-impact community; (5) evidence suggesting a shift

in the processes controlling community assembly from environmental preference and dispersal capacity to competition-colonization tradeoff; and, (6) a reduction in carbon emissions from the estuary due to decreases in the clam population.

Restoration efforts are ongoing in the Colorado River estuary under multiple binational agreements between the United States and Mexico. The results presented here represent baseline data that can be used to evaluate the success of those efforts and to inform the best strategies for restoration success. Counterintuitive as it may seem, restoration success likely means a reduction in the number of species living in the estuary and an increase in estuarine carbon emissions.

BIOGRAPHICAL SKETCH

Jansen Alexander Smith received his Bachelor of Arts degree from Macalester College in 2012. At Macalester, Smith was a double major in Geology and Biology. Beginning in Fall 2012, Smith matriculated at Cornell University to pursue his Doctorate of Philosophy in the field of Geological Sciences with minor fields of Animal Behavior and Paleontology. This document represents the culmination of his PhD study.

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PREFACE

The Colorado River estuary once thrived with life to such a degree that it inspired Aldo Leopold to write his essay, *The Green Lagoons*, about the lushness of the region. Fast-forward a few short decades and the essay reads more like science fiction than a first-hand account. Dams along the Colorado River shut off freshwater flow to the estuary, forever altering the once fertile paradise.

Today, it is clear the estuary has changed but, aside from Leopold's musings, we know almost nothing about life in the estuary prior to dam construction in the 1930s. Enter conservation paleobiology. Trillions of seashells have accumulated along the shores of the estuary and hold the key to understanding life before the dams.

For six years I have studied the snail and clam community represented by these seashells as well as the estuary's living community. This work follows as five chapters, each of which is focused on one of three levels of the ecological hierarchy: population (Chapter 1), community (Chapters 2-4), and ecosystem (Chapter 5). Although the chapters are interrelated, each is meant to be a standalone publication. Likewise, although the levels of ecological hierarchy are linked, each is considered independently to assess how processes at different levels of organization have responded to the habitat change in the Colorado River estuary.

Walking amongst the seashells, it is clear that one clam, *Mulinia*, was very common in the past; it composes more than 90% of the accumulations! Today, *Mulinia* is rare. To the contrary, the hard clam, *Chionista*, has increased from a mere 5% of the

community to more than 50% (Chapter 3). Still, the overall abundance of clams in the estuary has decreased and whereas processes of dispersal and environmental preference previously controlled membership in the community, tradeoffs between competition and colonization are likely more important today (Chapter 4).

The presence of a new predatory snail, *Notocochlis*, represents another notable difference in the living community (Chapter 1). Absent from the shell accumulations—likely due to unfavorable, low-salinity conditions in the past—*Notocochlis* indicates a more dangerous, predator laden environment for clams. With the introduction of a new predator, there is not only greater competition between predators for food, but also a shift in which types of food resources are consumed. In the pre-dam era community, the hyper-abundant clam, *Mulinia*, was not the most preferred prey of predators but because it was so abundant, it was consumed by predators with great regularity. Now, because *Mulinia* is rare, predators are likely consuming other food resources, like the hard clam *Chionista* (Chapter 2).

At the ecosystem level, reduction in the estuary's clam population has likely resulted in a decrease in carbon emissions (Chapter 5). As clams live, breath, and grow their shells, they produce carbon dioxide. Where there were once clam densities in excess of 100 clams per square meter there are now only three. Although it is tempting to claim the corresponding reduction in carbon emissions as a positive outcome, the reduction is vastly outweighed by new upstream emissions related to power plants and costs of transporting water to cities like Las Vegas.

Restoration efforts are ongoing in the Colorado River estuary and now, for the first time, we know how the community should look. Counterintuitive as it may seem, a restoration success means a reduction in the number of species living in the estuary and likely an increase in estuarine carbon emissions.

CHAPTER 1

THE VALUE OF GEOHISTORICAL DATA IN IDENTIFYING A RECENT HUMAN-INDUCED RANGE EXPANSION OF A PREDATORY GASTROPOD IN THE COLORADO RIVER DELTA, MEXICO¹

Abstract

Throughout the Colorado River basin, numerous dams have captured and diverted the entirety of the basin's $c. 1.85 \times 10^{10} \text{ m}^3/\text{yr}$. of water, altering the downstream delta ecosystem. In the absence of pre-dam studies, geohistorical data can play a critical role in reconstructing ecological aspects of the past ecosystem. Here, we use geohistorical data to test the hypothesis that a shell-drilling naticid gastropod predator, *Notocochlis chemnitzii*, has recently undergone a human-induced range expansion to the Colorado River estuary (CRE). Based on uncertainty in the literature surrounding the membership of *N. chemnitzii* in the CRE benthic community before the dams were built, we predicted, for pre-dam samples, *N. chemnitzii* would be absent and there would be less variance in predator size selectivity and drillhole stereotypy.

At two localities we sampled naticid shells and collected bivalve prey from the tidal flat and pre-dam era cheniers—dune-like structures composed primarily of molluscan remains. Naticids were sorted and counted by species. Variation in the stereotypic placement of drillholes in the pre- and post-dam construction eras was

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Smith, J.A., & Dietl, G.P. 2016. The value of geohistorical data in identifying a recent human-induced range expansion of a predatory gastropod in the Colorado River delta, Mexico, Journal of Biogeography: 43, 791-800, <https://doi.org/10.1111/jbi.12644>

assessed by grouping drillholes into a nine-sector grid superimposed on the prey's shell. Predator size was regressed on bivalve prey size to assess variation in predator size selectivity pre- and post-damming of the Colorado River.

As predicted, we found no *N. chemnitzii* in cheniers of pre-dam age whereas another naticid species, *Neverita reclusiana*, was common. *Notocochlis chemnitzii* and *N. reclusiana* were found in the actively forming chenier and on the tidal flat. As expected with the addition of another naticid species, the preferred site of drilling and size selectivity of prey by predators changed significantly between cheniers from the pre- and post-dam construction eras due to variation in prey-handling behavior by different naticid species.

Geohistorical evidence, from body and trace fossils, suggests that *N. chemnitzii* has recently expanded its geographic range to the CRE, whereas *N. reclusiana* has long dwelled in the delta. Geohistorical baseline data are an underutilized source of information that can provide unique ecological perspectives for restoration efforts in estuaries of dammed rivers worldwide.

Introduction

During the 20th century, humans dramatically altered rivers and their watersheds with countless dams, almost unanimously without consideration for ecological effects downstream (Rosenberg et al., 1997; Rosenberg et al., 2000; WCD, 2000; Glenn et al., 2013). As a result, habitat loss, biodiversity loss, and range shifts of species figure prominently as unintended costs (Rosenberg et al., 1997; Rosenberg et al., 2000 and references therein; Glenn et al., 2013 and references therein).

Throughout the Colorado River basin, for example, dams have captured and diverted the entirety of the basin's $c.$ $1.85 \times 10^{10} \text{ m}^3/\text{yr}$. of water in an attempt to quench the region's population and massive agricultural industry (Thompson, 1968; WCD, 2000). This complete allocation of the Colorado's water for societal use has stressed the downstream delta ecosystem (Glenn et al., 2013 and references therein). And, although it is certain that the ecosystem has been altered, a lack of pre-dam era studies has made assessing the extent of the dams' effect a considerable challenge (Kowalewski et al., 2000; Rodriguez et al., 2001; Cintra-Buenrostro et al., 2005).

In the absence of pre-dam studies, collecting baseline data on ecological aspects such as species geographic distribution and species interactions seems unlikely. Conservation palaeobiologists, however, through the application of palaeoecological theory and techniques, may be able to provide these critical data (Dietl et al., 2015 and references therein). Geohistorical records—data from the past that provide environmental and ecological information—are an untapped source of valuable information that can be directly applied to conservation issues ranging from the identification of invasive species (Chiba and Sato, 2014) to the documentation of range expansions in response to anthropogenic change (Yanes, 2012). We present a case study from the Colorado River delta (CRE) to demonstrate the application of geohistorical data in identifying the human-induced range expansion—defined here as a range expansion that occurs via natural processes but is induced by anthropogenic alterations to the ecosystem—of a predatory gastropod, *Notocochlis chemnitzii* Pfieffer, 1840.

In the CRE, a unique combination of sediment deposition and winnowing by wave action has created a set of dune-like structures, called cheniers, along the western shore of the northern Gulf of California (Thompson, 1968; Figure 1). The youngest chenier has been actively forming during the last 90 years. The two older cheniers formed in the pre-dam era between 90 – 1500 and 2000 – 5000 years ago (Kowalewski et al., 1994). These cheniers are composed of trillions of molluscan remains (Kowalewski et al., 2000) and represent the death assemblage—the taxonomically identifiable, dead remains encountered in a landscape or seabed (Kidwell, 2013)—from the pre-dam community. These molluscan remains hold the key to unlocking the ecological past of the delta's benthic community (e.g., Cintra-Buenrostro et al., 2005) and can provide baseline data that are urgently needed to inform restoration efforts in the region (e.g., Minute 319 environmental pulse flows; Flessa et al., 2013).

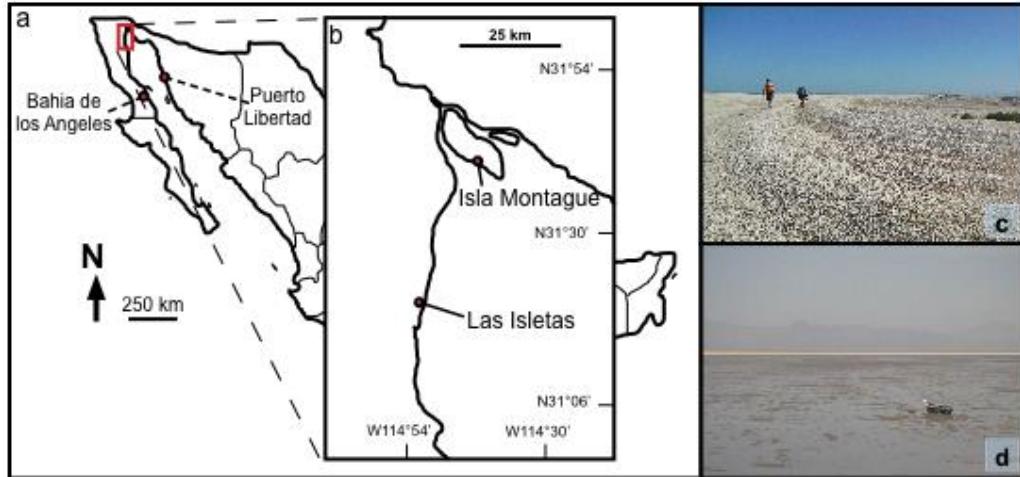


Figure 1 (a) Overview of sampling area. (b) Inset of 1a, sampling localities. (c) A pre-dam chenier at Las Isletas. (d) The tidal flat at Las Isletas.

To date, the application of geohistorical data in the CRE has focused on documenting the decline of the once abundant bivalve, *Mulinia modesta*, after the damming of the Colorado River (Kowalewski et al., 2000; Rodriguez et al., 2001; Cintra-Buenrostro et al., 2005). Prior to the upstream dams, when freshwater input reduced salinities below 10 PSU (Carbajal et al., 1997), *M. modesta* lived at densities of 50 individuals/m² and composed as much as 90% of the CRE molluscan fauna (Kowalewski et al., 2000; Rodriguez et al., 2001). Today freshwater input has ceased, however, and salinities in the estuary commonly exceed 40 PSU (Carriquiry and Sanchez, 1999). *Mulinia modesta* now composes less than 1% of the molluscan fauna, and the density of mollusks has dropped to 3 – 17 individuals/m² (Kowalewski et al., 1994; Avila-Serrano et al., 2006). The cessation of river inputs to the CRE has likely had widespread ecological consequences in the benthic community, especially for predators of *M. modesta* such as naticid gastropods, which drill a round hole through their prey's shell in order to feed (Cintra-Buenrostro et al., 2005; Figure 2).

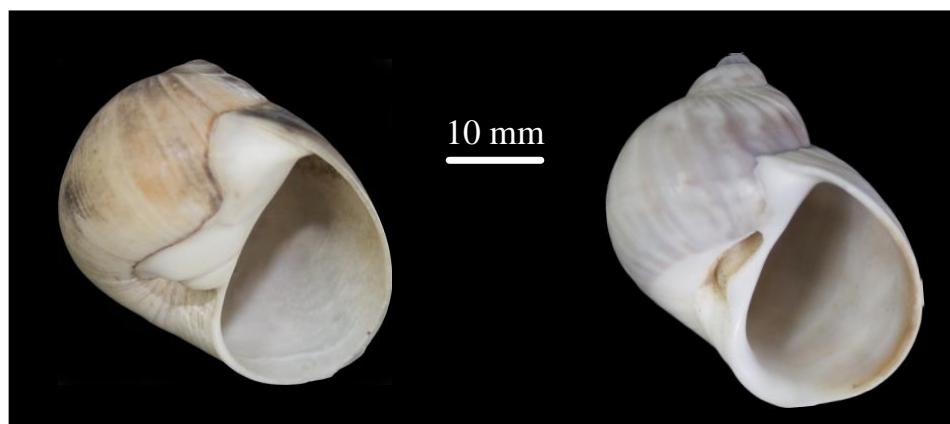


Figure 2 Specimens of *Neverita reclusiana* (top) and *Notocochlis chemnitzi* (bottom)

Two common naticid species have been reported from the CRE, *Notocochlis chemnitzii* and *Neverita reclusiana* (Kowalewski et al., 1994; Cintra-Buenrostro et al., 2005; Avila-Serrano et al., 2006; Figure 2). There is, however, some discrepancy in the literature regarding the presence and identification of these species. Kowalewski *et al.* (1994) identified ‘*Polinices* spp.’ in the cheniers, indicating that at least two species of naticids in the genus *Polinices* were present in the ‘modern’ (< 90 years ago) and ‘submodern’ (90 – 1500 years ago) cheniers. It is unclear whether multiple species were present at each chenier or whether naticids were simply lumped between localities, regardless of species. Cintra-Buenrostro et al. (2005) stated that *N. chemnitzii* was included within Kowalewski *et al.*’s (1994) *Polinices* spp. but did not provide any evidence for this assertion. The correct identification of the CRE naticid species is highly significant ecologically. If Kowalewski et al. (1994) were correct in their identification of *Polinices*, then *N. chemnitzii* should be considered a new addition to the CRE benthic community. If, however, Cintra-Buenrostro et al. (2005) were correct, *N. chemnitzii* has been a longstanding member of the benthic community.

Unfortunately, the specimens from Kowalewski et al. (1994) are no longer available for study to clarify this issue of species identity (Flessa, pers. comm. 2015). Museum collections, which can be excellent sources for baseline data (Winston, 2007; Lister and Climate Change Research Group, 2011), from the pre-dam era CRE are either absent or exist but do not contain *N. chemnitzii* (see Appendix 1). The absence of *N. chemnitzii* from the handful of pre-dam museum collections that are available does not eliminate the possibility that *N. chemnitzii* was present. In particular, because

benthic surveys only represent ecological snapshots of the molluscan community present at the time of sampling, it is conceivable that *N. chemnitzii* was missed. Here, we utilize geohistorical data, which are time-averaged over thousands of years, and represent the community average throughout the two millennia preceding the damming of the Colorado River (Kowalewski et al., 1998).

We use two lines of evidence from the geohistorical record to determine the proper status of *N. chemnitzii* in the CRE. First, we evaluate the occurrence of naticid body fossils from the cheniers and the modern tidal flat. Second, we examine a common naticid prey species, *Chionista fluctifraga*, for stereotypy in the location of drillholes and changes in prey selection by predators between the pre-dam and post-dam construction (hereafter post-dam) eras. Naticid predators exhibit a variety of species-specific prey-handling behaviors that can lead to interspecific variation in drillhole placement and differences in prey size selection (Kelley, 1988; Carriker and Gruber, 1999; Dietl and Kelley, 2006). We hypothesize that *N. chemnitzii* has recently expanded its range to the CRE and predict that: 1) *N. chemnitzii* body fossils will be absent from the pre-dam cheniers; and, 2) there will be greater variability in stereotypic drillhole placement and predator selectivity of prey size, evidenced by a lower correlation between predator and prey size, in the post-dam era due to the presence of a second naticid species.

Materials and Methods

Sample Collection

Specimens for this study were collected in 2012 and 2013 from the cheniers and tidal flat at Las Isletas, Mexico (Figure 1). This area is arid and hot, with an average annual precipitation < 70 mm, an evaporation rate up to 250 cm/yr. and water temperatures averaging between 15° and 30° C, seasonally (Thompson, 1968). Las Isletas was chosen for sampling due to its southern position in the CRE. This locality should be among the first areas where *N. chemnitzii* might be detected if it has recently expanded its range into the CRE. Additionally, Kowalewski et al. (1994) and Cintra-Buenrostro et al. (2005) based their conclusions on shells they identified from this locality.

At Las Isletas, cheniers of three ages, < 90 years, 90 – 1500 years, and 2000 – 5000 years, are present (Kowalewski et al., 1994) and each chenier was target and bulk sampled. Bulk samples—a method where all material from a randomly selected, volumetrically constrained area is sampled (Kowalewski, 2002)—were collected to ensure the inclusion of the smallest size specimens. At each chenier, two to three replicate bulk samples, approximately 0.006 m³ in volume, were collected at between two and six sites per chenier. Bulk samples were washed and sieved with 5-mm mesh.

Target samples, taken by between two and four collectors, were also collected at each Las Isletas chenier because less common and larger species are often missed in spatially restricted bulk samples (Ottens et al., 2012). Target sampling—a method in which all specimens of a taxon of interest are collected regardless of size or preservation quality within a specific area (Ottens et al., 2012)—was focused on *N.*

reclusiana, *N. chemnitzii*, and the bivalve species *C. fluctifraga*, a common prey item of naticids today. The tidal flat at Las Isletas, due to the sparseness of shells, was only target sampled and all naticids were collected, however, only recently dead *C. fluctifraga*, as indicated by their butterflyed appearance (Cadee, 2002) and intact ligament were collected.

In 2014, collections were made at a northern locality, Isla Montague, Mexico, near the mouth of the Colorado River to assess the possible geographic extent of the *N. chemnitzii* range expansion (Figure 1). At Isla Montague, bulk and target samples were taken from the single chenier at this locality. This chenier is still actively forming, as evidenced by partial submersion at high tide, although, it has been suggested that many of the shells composing this chenier are pre-dam in age (Rodriguez et al., 2001; Cintra-Buenrostro et al., 2005). It was not possible to survey the tidal flat at Isla Montague.

All naticids from both target and bulk samples at Las Isletas and Isla Montague were identified to the species level. All individuals were counted to test our first prediction that *N. chemnitzii* body fossils are absent from the pre-dam cheniers.

Trace Fossils

After collection, *C. fluctifraga* specimens from both localities, from bulk and target samples, were evaluated and those with complete shell margins were used to test our second prediction that variability in stereotypic drillhole placement and predator size selectivity changed in the post-dam era. Only specimens greater than 15 mm in shell length were included in analyses to eliminate potential size-related biases

between bulk and target sampling strategies (Ottens et al., 2012). Shells with drillholes were checked to ensure that naticid predators made the traces being considered (Figure 2). In the CRE benthic community, the predatory muricid gastropods *Muricanthus nigritus* and *Eupleura* spp. are potentially capable of drilling *C. fluctifraga*. *Muricanthus nigritus* have been observed in the field using a wedging behavior to grind away at the bivalves' shell margins, but they have not been observed drilling. Although other species of *Muricanthus* may be capable of drilling predation—*Muricanthus fulvescens* is known to drill and wedge bivalve prey on the southeastern Atlantic coast of the United States (Wells, 1958)—our observations of more than 30 *M. nigritus* (shell height c. 48 – 129 mm) on the tidal flat at Las Isletas suggest that they rely on wedging rather than drilling when feeding on *C. fluctifraga* (shell length c. 20 – 56 mm). *Eupleura*, however, have been observed drilling *C. fluctifraga* in the CRE. *Eupleura* in the CRE are small (maximum observed shell height = 55 mm) and the drillholes we have observed them making have been correspondingly small (mean outer diameter = 1.0 mm) and cylindrical in cross-section. Most drillholes examined for this study were too large (mean outer diameter > 2.0 mm) to have been made by *Eupleura*. In thin-valved prey, *Eupleura* and small naticid drillholes may be confused (Kowalewski, 1993), however, on thicker prey such as *C. fluctifraga*, the differences in typical outer drillhole diameter (ODD) and cross-sectional shape—naticid drillholes tend to be larger and parabolic (Kowalewski, 1993)—make the drillholes easily distinguishable. We are confident that the drillholes in our trace analysis originated during naticid predation events.

Drillhole stereotypy was determined by assigning each drillhole to a sector of the prey's shell using Kelley's (1988) nine-sector method (Figure 3). The correlation coefficient for the regression of predator size on prey size was estimated using ODD, a proxy for predator size, and prey shell length (Kitchell et al., 1981; Kelley, 1988). For each drilled valve, length—maximum distance from the umbo to the ventral shell margin—and ODD were measured to the nearest 0.1 mm.

Data Analysis

To test our first prediction, we used a Fisher's exact test to estimate any differences in the association of the naticid species, *N. reclusiana* and *N. chemnitzii*, with the pre- and post-dam era sampling time periods. Our second prediction contained two components: site stereotypy and size selectivity. For stereotypy, we used a Mann-Whitney U-test to evaluate differences in the distribution of drillholes. For selectivity, we used a one-tail Fisher's r-to-z transformation to convert the correlation coefficients of the regression between predator and prey size to statistically comparable z-values. Using the z-values, we tested the prediction that the correlation would be lower in the modern sample. All statistical analyses for this study were carried out using JMP PRO 10 (SAS Institute, 2012).

Results

Body Fossils

Notocochlis chemnitzii were only found in samples from the post-dam era whereas *N. reclusiana* were found in all samples regardless of age. A total of 88 *N.*

chemnitzii and 3783 *N. reclusiana*, in 58 target and 34 bulk samples, were collected from Las Isletas and Isla Montague (Table 1). In the two cheniers of pre-dam age from Las Isletas, no *N. chemnitzii* were found, as compared to 1194 *N. reclusiana* specimens. Similarly, at Isla Montague, five sites from the chenier were sampled resulting in the collection of zero *N. chemnitzii* and 947 *N. reclusiana*. *Notocochlis chemnitzii* were only found in the active chenier and on the tidal flat at Las Isletas (Fisher's Exact Test; $P < 0.0001$; Table 1).

Table 1 Specimen counts of *Neverita reclusiana* and *Notocochlis chemnitzii*.

Locality	Age (yrs)	Sites	Sample Type	# Samples	<i>Neverita reclusiana</i>	<i>Notocochlis chemnitzii</i>
Las Isletas	c. 0	*	Target	4	57	8
	< 90	2	Target	12	1344	73
			Bulk	6	241	7
	90-1500	6	Target	18	814	0
			Bulk	11	75	0
	> 2000	2	Target	6	195	0
			Bulk	2	10	0
	Isla Montague	< 90	5	Target	18	850
			Bulk	15	97	0

*Distinct sampling sites were not established due to the sparseness of shells on the tidal flat.

Trace Fossils

Stereotypy of drillhole placement and predator size selectivity both changed when comparing samples from the tidal flat to the chenier samples. Bulk and target samples yielded a total of 3486 shells of *C. fluctifraga*, of which 68% were collected from Las Isletas ($n = 2377$) and 32% from Isla Montague ($n = 1109$). Drilled *C. fluctifraga* specimens were only found at the pre-dam chenier ($n = 11$), active chenier ($n = 87$), and tidal flat ($n = 53$) at the Las Isletas locality. Thus, the trace fossil evidence presented hereafter will focus on specimens from Las Isletas.

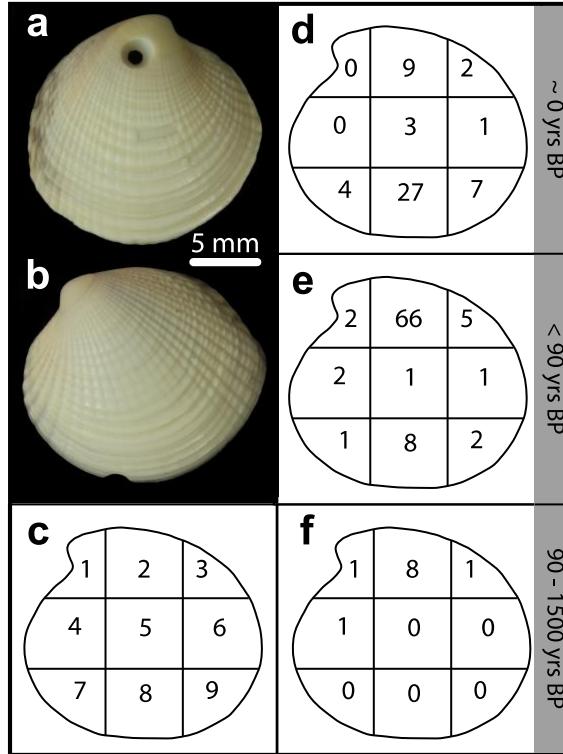


Figure 3 Drillhole stereotypy. (a) A wall drillhole in the sector 2 of *Chionista fluctifraga*, (b) An edge drillhole in sector 8 of *C. fluctifraga*. (c) Nine-sector grid of the bivalve shell (redrawn from Kelley, 1988). (d) Percentage of drillholes in each sector for *C. fluctifraga* from the tidal flat. (e) Percentage of drillholes in each sector for *C. fluctifraga* from the active chenier (< 90 years old). (f) Percentage of drillholes in each sector for *C. fluctifraga* from the middle age chenier (90 – 1500 years old).

When considering stereotypy, the distribution of drillholes on prey shells from the tidal flat was significantly different from both the active (Mann-Whitney U-test; $P < 0.0001$) and pre-dam chenier (Mann-Whitney U-test; $P < 0.0001$; Figure 3). The pre-dam and active chenier samples were not significantly different from each other (Mann-Whitney U-test; $P = 0.4333$). Drillholes from the pre-dam chenier were predominantly in sector 2 ($n = 8$; 73%), near the umbo of the shell. Sector 2 was also the most common location for drillholes from the active chenier ($n = 66$; 76%), but there was an additional cluster of drillholes in sector 8 ($n = 8$; 9%), along the shell margin. As with the other samples, tidal flat specimens had a large number of drillholes in sector 2 ($n = 9$; 17%), however, in this group the largest number of drillholes was in sector 8 ($n = 27$; 51%). Forty-six of the 48 (96%) drillholes in sectors 7, 8, and 9 were located on the edge of the shell (Figure 3).

The correlation coefficient for the relationship between predator size, using ODD as a proxy, and prey size was lower on the tidal flat ($r = 0.32$) than the active chenier ($r = 0.53$; one-tail Fisher's r-to-z transformation; $P = 0.0764$) and pre-dam chenier ($r = 0.77$), however, only the difference with the pre-dam chenier was significant (one-tail Fisher's r-to-z transformation; $P = 0.0344$). The correlation coefficient for the pre-dam sample is higher than the active chenier, but was not statistically different (one-tail Fisher's r-to-z transformation; $P = 0.117$).

Discussion

Multiple lines of evidence support the conclusion that *N. chemnitzii* is a recent addition to the CRE benthic community: (1) *N. chemnitzii* body fossils are absent from the pre-dam cheniers at Las Isletas and Isla Montague; (2) increased variability in drillhole stereotypy, and; (3) increased variability (i.e., scatter of points around the regression line) between prey size and outer drillhole diameter. This finding joins a growing list of examples documenting ecological change in the CRE since the diversion of water resulting from the damming of the Colorado River, such as declines in the *M. modesta* population (Kowalewski et al., 2000; Rodriguez et al., 2001).

Prediction 1: Body Fossil Evidence

Notocochlis chemnitzii body fossils were only found on the tidal flat and in the actively forming chenier at Las Isletas and were absent from all pre-dam era cheniers (Table 1), suggesting that *N. chemnitzii* only recently expanded its range to the CRE (see Appendix 2 for potential reasons why *N. chemnitzii* was restricted to a southern

range in the pre-dam era). Ecological change associated with water diversion is the most likely explanation, however, several other potentially biasing factors must be eliminated before accepting this conclusion. Kidwell (2013) proposed four alternatives, which are all based on arguments from negative evidence (see Appendix 3), that might explain the absence of a species from the death assemblage when it is rare (< 1% of individuals) in the live assemblage: under-sampling, collection bias, time-averaging, and taphonomic bias. We address and reject each of these alternative hypotheses below, strengthening our interpretation that ecological change in the CRE benthic community resulting from upstream water diversion is the most likely explanation for the *N. chemnitzii* range expansion.

Under-sampling

Under-sampling can potentially explain the presence of a species in a live assemblage when the species does not also occur in the death assemblage. In such a case, the death assemblage will have a relatively small sample size compared to the living assemblage and discordance (mismatch) between the live and death assemblages will be due solely to this discrepancy in sample sizes (Kidwell, 2013). In our collections, we found a total of 3783 naticid shells from the cheniers and tidal flats at two localities, Las Isletas and Isla Montague, using two different collecting methods, target and bulk sampling. Our pooled death assemblage differs from death assemblage samples (*sensu* Kidwell, 2013) in two ways: (1) shells from our chenier bulk samples have been condensed and transported from the nearby tidal flat with minimal between habitat mixing (Flessa et al., 1993; Kowalewski et al., 1998), and (2)

our target samples are focused on two species instead of the entire assemblage. Despite these differences, it is informative to use these samples to approximate the total size of the death assemblage that our naticid specimens would have been drawn from if we had sampled the entire assemblage.

Previous studies from the CRE tidal flat (Avila-Serrano et al., 2006) and cheniers (Kowalewski et al., 1994) have shown that naticids compose 0.26 – 0.4% of the total molluscan assemblage. In 112 samples at six tidal flat localities, Avila-Serrano et al. (2006) found 1954 individual specimens, including five naticids, distributed among 26 species. Kowalewski et al. (1994) collected 7870 molluscan specimens, including 34 naticids, belonging to at least 33 species in 61 samples from nine chenier localities. The agreement in low naticid abundance between these studies is not surprising given the well-documented high fidelity between live and death assemblages in estuaries (Kidwell, 2013). Assuming 0.26 – 0.4% is a representative range of naticid abundance from the hypothetical death assemblage to which our sampled naticids belonged, the 3783 total specimens we collected would have had to have come from a death assemblage sample size of 875,000 – 1,478,000 individuals. Under-sampling cannot explain the lack of *N. chemnitzii* in the death assemblage samples from the pre-dam cheniers.

Collection bias

Collection bias occurs when the sampling method being applied does not allow an equal probability for all individuals in a community to be sampled. This scenario is more commonly responsible for live-dead discordance when a species occurs in the

dead but not live assemblage, for instance, when a deep-living species is not collected because the sampling method used only sampled the top layers of sediment (Kidwell, 2013). Consequently, Kidwell (2013) lists collection bias as unlikely to account for the occurrence of rare species in only the live assemblage. This unlikelihood is especially true in our case given our target sampling method. Target sampling of death assemblages on cheniers and the tidal flat can cover the entire surface of a large sampling area (Ottens et al., 2012). Even if exceedingly rare in the ‘death assemblage,’ our sampling should have recovered at least a single *N. chemnitzii* specimen and, in fact, during our sampling we encountered many rare species including gastropods of the genera *Conus*, *Malea*, *Turritella*, *Fusinus*, *Ficus*, *Knefastia*, and *Bursa*. Collection bias cannot explain the presence of *N. chemnitzii* in the live assemblage and its absence from the pre-dam chenier death assemblage.

Time-averaging

Time-averaging can account for the live-only occurrence of a rare species when there is very little time-averaging in the death assemblage, such as in lagoonal environments where sedimentation rate is high and death assemblages are rapidly buried, or when the residence time of shells in the death assemblage is short due to low durability (see Taphonomic Bias below). We do not consider time-averaging to be a valid alternative on the CRE tidal flats, however, given that sedimentation rate in the CRE has dropped drastically since the damming of the Colorado River (Thompson, 1968), and that the chenier deposits are known to be time-averaged over at least 500 years (Kowalewski et al., 1998). More importantly, the process of chenier formation

includes a stage of sediment winnowing (Augustinus, 1989). As a result, in the CRE, the cheniers are composed almost entirely of molluscan shell remains (Thompson, 1968) and are not at risk of rapid burial as described by Kidwell (2013). Finally, the scale of time-averaging in the CRE greatly exceeds the time scale over which any live assemblage will be collected. For example, the live survey conducted by Avila-Serrano et al. (2006) spanned two years. In comparison to these snapshot census samples, 500 years does not qualify as ‘very little time-averaging.’ Time-averaging cannot explain the live-only occurrence of *N. chemnitzii*.

Taphonomic Bias

Taphonomic bias can explain the live-only occurrence of a species if that species has intrinsically low preservation potential (Kidwell, 2013). Processes such as shell transport in and out of habitats, fragmentation, differential weathering based on mineralogy, and the time-averaged nature of shell accumulations, are a few of the host of issues that can present challenges for conservation palaeobiologists when interpreting geohistorical data (Flessa et al., 1993; Kowalewski et al., 1998). In the CRE cheniers, the most apparent taphonomic effects on molluscan shells are a decrease in the luster of shells and, to a lesser degree, physical processes such as peeling, cracking, and fragmentation (Kowalewski et al., 1994). Whereas these effects may diminish the quality of preservation, it is highly unlikely that *N. chemnitzii* would have been uniquely affected by any of the above processes to the degree that it would have been removed entirely from the assemblage. It is also improbable that *N. chemnitzii* would have been removed completely by wave transport, as it has been

reported that between-habitat transport is uncommon in the northern Gulf today (Flessa et al., 1993), as well as in the geologic past (Meldahl, 1993).

In comparison to *N. reclusiana*, *N. chemnitzii* is similar in many of the aspects that would affect rates of taphonomic loss. For instance, they both have a globose shell and grow to similar sizes (mean height of c. 30 mm, measured from apex to base of aperture), meaning they should respond similarly in the same environmental context, such as under wave transport or burial. Based on these similarities and the abundant presence of *N. reclusiana* in our samples, one would expect that *N. chemnitzii* would be present in the cheniers if it had inhabited the tidal flat of the pre-dam CRE. Furthermore, *N. chemnitzii* has been reported from southern archaeological middens of similar age to the chenier deposits (Laylander et al., 2013) and Late Pleistocene fossil assemblages that greatly exceed the cheniers in age (Stump, 1975); if *N. chemnitzii* were preserved in these settings, they should also have been preserved in the comparably young chenier deposits. Taphonomy cannot explain the absence of *N. chemnitzii*.

Prediction 2: Trace Fossil Evidence

Trace fossil evidence from drillhole placement stereotypy and predator size selectivity support the conclusion from body fossils that *N. chemnitzii* only recently expanded its range to the CRE. Variance in stereotypy increased in the post-dam era due to the occurrence of drillholes on the edge of *Chionista fluctifraga* shells in sectors 7, 8, and 9 (Figure 3). The appearance of these edge drillholes suggests that a new predatory behavior has been introduced into the CRE, likely originating with *N.*

chemnitzii. Edge drilling, where a predator places its drillhole along the thin margin of its bivalve prey (Figure 3), shortens the duration of the predation process relative to the alternative behavior of drilling through the prey's thicker shell wall (Dietl and Herbert, 2005). This behavior has been noted in several naticid and muricid species (e.g., Dietl et al. 2004; Chattopadhyay et al. 2014). Although we have no direct evidence of *N. chemnitzii* edge drilling, edge drilled prey have only been found in post-dam samples associated with *N. chemnitzii* body fossils, suggesting that this species is most likely responsible for the traces. All other potential edge-drilling gastropod predators, including *Eupleura* spp., *Muricanthus nigritus*, and *N. reclusiana*, were present in deposits of both pre- and post-dam age, with and without edge-drilled bivalves. *Notocochlis chemnitzii* is the only species that is uniquely found alongside edge drilled prey and its congener, *N. unifasciata*, was recently reported to edge drill bivalve prey along the Pacific coast of Panama (Dietl et al. 2010). This evidence suggests that *N. chemnitzii* is responsible for the novel edge-drilling behavior in the CRE and we expect that field observations or lab experiments with live *N. chemnitzii* will validate this hypothesis.

The degree to which data points were scattered around the regression of predator size on prey size increased from the pre-dam chenier to the active chenier and to the tidal flat. Although the only significant increase in this variability (i.e., lower correlation coefficient) was between the pre-dam chenier and tidal flat, variability did increase from the tidal flat to the active chenier and from the active chenier to the pre-dam chenier. This increase is the expected result when a new naticid is added to the system and is due to the differing capabilities and preferences of naticids for capturing

prey (Carriker and Gruber, 1999; Dietl and Kelley, 2006). That is, similarly sized individuals from different predatory species tend to consume differently sized prey. Thus, there was a stronger correlation between predator and prey size when only *N. reclusiana* was present in the CRE than with the addition of *N. chemnitzii*, today. In addition to increasing the variability, the addition of *N. chemnitzii* changed the slope of the predator-prey size relationship (Figure 4). The slope of the relationship between sizes in the pre-dam era is relatively steep (0.09), drops slightly for the active chenier (0.07), and flattens considerably for the tidal flat (0.03). The statistically non-significant reduction in slope from the pre-dam to active chenier (ANCOVA, $P = 0.4979$) reflects the ages of shells composing the active chenier. The active chenier is composed of a large proportion of pre-dam age shells and relatively few post-dam age shells (Kowalewski et al., 1994; 1998), meaning the *N. chemnitzii* range expansion is only slightly detectable in predatory traces on *C. fluctifraga*. On the contrary, *C. fluctifraga* from the tidal flat are exclusively from the post-dam and the predatory traces fully reflect the addition of *N. chemnitzii*. This significant change from the pre-dam (ANCOVA; $P < 0.0001$) and active chenier (ANCOVA; $P = 0.0121$) in slope suggests a smaller *N. chemnitzii* is capable of consuming the same size prey as a larger *N. reclusiana*, and, given that the two species reach similar sizes, *N. chemnitzii* are capable of consuming larger prey overall. This inference is further supported when considering the size of prey drilled by wall and edge drilling. Edge drilled *C. fluctifraga* ($n = 46$; mean c. 27 mm) were significantly larger (Mann-Whitney U-test; $P < 0.0001$) than wall drilled *C. fluctifraga* ($n = 105$; mean c. 20 mm). Again, we expect future field observations and experimentation will support this interpretation.

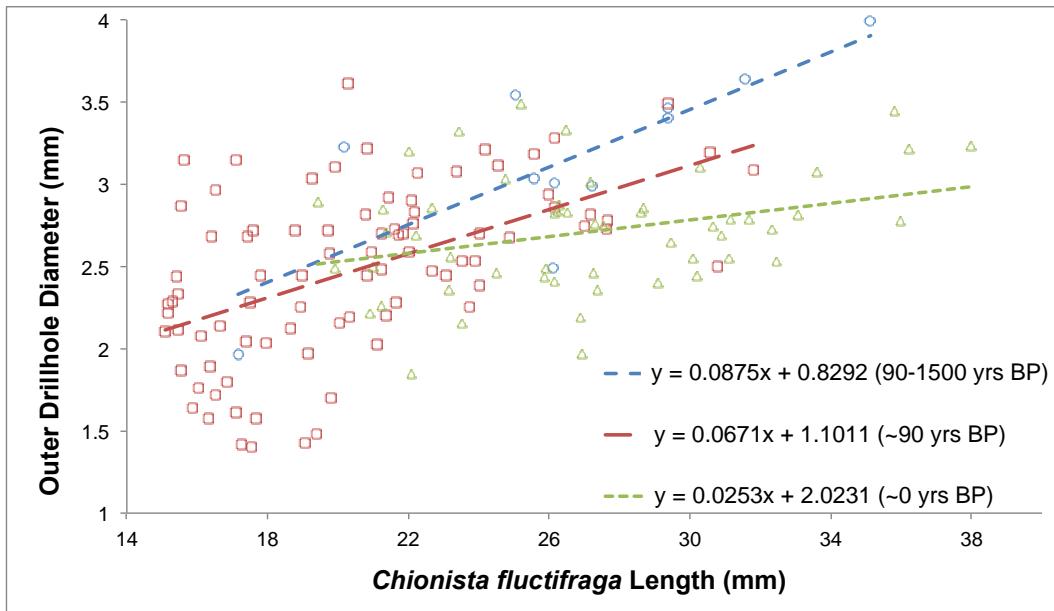


Figure 4 Regression of outer drillhole diameter, a proxy for predator size, on *Chionista fluctifraga* prey size. Regression excludes individuals smaller than 15 mm to account for potential bias in size between bulk and target sampling methods. Circles indicate data from the pre-dam chenier (90 – 1500 yrs BP). Squares are data from the active chenier (c. 90 yrs BP). Triangles represent data from the tidal flat (c. 0 yrs BP).

Ecological Implications

The presence of *N. chemnitzii* in the post-dam CRE may have broad ecological implications for the molluscan prey populations. Since the decline in *M. modesta* populations, *C. fluctifraga* has become one of the most abundant bivalves on the CRE tidal flat (Kowalewski et al., 1994) and may experience greater predation intensity as a result (Cintra-Buenrostro et al., 2005). With the expansion of *N. chemnitzii* and their ability to consume larger prey, this increased pressure may also extend to large *C. fluctifraga* that would have been too large for *P. reclusianus* to consume. Thus, predation by *N. chemnitzii* has likely affected *C. fluctifraga* population dynamics and may lead to declines in the *C. fluctifraga* population, as has occurred with other

introduced large predatory gastropods in other communities (e.g., predation by the invasive muricid gastropod *Rapana venosa* on bivalves in Chesapeake Bay; Harding, 2003; Harding et al., 2007).

Notocochlis chemnitzii may also be influencing the population of *N. reclusiana* through competition for prey, such as *C. fluctifraga*. Competition between these two naticid gastropods may occur in one of four ways: 1) no overlap in prey resources; 2) *N. chemnitzii* and *N. reclusiana* compete for prey but can coexist due to different prey size preferences; 3) *N. reclusiana* outcompetes *N. chemnitzii* for bivalve prey; and, 4) *N. chemnitzii* outcompetes *N. reclusiana* for bivalve prey. Given that *N. chemnitzii* are capable of preying on larger bivalve prey and that by edge drilling they can drill prey in less time than *N. reclusiana*, it seems likely that there already have been and will continue to be declines in the *N. reclusiana* population (see also Harding et al., 2007 for a similar effect of a novel behavior of an invasive predatory gastropod, *Rapana venosa*, on populations of the native drilling gastropod, *Urosalpinx cinerea*, in Chesapeake Bay). Furthermore, the addition of *N. chemnitzii* has created potential opportunities for interactions with dangerous prey (i.e., confamilial predation between *N. chemnitzii* and *N. reclusiana*; Dietl and Alexander, 2000). Future work should focus on differentiating among these alternatives and the direct and indirect ecological effects for the CRE benthic community.

Taxonomic Clarification

In light of our results, we suggest Cintra-Buenrostro et al. (2005) were partially correct in their interpretation of Kowalewski et al.'s (1994) species identifications:

Kowalewski et al. (1994) appear to have included *N. chemnitzii* under *Polinices* spp. Cintra-Buenrostro *et al.* (2005) were not, however, entirely correct in their assertion that *N. chemnitzii* was present in the pre-dam era. Instead, based on the results presented here, it is highly likely that Kowalewski et al. (1994) encountered *Polinices* in all cheniers and only found *N. chemnitzii* in the actively forming chenier, but, by not identifying naticids to the species level, conflated the species under the genus *Polinices*.

The Value of Geohistorical Data

The human-induced range expansion of *N. chemnitzii* documented in this study reveals the importance of incorporating geohistorical data into restoration efforts of dammed river systems, especially given the general lack of baseline data in these systems (WCD, 2000). To the best of our knowledge, *N. chemnitzii* is the first documented case of a marine molluscan range expansion related to the damming and diversion of the Colorado River. Without geohistorical data, *N. chemnitzii* appears to be a natural part of the molluscan community in the CRE and, in the event of a restoration effort (such as the environmental pulse-flows recently initiated in the CRE; Flessa et al., 2013), restoration goals might include enhancing *N. chemnitzii* populations alongside other species such as *M. modesta*. The geohistorical baseline data presented here, however, suggest that *N. chemnitzii* will not flourish under a return to pre-dam conditions and no ‘recovery’ should be expected, or encouraged.

Beyond the CRE, in other estuaries of dammed river systems around the world, species assemblages and their geographic ranges also often do not represent historical

(i.e., pre-dam) conditions given the wide-ranging effects of dams on estuaries (Rosenberg et al., 1997; Rosenberg et al., 2000; WCD, 2000; Dietl et al., 2015). In the absence of pre-dam baseline studies, geohistorical data are the lone source of information that can be used to elucidate past species distributions and other ecological attributes (Dietl and Flessa, 2011; Dietl et al., 2015) and could prove invaluable to restoration efforts in dammed river systems worldwide.

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CHAPTER 2

EFFECTS OF DAMS ON DOWNSTREAM MOLLUSCAN PREDATOR-PREY INTERACTIONS IN THE COLORADO RIVER ESTUARY

Abstract

River systems worldwide have been modified for human use and the downstream ecological consequences are often poorly understood. In the Colorado River estuary, where upstream water diversions have limited freshwater input during the last century, mollusk remains from the last several hundred years suggest widespread ecological change. The once abundant clam, *Mulinia modesta*, has undergone population declines of ~94% and populations of predators relying on this species as a food source have likely declined, switched to alternative prey species, or both. We distinguish between the first two hypotheses using a null model of predation preference to test whether *M. modesta* was preyed upon selectively by the naticid snail, *Neverita reclusiana*, along the estuary's past salinity gradient. To evaluate the third hypothesis, we estimate available prey biomass today and in the past, assuming prey were a limiting resource. Data on the frequency of drill holes—identifiable traces of naticid predation on prey shells—showed several species, including *M. modesta*, were preferred prey. *Neverita reclusiana* was likely able to switch prey. Available prey biomass also declined, suggesting the *N. reclusiana* population also likely declined. These results indicate a substantial change to the structure of the benthic

food web. Given the global scale of water management, such changes have likely also occurred in many of the world's estuaries.

Introduction

Nearly two-thirds of the world's major rivers have been captured, diverted, or otherwise modified for human use (Nilsson et al., 2005). Given the world's growing population, the utilization of riverine resources (e.g., hydroelectric power, potable water) will remain high for the foreseeable future (Christensen et al., 2004; US Department of Interior, 2011; Wada and Bierkens, 2014). At the same time, the downstream ecological implications (i.e., trade-offs) of upstream water management decisions are not well understood, often for a lack of pre-management data (Auerbach et al., 2014; Cloern et al., 2016; Smith et al., 2016). That is, we have an incomplete accounting of how management decisions (e.g., dam construction, water diversions) affect downstream communities and species interactions, particularly in estuaries. In estuarine environments, where sedimentation rates are high and many organisms (e.g., mollusks) have hard skeletal components, pre-management data may still be within reach (e.g., (Kowalewski et al., 2000; Dietl and Smith, 2017; Martinelli et al., 2017)).

In the Colorado River estuary (CRE), for example, accumulations of molluscan remains have been utilized to better understand the community that existed prior to widespread damming and water diversion along the Colorado River during the twentieth century (Kowalewski et al., 2000; Rodriguez et al., 2001; Cintra-Buenrostro et al., 2005). Much of this previous work focused on the once dominant clam, *Mulinia modesta* (formerly *M. coloradoensis*; see Coan and Valentich-Scott, 2012). Densities

of *M. modesta* exceeded 50 individuals/m² during the pre-dam era—defined as the time period prior to the beginning of dam construction in the 1930s—and are scarce on the tidal flat today (Kowalewski et al., 2000; Rodriguez et al., 2001; Avila-Serrano et al., 2006; Dietl and Smith, 2017). Consequently, *M. modesta* is no longer the most abundant clam in the CRE (Kowalewski et al., 2000; Dietl and Smith, 2017) and its role in estuarine carbon cycling has diminished proportionately (Smith et al., 2016). Furthermore, upon examination of the shells of 600 pre-dam era *M. modesta* individuals for traces of predation at Las Isletas (Figure 5), Cintra-Buenrostro et al. (Cintra-Buenrostro et al., 2005) found 23% had drill holes made by predatory snails (naticids and muricids; see Figure 5d), 27% had damage on the margins of their shells consistent with successful crab predation, and 34% had repair scars from unsuccessful crab attacks. These results led Cintra-Buenrostro et al. (2005) to propose three related hypotheses based on the importance of *M. modesta* as a food source for snails and crabs. They hypothesized *M. modesta* population declines likely resulted in corresponding declines in the populations of predatory species (hypothesis 1), switching by predators to alternative prey species (hypothesis 2), or a combination of both effects (hypothesis 3).

Here we evaluate the preference—defined as deviation from a random diet—of the shell-boring naticid *Neverita reclusiana* (Figure 5c) for *M. modesta*, with respect to potential alternative prey in the pre-dam era molluscan community, to differentiate between these hypotheses. As with many naticid species, *N. reclusiana* use a combination of acidic secretions and a scraping radula to bore characteristic drill

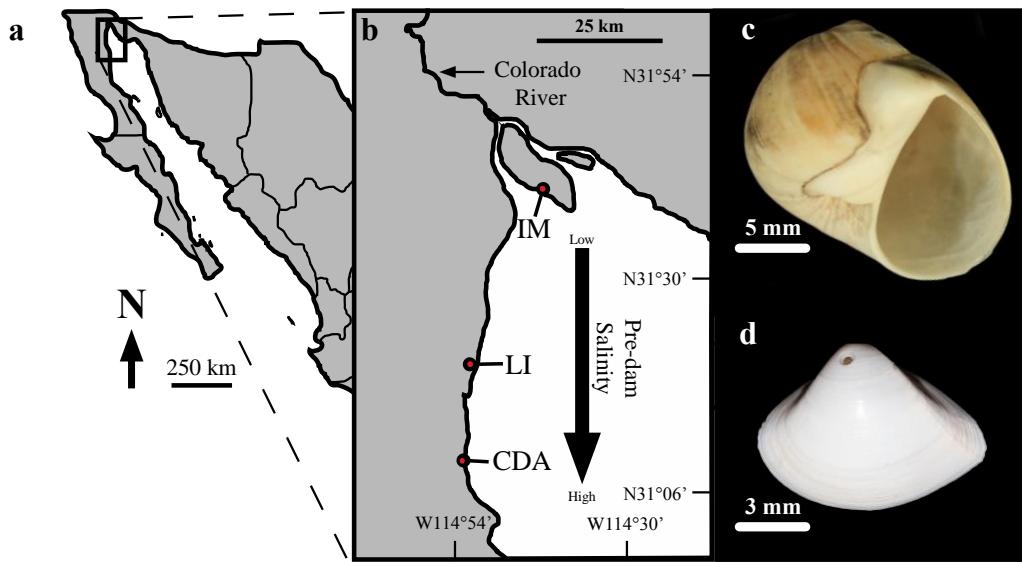


Figure 5 (a) Location of the Colorado River estuary with (b) an inset showing the study sites. Specimens of the (c) drilling snail *Neverita reclusiana* and (d) once-common clam *Mulinia modesta*. Note the predatory drill hole near the umbo of *M. modesta*. IM = Isla Montague; LI = Las Isletas; CDA = Campo don Abel.

holes into the shells of their prey (Figure 5d; (Carriker, 1961)). These trace fossils are readily preserved and record a reliable record of past predator-prey interactions (Kowalewski et al., 1998a). Although naticid drill holes made by individuals of different species can be challenging to differentiate (Dietl and Kelley, 2006) and two naticid species are present in the CRE today, *N. reclusiana* was likely the only naticid present in the pre-dam era (Smith and Dietl, 2016). Thus, using the trace fossil record of *N. reclusiana* and a metric of prey preference by predators (Manly's alpha; Manly et al., 1972; Chesson, 1978, 1983) we evaluate the potential ecological effects of dam construction and water diversion on predator-prey interactions in the CRE. If *N. reclusiana* disproportionately preyed on *M. modesta* (i.e., a non-random diet composed mainly of *M. modesta*) then the *N. reclusiana* population will likely have

declined alongside the *M. modesta* population (hypothesis 1). Alternatively, if *N. reclusiana* selectively consumed other prey, in addition to *M. modesta*, it is more likely that switching from *M. modesta* will have occurred, as *N. reclusiana* compensated for the population decline of *M. modesta* (hypothesis 2). Because support for hypothesis 2 cannot conclusively rule out the possibility of a *N. reclusiana* population decline, we subsequently use estimates of past and present prey densities on the CRE tidal flat to assess whether the potentially supportable population size of *N. reclusiana* has changed (hypothesis 3).

Methods

Sampling

Samples were taken from the molluscan death assemblages at three sites in the CRE—Isla Montague, Las Isletas, and Campo don Abel—following the north-south salinity gradient that existed prior to widespread damming and water diversions in the Colorado River basin, which began in the 1930s (Cintra-Buenrostro et al., 2012); Figure 5). Shells in the death assemblages are time-averaged, but dating via amino acid racemization of *Chionista fluctifraga* has shown that more than three-fourths of shells originated 100–300 years ago, during the pre-dam era (Kowalewski et al., 1998). The death assemblage samples were collected from cheniers—sedimentary deposits that are formed through shoreward tidal movement and accumulation of large clasts (e.g., shells) and the removal of smaller clasts (e.g., clays, silts) by longshore currents (Augustinus, 1989)—at each site. Three samples (~10 L) were collected at Isla Montague and Las Isletas and five (~2 L) were collected at Campo don Abel.

Samples were taken at random at a spacing of approximately 30 m from the top 10 cm of chenier surfaces (~0.25–0.50 m²), which are well-mixed with the subsurface (Kowalewski et al., 1998). All samples were wet sieved using a 5-mm mesh in the laboratory, all individuals were identified to the species level, and all predatory drill holes were tallied. Only specimens judged to be at least 85% complete were included and clam count totals were halved to estimate their abundance to account for each individual specimen having two elements (i.e., left and right valves of the shell; Kowalewski, 2002). For each sample, species with more than 150 specimens were randomly subsampled (see Appendix 4). Because drilling predation by species of the snail family Muricidae can be readily confused with naticid drill holes in thin-shelled clam prey (Kowalewski, 1993), all drill holes were measured across their outer diameter and their position on the prey shell recorded to distinguish between predators. Drill holes that were small (<1.0 mm in outer diameter) or did not have the characteristic countersunk appearance of a naticid drill hole were not included in the analysis as there is greater likelihood that they were made by a muricid rather than a naticid snail (Kowalewski, 1993, 2002). If after this filtering there was still ambiguity as to the origin of the drill hole, the location of the drill hole on the shell was evaluated because naticid predation is highly stereotyped in site selection (e.g., Kelley, 1988)—particularly as compared to the most common drilling muricid, *Eupleura limata*, in the CRE (pers. obs; Kowalewski, 1993)—such that drill holes are commonly found near the umbo in clam prey (Figure 5d).

Analysis of Preference

We applied the preference metric proposed by Manly et al. (Manly et al., 1972) and further developed by Chesson (1978, 1983; see also Manly et al., 2007)—hereafter referred to as Manly’s alpha—to distinguish between the first two hypotheses. Manly’s alpha incorporates drilling frequency and normalizes species-specific drilling frequencies for the entire community:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^m r_j/n_j}, i = 1, \dots, m \quad (1)$$

where r_i is the number of prey type i that are drilled, n_i is the number of individuals from species i in the community, and m is the number of prey types (Smith et al., 2018). To calculate a normalized α_i , species-specific r_i/n_i (i.e., drilling frequency) is divided by the sum of all species’ drilling frequencies (Chesson, 1983). If the predator only consumes prey type i , the value of α_i will be 1, whereas if prey type i is always avoided the value of α_i will be 0. If a predator is not selective, α_i will be equivalent to $1/m$ prey types in the community. We applied this non-selective scenario as a null model for predator preference to test the hypothesis that *M. modesta* was the preferred prey of *N. reclusiana* during the pre-dam era in the Colorado River estuary.

At each site, specimen and drill hole counts for those species that were drilled at least once were used to calculate species-specific Manly’s alpha values according to equation 1. As such, the results discussed below provide a conservative estimate of *N. reclusiana* preference because the removal of species not likely to be in the diet of *N. reclusiana* increases the null threshold ($\alpha_i = 1/m$) used to evaluate the preference for each species. Independently at each site, species-specific alphas were compared to the

null alpha value ($\alpha_i = 1/m$) using Bayesian posterior distributions to evaluate the probabilities that naticids exhibited preference for the respective prey species. Additionally, using a Bayesian formulation, each species' alpha was compared to the *M. modesta* alpha value to give the probability that *M. modesta* was more greatly preferred than the second species. Low species-specific sample sizes (e.g., $n < 25$), which commonly occur in paleocommunities and in the CRE dataset, can make interpretations difficult due to the high degree of uncertainty associated with small samples (Kowalewski, 2002). Although it does not completely alleviate the issue, the Bayesian formulation employed here provides more information than a traditional, frequentist approach, including true probability statements derived from posterior distributions and credibility intervals (Korner-Nievergelt et al., 2015). Analyses were conducted in R (see Smith et al., 2018 for R code and a discussion of practical considerations when applying Manly's alpha to paleoecological data).

Molluscan Biomass in the CRE

Estimates of *N. reclusiana* densities have not previously been made for the pre- or post-dam era. Therefore, in order to evaluate hypothesis 3, that *N. reclusiana* switched prey and its population declined, we used estimates of prey density on the CRE tidal flat and naticid energetic needs to estimate the maximum *N. reclusiana* populations that could potentially be supported during the pre- and post-dam eras. We restrict prey here to clams, as data on snails are limited. After accounting for breakage of shells in the cheniers, Kowalewski et al. (2000) estimated densities of large (> 12.5 mm) *M. modesta* in excess of 50 individuals/m² in the pre-dam era. In contrast, today,

the density of large clams—predominantly *C. fluctifraga* and *M. modesta* (Dietl and Smith, 2017)—is approximately three individuals/m². Given that the CRE tidal flat is approximately 1.2 x 10⁸ m² (Kowalewski et al., 2000), a density of 50 clams/m² is equivalent to a population of 6.0 x 10⁹ clams. Comparatively, a density of three clams/m² amounts to a population of 3.6 x 10⁸ clams (see Appendix 5).

Using estimates of naticid energetic requirements from the literature for a phylogenetically closely related species, *Neverita duplicata*, it is possible to estimate the number of *N. reclusiana* that could be sustained on those prey populations, assuming prey were a limiting resource and that all other variables (e.g., pathogens; predation on *N. reclusiana*) remained constant. Studying the western Atlantic species *N. duplicata*, Edwards and Huebner (1977) estimated annual energetic requirements of approximately 385 kilojoules for a large individual (~39 mm in maximum diameter), or 218 kilojoules for a small individual (~25 mm in maximum diameter). Using a prey size of 25 mm in shell length—a prey size both “small” or “large” naticids could likely consume—we apply an energetic value of 3.09 kilojoules/ind. for *M. modesta* and 3.31 kilojoules/ind. for *C. fluctifraga* (see electronic Appendix 5 for calculations and conversion factors) to estimate the size of the *N. reclusiana* population that could be supported during the pre-dam era and today.

Results and Discussion

Predator Preference in the CRE

Neverita reclusiana exhibited preferences for multiple prey species at each of the three sites in the pre-dam era CRE and those preferences were variable among

sites (Figure 6). These results (see electronic Appendix 6 for species-specific data) were confirmed when considering all species in the analysis regardless of whether they were drilled (Appendix 6) and only the subset of species shared between sites (Appendix 7).

At Isla Montague, which had the lowest average salinities due to its northern position near the mouth of the Colorado River (Cintra-Buenrostro et al., 2012), nine species were included in the analysis and *M. modesta* was a preferred prey ($\alpha_{M.m} = 0.205$; Probability $\alpha_{M.m} > \alpha_0 = 0.827$; $\alpha_0 = 0.111$). Additionally, the Bayesian formulation of alpha values found that *Eupleura limata* ($\alpha_{E.l.} = 0.209$; Probability $\alpha_{E.l.} > \alpha_0 = 0.830$) and *Felaniella sericata* ($\alpha_{F.s.} = 0.386$; Probability $\alpha_{F.s.} > \alpha_0 = 0.872$) were preferred (Figure 6a). The probabilities that *M. modesta* had a higher alpha value than the latter two species were relatively low (Probability $\alpha_{M.m} > \alpha_{E.l.} = 0.477$; Probability $\alpha_{M.m} > \alpha_{F.s.} = 0.302$), supporting the conclusion that alternative prey species were preferred along with *M. modesta*.

Thirteen species were included in the analysis of *N. reclusiana* preference at the middle site, Las Isletas. Several species were preferred ($\alpha_0 = 0.077$)—*Chionopsis gnidia* ($\alpha_{C.g.} = 0.239$; Probability $\alpha_{C.g.} > \alpha_0 > 0.999$), *E. limata* ($\alpha_{E.l.} = 0.123$; Probability $\alpha_{E.l.} > \alpha_0 = 0.957$), *Lamelliconcha concinnus* ($\alpha_{L.c.} = 0.137$; Probability $\alpha_{L.c.} > \alpha_0 = 0.794$), *Cosmioconcha palmeri* ($\alpha_{C.p.} = 0.106$; Probability $\alpha_{C.p.} > \alpha_0 = 0.780$)—however, *M. modesta* was not among them ($\alpha_{M.m} = 0.081$; Probability $\alpha_{M.m} > \alpha_0 = 0.571$; Figure 6b). Furthermore, all four species were likely more preferred than

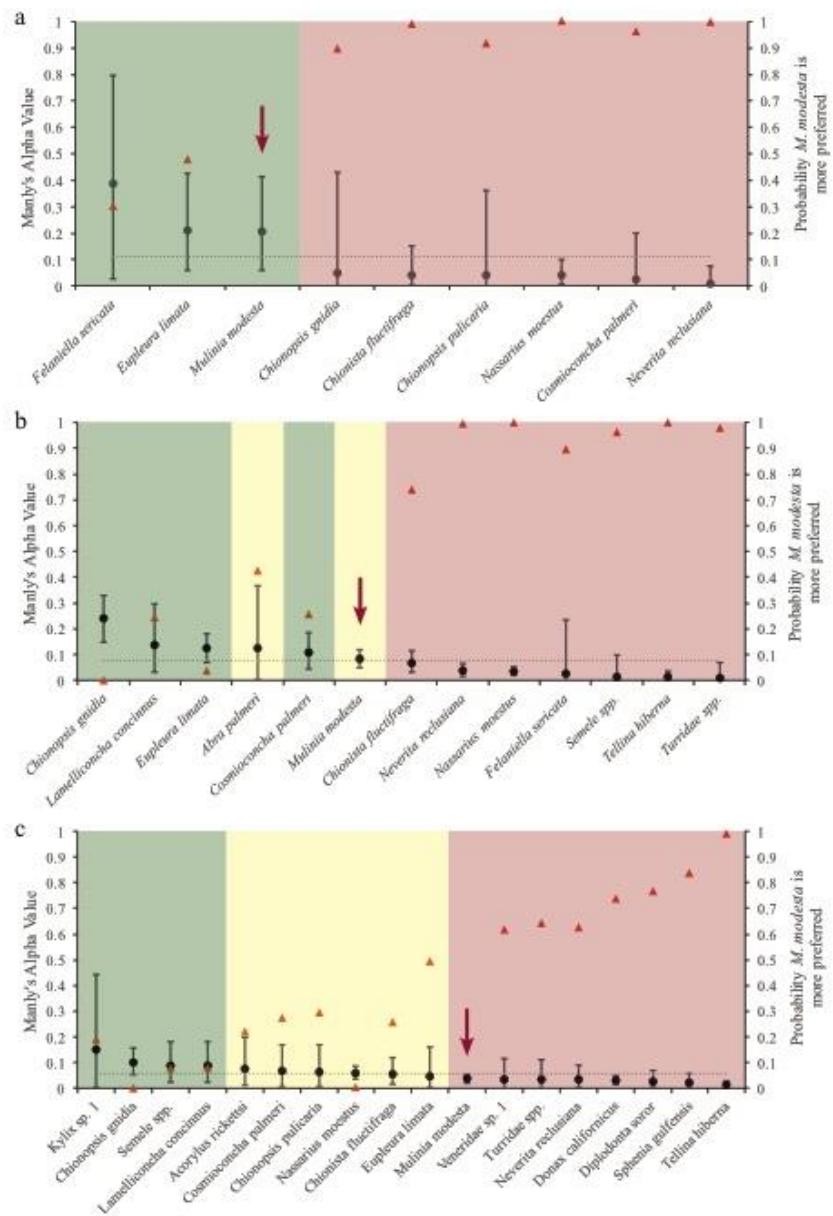


Figure 6 *Neverita reclusiana* preferences (primary axis) for molluscan prey species at Isla Montague (a), Las Isletas (b), and Campo don Abel (c) and probabilities that *Mulinia modesta*, indicated by the red arrow in each panel, was more preferred than the other prey species (secondary axis, red triangles). Green shading indicates prey species were likely more preferred than predicted by the null condition ($\alpha_i = 1/m$). Yellow shading indicates preference was indistinguishable from the null condition. Red shading indicates prey species were likely less preferred than predicted by the null condition. The dashed line in each panel represents the site-specific null alpha value and the black bars around the estimates of Manly's alpha give the 95% credibility interval.

M. modesta by *N. reclusiana*, as probabilities of *M. modesta* having a greater alpha value were < 0.001, 0.038, 0.242, 0.257, respectively. The results from Las Isletas support the second hypothesis that *N. reclusiana* preferred prey species other than *M. modesta*.

Mulinia modesta ($\alpha_{M.m} = 0.035$; Probability $\alpha_{M.m} > \alpha_0 = 0.017$; $\alpha_0 = 0.056$) was not a preferred prey species of *N. reclusiana* at the southernmost site, Campo don Abel, where salinities during the pre-dam era were approximately normal marine (i.e., 34 psu) during much of the year (Cintra-Buenrostro et al., 2012). Of the remaining 17 prey species, four had alpha values indicating a greater than 70% probability of being preferred and an additional five species were likely preferred over *M. modesta* (Figure 6c). With respect to the hypothesis being tested here, that *M. modesta* is more preferred than other potential prey species in the community (hypothesis 1), the evidence from these prey species (e.g., *C. gnidia*: $\alpha_{C.g.} = 0.099$, Probability $\alpha_{C.g.} > \alpha_0 = 0.969$, Probability $\alpha_{M.m} > \alpha_{C.g.} < 0.001$; *L. concinnus*: $\alpha_{L.c.} = 0.085$, Probability $\alpha_{L.c.} > \alpha_0 = 0.737$, Probability $\alpha_{M.m} > \alpha_{C.p.} = 0.078$) suggests that many other species were preferred over *M. modesta*.

In the pre-dam era CRE, *M. modesta* was one of the only preferred prey species in the north, but was not a preferred prey species at the middle or southern sites (Figure 6). The increase in salinity from north to south during the pre-dam era (Cintra-Buenrostro et al., 2012) likely explains the observed differences in *N. reclusiana* preference for prey (see Appendix 7 for discussion and dismissal of alternative explanations of the preference trend).

As described by the Estuarine Quality Paradox (Remane and Schlieper, 1958; Dauvin, 2007; Elliott and Quintino, 2007), brackish environments often exclude species because the natural conditions in those environments are physiologically unfavorable (Gainey and Greenberg, 1977; McLusky and Elliott, 1981). Likewise, naticid predation intensity has been shown to decrease as salinities approach brackish conditions (e.g., Hanks, 1953; Broom, 1982). Accordingly, community-wide drilling frequency and prey species richness in the CRE increased southward, away from the brackish salinities (Figure 7). Drilling frequency on *M. modesta* followed a similar trend but alpha values for *M. modesta* did not (Figure 7). *Mulinia modesta*, like the congeneric Atlantic *M. lateralis* (Levinton and Bambach, 1970), is an opportunistic species that thrives in disturbed habitats, such as the brackish CRE (Rodriguez et al., 2001), setting it apart from many of the species in the CRE metacommunity that were absent in the north. With the southwardly increasing prey richness and predation

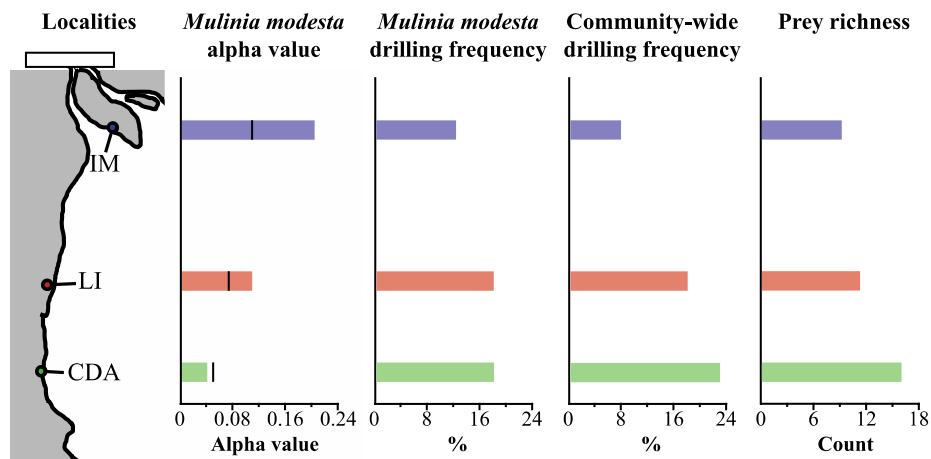


Figure 7 Summary of *Neverita reclusiana* predation on *M. modesta* (alpha, drilling frequency) compared to community-wide drilling frequency and richness of prey species along north-south salinity gradient in the Colorado River estuary. Black bars indicate the null condition for alpha values at each site.

intensity, a more complete picture of *N. reclusiana* prey preference presents itself. *Mulinia modesta* was likely preferred in the north due to the scarcity of more highly preferred prey species (i.e., $n < 10$; see Appendix Table 6; Smith et al., 2018). Moving to the southernmost site, *M. modesta* was still abundant in the community (27%; Rodriguez et al., 2001), suggesting that it should have been commonly encountered by *N. reclusiana*. Yet, more favorable prey (e.g., more energetically favorable; *sensu* Kitchell et al., 1981) became available to *N. reclusiana* as the environmental conditions became more amenable to a wider range of prey species. Indeed, the *M. modesta* alpha value (0.035) indicates that, if all species present in the south were equally abundant, *M. modesta* would only compose 3.5% of the *N. reclusiana* diet. In contrast, when *N. reclusiana* had fewer species to select from in the north, *M. modesta* would have contributed 20.5% to the *N. reclusiana* diet (Figure 7). Based on these results for the preference of *N. reclusiana*, it is likely that this predatory species was able to switch to alternative prey species as the *M. modesta* population declined during the post-dam construction era, supporting hypothesis 2.

Molluscan Biomass in the CRE

The analysis performed here clearly demonstrates *N. reclusiana* had preferences for a variety of prey species in the pre-dam era and it was likely capable of switching to alternative prey (hypothesis 2). Preference for alternative prey is not, however, sufficient evidence to dismiss the possibility of a concurrent reduction in the *N. reclusiana* population. Using estimates from the literature on clam abundance and energetics (Appendix 5), we found that a naticid must consume between 66 (all *C.*

fluctifraga, small naticid) and 125 (all *M. modesta*, large naticid) prey individuals each year to meet its minimum energetic requirements. Assuming a constant *M. modesta* population (50 ind./m²) and applying these values to the total tidal flat area (1.2 x 10⁸ m²; Kowalewski et al., 2000) yields a maximum pre-dam era density of 0.40 – 0.71 naticids/m², or a standing population of 4.82 x 10⁷ – 8.51 x 10⁸ individuals. Comparatively, the clam population on the tidal flat today (3 ind./m²)—predominantly *C. fluctifraga* and *M. modesta* (Kowalewski et al., 2000; Dietl and Smith, 2017)—can only support a maximum density of 0.02 – 0.05 naticids/m², or a population of 2.89 x 10⁶ – 5.47 x 10⁶ naticids. These estimates are only a conservative approximation of the naticid population, as they do not incorporate snail prey species and the parameters used in the calculations were not derived from CRE species. Nonetheless, these estimates demonstrate the potential implications of the decline in clam density in the CRE if prey were a limiting resource. Specifically, it is highly likely that the *N. reclusiana* population has also declined in response to the reduction in clam biomass on the CRE tidal flat, supporting hypothesis 3.

Ecological Change in the CRE

Our analyses suggest that *N. reclusiana* has very likely switched to alternative prey species in the absence of *M. modesta* and its population has likely also declined due to a reduction in biomass of potential clam prey on the CRE tidal flat. With respect to the hypotheses proposed by Cintra-Buenrostro et al. (2005) it would seem that their third option, “both effects,” has the most support. We have, of course, only evaluated the hypothesis for one of the three groups of predators considered by Cintra-

Buenrostro et al. (2005), with muricid snails and crabs remaining unstudied. The response of the shell-boring *E. limata* is likely most similar to *N. reclusiana* given the mode of predation. The response of other predators—including the shell-grinding muricid, *Hexaplex nigritus*, and shell-crushing or shell-peeling crabs—to the reduction in clam biomass may differ due to differences in predatory behaviors, perhaps with greater effect depending on their prey preferences. As the thick-shelled *C. fluctifraga* has become the most abundant clam in the CRE (Dietl and Smith, 2017), predatory behaviors that were sufficient for thin-shelled *M. modesta* prey may no longer be effective. Indeed, Smith and Dietl (Smith and Dietl, 2016) reported the human-induced range expansion of the naticid snail, *Notocochlis chemnitzii*, into the CRE and its novel utilization of edge-drilling behavior to more efficiently drill thick clam prey at their thinner shell margin rather than through the relatively thick umbonal region. Although none of the species discussed here have become locally extinct since the pre-dam era, their relative abundances and strengths of interactions in the CRE have undeniably changed. Given the importance of snail and crab predators in the benthos (Virnstein, 1979; Broom, 1982; Peterson, 1982; Mansour and Lipcius, 1991; Anderson, 1992), it is highly likely that the entire food web has been affected.

A Tangled Web of Altered Estuarine Interactions for the World's Major River Systems

Just as upstream water management decisions along the Colorado River have altered species interactions and food web dynamics in the downstream CRE, there have likely been substantial ecological consequences in the estuaries of other major

rivers that have been altered for human use (Cloern et al., 2016). As with the CRE, pre-impact ecological data were not recorded in most estuaries but are likely attainable through the utilization of the geohistorical data recoverable from molluscan remains (Dietl and Smith, 2017; Martinelli et al., 2017). Given that estuaries tend to be highly productive ecosystems and are consequently of economic importance (Costanza et al., 1997), understanding shifts in estuarine food web dynamics resulting from past, present, and future water management decisions may have profound implications for the people relying on estuarine ecosystems for goods (e.g., shellfisheries for food) and services (e.g., nutrient cycling). If, in the future, society chooses to attempt the restoration of these estuarine ecosystems, or elects to alter them further, species interactions, not just species abundances and distributions, must be considered.

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CHAPTER 3

LIVE-DEAD ANALYSIS REVEALS LONG-TERM RESPONSE OF THE ESTUARINE BIVALVE COMMUNITY TO WATER DIVERSIONS ALONG THE COLORADO RIVER²

Abstract

Dam construction and water diversions along the Colorado River during the twentieth century have altered the downstream estuarine ecosystem. Although it is clear that the ecosystem has changed, a lack of pre-impact studies has made it challenging to determine the magnitude and direction of change. By using a paleontological approach, we can retrospectively estimate ecological conditions in the estuary from before dam construction, particularly for benthic organisms with preservable hard parts, such as the shells of bivalve mollusks. Here, for the first time, we quantify differences in evenness, richness, taxonomic similarity, and rank-order abundance between the bivalve community living in the estuary today and two potential geohistorical baselines, the accumulated dead shells on the tidal flat and an older accumulation—known to pre-date dam construction on the river—in nearby shell-rich beach ridges called cheniers.

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Analysis of more than 12,000 live and dead bivalves distributed among 18 species collected from the tidal flat and cheniers on Isla Montague—an island at the mouth of the Colorado River—indicates that the pre-dam bivalve community was dominated by *Mulinia modesta* and was characterized by low rarefied species richness and evenness (indexed by Hurlbert's Probability of Interspecific Encounter). The increase in these metrics in the live relative to the chenier assemblage reflects a shift in the estuary from brackish to full marine conditions after damming and water diversions reduced freshwater flow to the estuary during the twentieth century. The tidal flat death assemblage was more similar to the live assemblage, which suggests that it represents a shifted baseline, due to a large input of recent shells, whereas the chenier assemblage is a robust pre-impact baseline. Taxonomic similarity and rank-order abundance, indexed by Jaccard-Chao and Spearman's Rho metrics, respectively, were too conservative to detect these differences.

These baseline data, most notably the documented changes between the live and chenier assemblages, can be used to assess the efficacy of restoration efforts in the estuary, such as the Minute 319 environmental pulse flows. If restoration efforts stimulate a response in the bivalve community, metric values for evenness and richness are expected to decrease and become more similar to those we report here for the pre-impact chenier assemblage.

Introduction

The management of river systems throughout the world has led to widespread human-induced changes in downstream habitats from riparian corridors to estuaries

(World Commission on Dams, 2000; Nilsson, 2005; Cloern et al., 2015). The effects in estuaries can be particularly acute and include the alteration of nutrient cycles (Casey et al., 2014), physical habitat structure (Yang et al., 2011), and other abiotic conditions (Herbert et al., 2011). It is also possible for multiple effects to occur in concert, further increasing the stress on ecosystems (Cloern et al., 2015). In the Colorado River estuary (CRE), for instance, damming and water diversions along the Colorado River have resulted in a net fining of the sediments in the CRE and an increase in salinity from brackish to full marine conditions (Thompson, 1968; Cintra-Buenrostro et al., 2012). In the last several decades, subsequent ecosystem changes have ranged from decreased wetlands coverage (Zamora-Arroyo et al., 2005; Zamora-Arroyo and Flessa, 2009) to reduced nursery habitat for economically viable shrimp and fish populations (Galindo-Bect et al., 2000; Rowell et al., 2005).

While it is clear that the CRE has changed since the beginning of dam construction along the Colorado River in the 1930s, a lack of pre-dam era (prior to 1930) data has made it challenging to elucidate the full range of the ecological effects. Nearly one hundred years later, ecological data from the pre-dam era may seem unattainable, however, through the application of geohistorical records—sediment cores, tree ring series, fossils, and other natural archives that provide environmental or biological information about the past (NRC, 2005)—such data are within reach (Dietl et al., 2015). The utility of information derived from fossils (*sensu* Kowalewski, 2009), the main source of pre-dam era ecological data in the CRE, is largely limited to taxa with preservable hard parts (e.g., mollusks, echinoderms, corals), but when

considering such taxa the records can be highly reliable, particularly when using count data (Kidwell, 2013).

For CRE bivalve mollusks, which are excellent indicators of ecological change due to their relatively long lifespan (years to decades) and sensitivity to the environment (Warwick et al., 1990; Zenetos, 1996; Mahmoud et al., 2010; La Valle et al., 2011; Nerlović et al., 2011; Coelho et al., 2014; Velez et al., 2016), geohistorical data form the basis for understanding the scope of ecological change in the post-dam construction era (hereafter, "post-dam era"; Kowalewski et al., 2000; Cintra-Buenrostro et al., 2005, 2012). In the pre-dam era, *Mulinia modesta* accounted for as much as 95% of the bivalve community (Kowalewski et al., 1994; Rodriguez et al., 2001a) and it has been suggested that they were an important food source for predators such as crabs and fish (Cintra-Buenrostro et al., 2005). Based on volumetric estimates of pre-dam era shell accumulations and the density of *M. modesta* in those accumulations, Kowalewski et al. (2000) estimated that *M. modesta* lived at densities in excess of 50 individuals/meter² on the pre-dam era tidal flat. In contrast, surveys of the live community show that *M. modesta* are rare today and the density of bivalves has dropped to 3–17 individuals/meter² (Kowalewski et al., 2000; Avila-Serrano et al., 2006). The reduction of the *M. modesta* population is likely an ecologically meaningful change, however, to date, there has not been a quantitative assessment of abundance and composition changes for the entire bivalve community. That is, aside from *M. modesta* abundance, we do not know how other species in the bivalve community responded to changing ecological conditions related to dam construction and water diversions from the Colorado River in the past.

Whereas a survey of the live community (e.g., Avila-Serrano et al., 2006) can improve our understanding of the structure and composition of the current bivalve community, it does not provide any context for how the community has been affected by reduced freshwater and fining sediments in the CRE. A geohistorical approach, using the bivalve death assemblage (DA)—the taxonomically identifiable, dead remains encountered in a seabed or landscape (Kidwell, 2013)—can provide this much needed insight from the past. Death assemblages in estuaries accumulate over an extended period of time (i.e., decades to centuries) and so provide a record of the average ecological and environmental conditions (Kidwell, 2013). Thus, by comparing the DA with the live assemblage (LA) it is possible to assess changes in the community over time in response to impacts as varied as waste water input (Leshno et al., 2015) and fishing pressure (Casey et al., 2014). In the CRE, the scale of time-averaging in the DA has not been documented, but, because DAs in estuaries tend to be averaged over decades or centuries (Kidwell, 2013), it likely is heavily influenced by post-dam era inputs; that is, the baseline may have shifted. Shifting baselines are a well-documented phenomenon wherein the basis for comparison does not reflect true historical conditions (Pauly, 1995; Jackson et al., 2012). Geohistorical records can be useful for elucidating baseline shifts by providing a means to recognize that ecological conditions have changed, establishing the timing and drivers of that change, and, ultimately, establishing a true baseline for “what was natural” (Jackson et al., 2012; Dietl et al., 2015).

Consequently, it may be necessary to go deeper in time to establish a robust pre-dam baseline, which is possible in the CRE due to shell-rich ridges composed

primarily of molluscan remains, called cheniers (Kowalewski et al., 1998). The cheniers on the beachfront are actively forming but Kowalewski et al. (1998) found that 83% (n=40) of dated shells originated between 100 – 300 years ago (i.e., during the pre-dam era). Here, using geohistorical data from the chenier death assemblage (cDA) in tandem with the tidal flat death assemblage (tDA), we establish a baseline for the ecological structure of the pre-dam era bivalve community for the first time. Additionally, through comparison with the LA, the DA (chenier and tidal flat) data provide a context-based set of reference conditions for the post-dam era that can be used in the future to assess restoration actions that have implications for the bivalve community. Although the entire CRE will likely never be restored to its pre-dam era state, the results presented here will clarify what is possible through restoration and give an indication of what is required to recover a natural range of variability for faunal composition, structure and dynamics (Palmer et al., 2006).

Methods

Sample Collection

Samples for this study were collected in March 2014 at two sites on Isla Montague, Mexico (Figure 8). Isla Montague was chosen as the sampling area due to its location in the mouth of the Colorado River. Live and dead samples were collected over the course of multiple low tides to approximate a rectangular grid pattern. The coordinates of each sample location were recorded with a hand-held Garmin GPS (+/- 10 m). At site 1, the sampling area was 300 m by 400 m and a total of 36 samples were taken at intervals of 40 to 70 m (Figure 7c). At site 2, 55 samples were collected

from an area of 210 m by 320 m at intervals of 20 to 40 m (Figure 7d). At each sampling point, a 25 cm x 25 cm quadrat was tossed at random and, at the point where it fell, the top 20 cm of sediment was exhumed. Each sample was sieved onsite with a 5-mm mesh and all live and dead specimens were collected. Five cheniers adjacent to the tidal flat on Isla Montague were also sampled (Figure 7b). These cheniers are similar to the actively forming cheniers dated by Kowalewski et al. (1998). Because

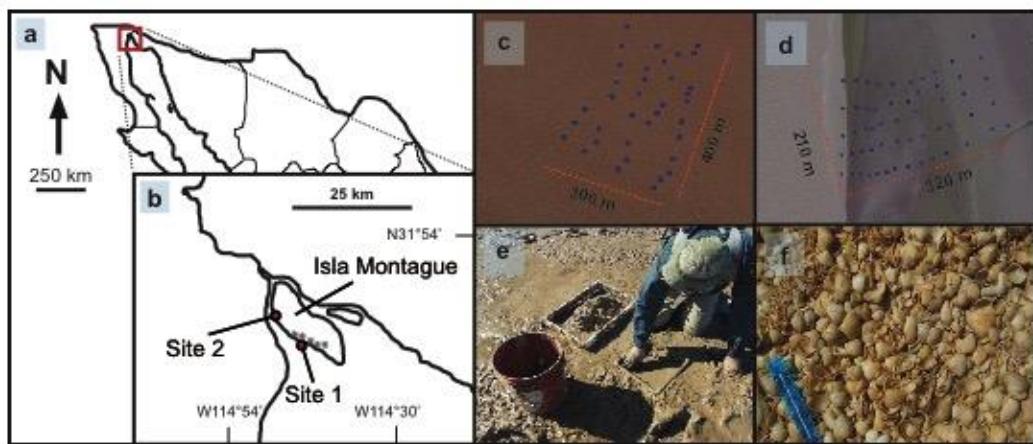


Figure 8 (a) Overview of sampling area. (b) Inset of 1a; sampling sites at Isla Montague. Gray asterisks are chenier locations. (c) Live assemblage and tidal flat death assemblage samples at Site 1. (d) Live assemblage and tidal flat death assemblage samples at Site 2. (e) Example of sampling on tidal flat. (f) Close up of shells in a chenier. Notice the dominance of *Mulinia modesta*.

they are highly condensed shell accumulations, $\sim 0.006 \text{ m}^3$ bulk samples—which contained all of the material from a randomly selected, volumetrically constrained area (Kowalewski, 2002)—were taken at each chenier. The bulk samples were subsequently sieved with a 5-mm mesh. All individuals from the LA, tDA, and cDA were identified to the species level and counted. Live assemblage samples were counted based on whole individuals. For DA samples, a single identifiable component, the umbo, was counted to account for shell breakage. Given that bivalves have two

elements (i.e., left and right valves), DA count totals were halved to provide a conservative estimate of abundance (Kowalewski, 2002).

Data Analysis

Four community metrics (taxonomic similarity, rank-order abundance, evenness, and richness) were utilized to detect any shifts in response to changes in the environment related to the reduced freshwater flow to the estuary after damming of the Colorado River was completed, as some species will not tolerate the changing ecological conditions and others might thrive. Multiple metrics were applied to the LA and DA data in order to maximize the detection of differences between assemblages (Kidwell and Tomasovich, 2013; Casey et al., 2014; Korpanty and Kelley, 2014; Leshno et al., 2015). For analysis, live and dead data from all samples were combined to provide an averaged assemblage, accounting for potential biases due to spatial variability on the tidal flat. Given that cheniers form through the consolidation of shell material from the entire tidal flat (Augustinus, 1989), pooling the tidal flat data increases the similarity between assemblages by minimizing differences in the amount of spatial averaging (see Olszewski and Kidwell, 2007).

Taxonomic similarity and rank-order abundance

The effect of reduced freshwater flow on the taxonomic composition of the local community was quantified with the Jaccard-Chao (JC) taxonomic similarity index. JC values were compared between the LA, tDA, and cDA. The index ranges from 0 (no shared taxa) to 1 (all taxa shared) and is preferred to other metrics for

taxonomic similarity (e.g., Jaccard, Bray-Curtis) because it gives a better account of rare taxa and alleviates statistical artifacts arising from differences in sample size between assemblages (Chao et al., 2005; Kidwell, 2007). To calculate JC, count data from each assemblage, were input to and run in the statistical program EstimateS 9.1.0 (Colwell, 2013).

Spearman's rank-order abundance (Rho) was calculated using species count data via Wessa's (2016) rank-correlation calculator to detect shifts in the abundance structure of the bivalve community. When the rank-order abundance of species in one assemblage is opposite to that which it is being compared, the resulting Rho value is -1. If the rank-order is identical, Rho will be 1. Rho is highly sensitive to major changes in order (e.g., a species shifting from first to last) but does not change appreciably when changes are minor (e.g., a species shifting from second to third; Kidwell, 2009).

Taxonomic similarity and rank-order abundance are often plotted together to determine changes to the structure of molluscan communities (after Kidwell, 2007) and this approach was followed here. Data points falling in the upper right quadrant of the JC-Rho plot are taken to indicate good agreement between assemblages. Any points falling in the other three quadrants suggest disparity between assemblages (Kidwell, 2007).

Evenness

Evenness was calculated using Hurlbert's (1971) Probability of Interspecific Encounter (PIE). PIE values will be low—close to 0—when one or few species

dominate an assemblage. As the abundance of species becomes more uniform in an assemblage PIE values approach 1, with a value of 1 representing a completely uniform distribution of individuals between species.

Richness

Rarefaction curves were generated for each assemblage using Holland's (2015) Analytic Rarefaction to elucidate any differences in species richness (number of species). In order to compare richness between samples of different sizes, the curves were truncated at the lowest sampling interval ($n=84$, LA). Curve shapes were assessed and compared visually, with steep curves indicating that a large fraction of species have not been sampled and flat curves indicating that most species have been sampled.

Results

A total of 12,382 bivalve specimens distributed amongst eighteen species was collected at the two sampling sites (Table 2). The LA ($n=84$) contained only four species, of which, 73% ($n=61$) were from a single species, *Chionista fluctifraga*. Fourteen species were sampled from the tDA ($n=2,665$), which was dominated by *Mulinia modesta* ($n=2,257$; 85%). Similarly, *M. modesta* composed 98% ($n=9,410$) of the cDA ($n=9,633$) despite the presence of twelve additional species.

Taxonomic similarity and rank-order abundance

All of the data points fall within the upper right quadrant of the JC-Rho plot indicating that there is no distinguishable difference between the LA, tDA, and cDA comparisons (Figure 9). The Rho values vary from 0.30 to 0.78 but, given that Rho can range from -1 to 1, these values indicate good agreement between the rank-order abundance of the different assemblages. Likewise, there is strong agreement between assemblages when examining taxonomic similarity, as JC values ranged from 0.99 to 1.00.

Evenness

PIE values increase from the oldest to the youngest assemblage (Figure 10). In the cDA, PIE was 0.05 and increased to 0.27 in the tDA. PIE was greatest in the LA, at 0.43. These data indicate that the modern bivalve community is considerably more even than the community from the pre-dam era, while tDA evenness was intermediate.

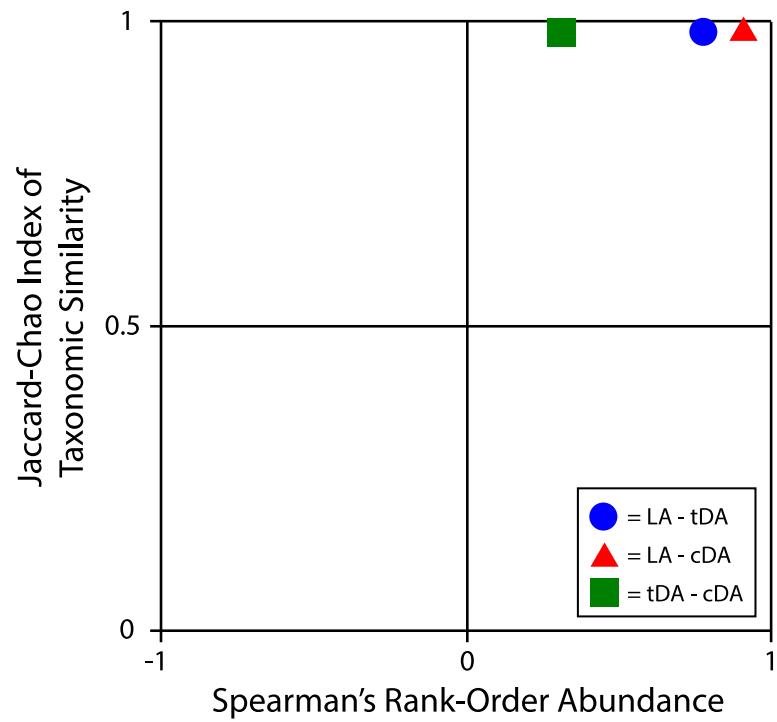


Figure 9 Plot of Jaccard-Chao taxonomic similarity (JC) versus Spearman's rank-order abundance (Rho). LA = live assemblage; tDA = tidal flat death assemblage; cDA = chenier death assemblage. Legend shows comparisons.

Table 2 Species abundances in the live assemblage (LA), tidal flat death assemblage (tDA), and chenier death assemblage (cDA).

Species	LA	tDA	cDA
<i>Anomia peruviana</i>	0	1	1
<i>Argopecten</i> sp.	0	3	1
<i>Chionista fluctifraga</i>	61	164	119
<i>Chionopsis gnidia</i>	0	3	1
<i>Cumingia pacifica</i>	3	20	6
<i>Cyclinella saccata</i>	0	1	0
<i>Donax gracilis</i>	0	0	1
<i>Fellaniella sericata</i>	0	1	1
<i>Kurtiella regueroae</i>	0	0	1
<i>Macoma</i> sp.	0	3	0
<i>Mulinia modesta</i>	19	2257	9410
<i>Petricola parallelia</i>	0	17	0
<i>Pitar concinnus</i>	0	0	1
<i>Protothaca</i> sp.	0	0	2
<i>Strigilla cicercula</i>	0	2	0
<i>Tagelus affinis</i>	1	188	88
<i>Tellina</i> sp. 1	0	3	0
<i>Tellina</i> sp. 2	0	2	1
TOTAL	84	2665	9633

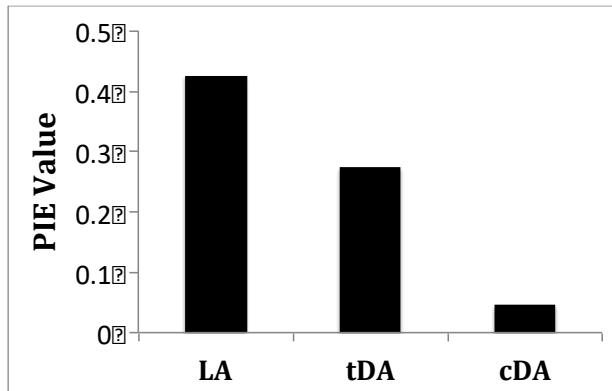


Figure 10 PIE values for the live assemblage (LA), tidal flat death assemblage (tDA), and chenier death assemblage (cDA).

Richness

Rarefaction of the bivalve community with a standardized sample size of 84 individuals shows the cDA has the lowest richness ($n=2.3$), whereas the LA ($n=4$) and tDA ($n=4.4$) have higher, nearly equal values (Figure 11). The tDA has the highest value. The slope of the tDA curve is slightly steeper than that of the LA, suggesting that there are more species remaining to be sampled in the tDA than in the LA.

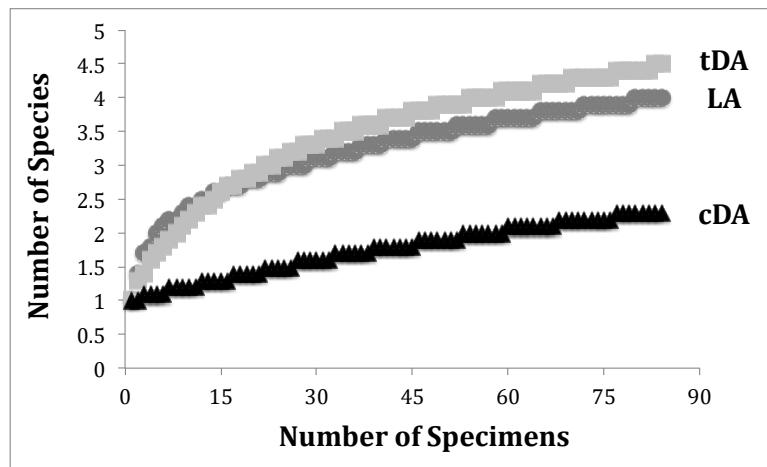


Figure 11 Rarefaction curves for the live assemblage (LA), tidal flat death assemblage (tDA), and chenier death assemblage (cDA). Sample size was standardized to 84 specimens.

Discussion

Evenness and richness give a clear indication of ecological change in the CRE during the post-dam era but taxonomic similarity and rank-order abundance (as evident in the JC-Rho plot) do not detect this change. It seems likely that the tDA is not a true pre-dam era baseline; that is, it appears to be heavily influenced by inputs from the post-dam era. While the tDA baseline has shifted, the cDA provides a robust pre-dam era baseline that can be used to guide restoration actions towards a more resilient CRE ecosystem (Palmer et al., 2006).

Comparison of metrics

JC and Rho remained relatively unchanged between assemblages due to the similarity of the species and their relative abundances. All of the species found in the LA were also found in the tDA and cDA (Table 2), which explains the high JC values. Likewise, for Rho, the changes in relative abundance are minor; that is, species only shift one or two positions in rank-order. Hence, in the absence of large shifts (e.g., first to last), Rho values remain high. The lack of change detected by these metrics is not an artifact of small sample size, as the minimum recommended JC-Rho sample size of 20 individuals (Kidwell, 2007) is exceeded here by four-fold.

In order for JC and Rho to detect change, a significant turnover is required in the community (Kidwell, 2007). Although the size of the *M. modesta* population has declined considerably (Kowalewski et al., 2000), this shift seems to have been the only major change in the abundance structure of the CRE bivalve community. And, while this decline may have wide-reaching ecological implications (Cintra-Buenrostro

et al., 2005), *M. modesta* is still the second most common bivalve species in the CRE. Thus, we suggest that in communities dominated by single species, the JC-Rho approach (*sensu* Kidwell, 2007) may be too conservative (see also Casey et al., 2014; Leshno et al., 2015). Furthermore, a post-hoc manipulation of the cDA data showed that neither JC nor Rho values changed appreciably even with the reduction of *M. modesta* abundances by an order of magnitude or more (Appendix 8). In cases such as these, metrics (e.g., PIE) that are more sensitive to within-species abundance fluctuations may be better suited to detect ecological changes, as evenness does in the CRE bivalve community.

In contrast to the JC-Rho data, the LA, tDA, and cDA PIE values show a stepwise increase in evenness from the past to the modern. Given the reported dominance of *M. modesta* in the pre-dam era (Kowalewski et al., 2000), the low PIE value of 0.05 is to be expected. The PIE value from the tDA (0.27) is much more similar to the LA (0.43), suggesting that the tDA is composed largely of post-dam era shells. In many cases DA PIE values are, on average, 0.20 greater than LA PIE values due to time-averaging and taphonomic bias (Olszewski and Kidwell, 2007). Hence, the true tDA PIE value likely falls between 0.07 – 0.27, reflecting an average of the LA and cDA as would be expected if the tDA is influenced by shell inputs from both the pre-and post-dam eras. Whereas the tDA PIE value should be viewed cautiously due to this bias, the difference between the LA and cDA PIE values should be given more weight. Given that the cDA PIE value is already approaching zero (due to a 98% *M. modesta* composition), the LA-cDA difference is strong evidence for ecological

change, especially because alternative factors that might influence comparisons between assemblages can be eliminated (See Appendix 9).

The richness data are in agreement with the evenness data and suggest that ecological change has occurred in the post-dam era. The rarefaction curve showed that richness in the cDA was much lower than in the LA and tDA. With regard to time-averaging, this is an unexpected result. Time-averaging typically leads to the accumulation of rare taxa, and a corresponding increase in species richness, correlated to the timespan over which an assemblage is averaged (Olszewski and Kidwell, 2007; Tomašových and Kidwell, 2010). The cheniers, which are time-averaged over centuries (Kowalewski et al., 1998), should thus have higher richness than the tDA, which is likely averaged over decades (Kidwell, 2013), and much greater richness than the LA, which is a snapshot in time. This disparity in richness is highlighted further upon closer examination of the tDA and cDA datasets. Although the total number of species sampled in these assemblages was similar, 13 in the cDA and 14 in the tDA, the total number of specimens differs greatly, 9,633 compared to 2,665, respectively (Table 2). These data further support the conclusion that ecological change has occurred in the CRE.

Evenness and richness both suggest that an ecological change has occurred in the CRE in response to changing salinities and fining sediments in the post-dam era but the direction of change is counterintuitive. For both metrics, high values are considered “good” and low values are generally taken to be indicative of poor ecosystem “health” (Gray, 2001; Johnston and Roberts, 2009). It may seem strange then to argue that restoration efforts in the CRE should aim to restore a community

with low values for both metrics. It is, however, important to consider that in the pre-dam era the CRE was a brackish estuary, whereas today it is a fully marine system (Rodriguez et al., 2001b). Brackish conditions are often considered stressful and such conditions can limit the number of species in the ecosystem (Dauvin, 2007; Elliott and Quintino, 2007), although not all species are adversely affected. *Mulinia modesta* thrives in brackish conditions (Rodriguez et al., 2001a), hence its dominance in the pre-dam era. On the contrary, with marine salinities, more species are able to cope with the abiotic conditions, resulting in increased evenness and richness. Thus, in the CRE, what seems to be a counterintuitive result based on colloquial conceptions of evenness and richness for a ‘healthy’ ecosystem is an expected result and indicates a significant ecological change resulting from the abiotic alterations associated with the damming and diversion of the Colorado River during the twentieth century.

Shifting baselines and geohistorical data

The similarity between the LA and tDA in this study demonstrates the necessity of a deeper-time baseline, when evaluating anthropogenic effects that occur on the scale of tens to hundreds of years. Without the inclusion of the older cDA here, the results of this study would have suggested that no change had occurred in the CRE bivalve community between the pre- and post-dam eras. This study highlights the need for baselines to be chosen on a scale that is appropriate for the potential ecological changes, which can vary from decades to millennia, that are being assessed (Kidwell, 2009; Weber and Zuschin, 2013; Casey et al., 2014). In many cases (e.g., the CRE bivalve community), geohistorical records are the only available source of data that

can provide temporally appropriate baselines and offer a means to avoid the issue of shifting baselines (Pauly, 1995; Jackson et al., 2012; Dietl et al., 2015).

Extending live-dead studies beyond the baseline

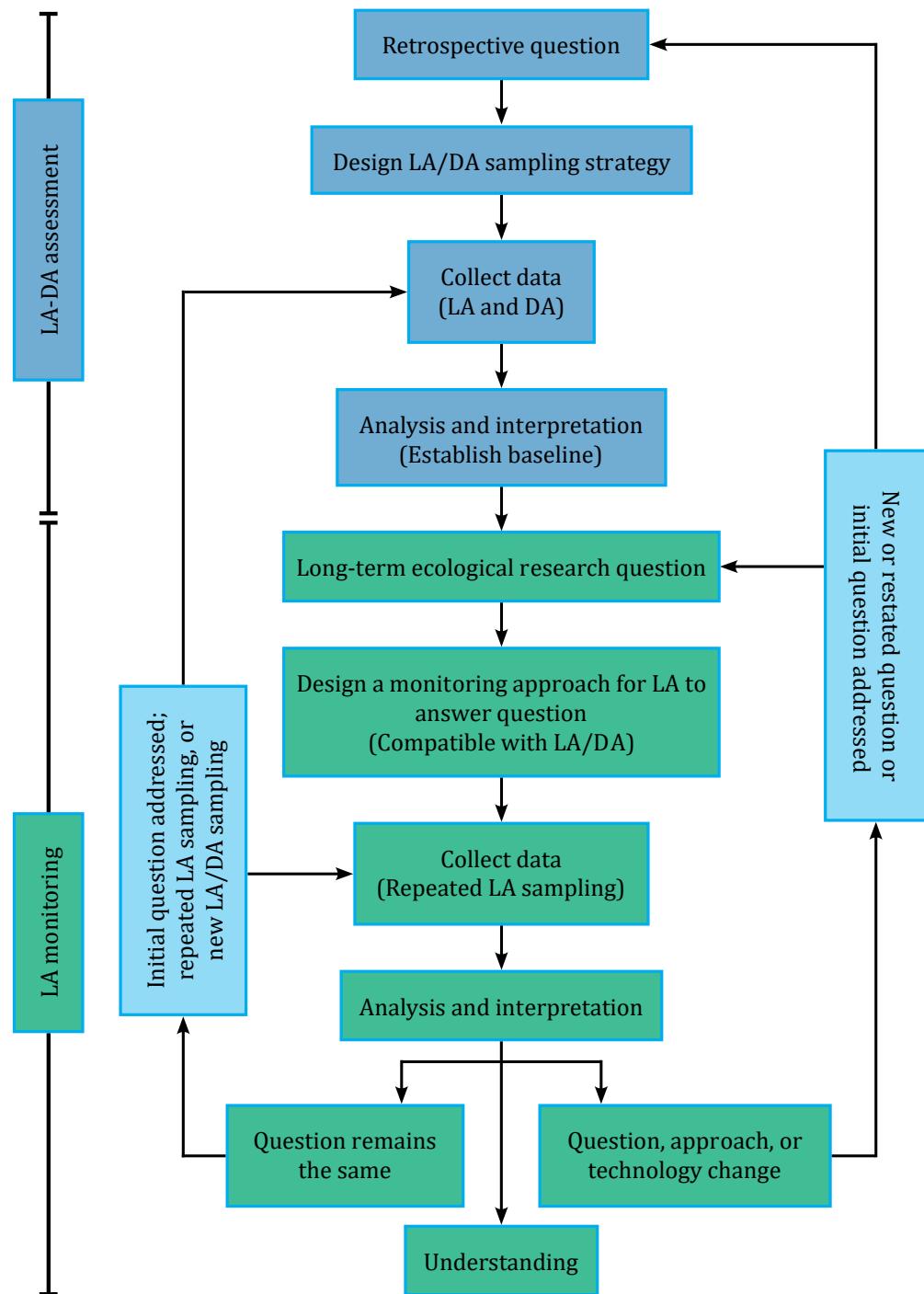
Live-dead studies retroactively assess the response of ecosystems to anthropogenic activities using baseline conditions (Kidwell, 2007), just as the present study considers the effects of damming and water diversions on the Colorado River during the twentieth century. Live-dead studies do not, however, tend to be used in long-term ecological research and monitoring, but this need not be true.

Typical live-dead studies in conservation paleobiology (Dietl et al., 2015) address the question, “How, if at all, has previous human activity changed the community?” This question remains valuable, as it serves to establish baseline conditions. But, in order to determine whether the underlying nature of a community is continuing to change relative to a baseline condition, and by how much and in what direction, the approach needs an additional component to accommodate ongoing and future environmental changes. Hence, we suggest additional LA sampling over multiple years to complement standard live-dead data. The traditional live-dead assessment, as a retrospective method, is not considered monitoring (Strayer et al., 1986; Davis, 1989; Lindenmayer and Likens, 2009), however, adding multiple years of LA sampling, particularly in an iterative framework (Figure 12; Lindenmayer and Likens, 2009), can transform this method. Adding this monitoring component to a traditional live-dead study can provide long-term ecological data, which can be extended in time with DA data (Davis, 1989). The resulting data could be used: (1) to quantify ecological

responses to ecosystem change; (2) to understand long-acting ecological processes; (3) to develop and parameterize ecological models; (4) to promote collaborative studies and multidisciplinary research; and (5) to provide data at scales relevant to management for the evaluation of success and development of policy (Lindenmayer et al., 2012).

When restorative actions are taken, comparing multiple years of LA sampling (i.e., monitoring data) to the DA can be invaluable for assessing the efficacy of the restorative action. This combination of retrospective baseline development and monitoring already form the core of restoration ecology (at least in theory; see Wortley et al., 2013), but this paleontologically based approach has yet to be realized. In doing so, the live-dead approach can become one associated with monitoring in addition to a method for establishing baselines. By asking additional questions, the application of this method shifts from the development of static baselines designed to assess whether a site was influenced by human impacts to a dynamic evaluative tool designed to measure the success of restoration projects.

Figure 12 Extending live-dead studies beyond the baseline. Key steps in a traditional live-dead study are added to the adaptive monitoring framework developed by Lindenmayer and Likens (2009) to establish a time-averaged death assemblage (DA) baseline that can be compared with repeated live assemblage (LA) monitoring data. A fundamental aspect of the adaptive framework is that it is question driven. Each component — question setting, sampling design, data collection, data analysis and interpretation — is an iterative step. A live-dead assessment can thus change in response to new opportunities or questions as long as the implementation of a new sampling strategy for the LA or DA remains compatible with the long-term dataset. Modified from Lindenmayer and Likens (2009).



The environmental flows under Minute 319—the binational agreement between the United States and Mexico (IBWC, 2012) that led to the release of a large pulse of water into the dry, lowermost channel of the Colorado River during the spring of 2014 (Flessa et al., 2013; Glenn et al., 2013)—presents a fortuitous opportunity to apply this concept. Our results have potential to be used as a baseline to assess the effects of this engineered experimental spring flood on the CRE bivalve community in the future. Although the results presented here do not go beyond the typical live-dead approach, our study, in tandem with future monitoring efforts, could be used to address the question: “Was the water released during the Minute 319 environmental pulse flow enough to shift the bivalve community at Isla Montague back towards its pre-dam state?”

Given the location of Isla Montague in the mouth of the Colorado River, the bivalve community at this locality may have been affected by the experimental pulse. Whether the 130 million cubic meters of water released via the 2014 flows, of which 1% reached Isla Montague (Flessa et al., 2014), was enough water to elicit a response from the bivalve community should be the focus of future monitoring efforts. Using the present study as a benchmark, two simple responses can be predicted (Dietl et al., 2014). First, if the amount of water was not sufficient to cause a response from the bivalve community, there will be no change in metrics such as evenness and richness. That is, a future survey of the living bivalve community will resemble the LA reported here. Alternatively, if the water did stimulate a response, the bivalve community may return to a low richness, low evenness state, as found in the cDA, with *M. modesta* composing a large proportion of the community.

Conclusions

We conclude that the CRE bivalve community has undergone substantial ecological change in response to damming and water diversions along the Colorado River during the twentieth century. The pre-dam bivalve community was dominated by *M. modesta* and was characterized by low richness and evenness. The long-term response of the CRE bivalve community was an increase in both richness and evenness, evidencing a shift from a brackish to a full marine environment as a consequence of Colorado River damming and water diversions. These baseline data, most notably the documented changes between the LA and cDA, can be used to assess the efficacy of restoration efforts in the CRE, such as the Minute 319 environmental flows. If the quantity of water that reached the CRE from the flows was enough to elicit a response from the bivalve community, future LA monitoring will likely find a community with reduced evenness and richness values reminiscent of the cDA pre-dam era baseline.

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CHAPTER 4

ENVIRONMENTAL PREFERENCE AND DISPERSAL CAPACITY EXPLAIN COMMUNITY ASSEMBLY PATTERNS FOR MARINE MOLLUSKS ALONG A PAST SALINITY GRADIENT

Abstract

Emergence of the metacommunity concept has highlighted the need to understand interactions between local and regional processes in community assembly. Here, we utilize accumulations of molluscan shells from the past 100 – 300 years at three sites along a salinity gradient in the Colorado River estuary to determine which of the four major paradigms of metacommunity theory (environmental filtering, mass effects, patch dynamics, and neutrality) best explained community assembly. Differentiating between dominant paradigms is important, as the efficacy of ongoing conservation efforts in the anthropogenically altered estuary may depend on the dominant paradigm controlling community assembly. We differentiate between paradigms using model fits of species abundance distributions and their subsequent deconstruction by commonness. Commonness was modelled against species' environmental preferences using a Bayesian binomial model.

Patch dynamics was dismissed because the assumption of homogeneous environmental conditions was violated. Neutrality was rejected because fits of niche-based models outperformed the neutral model. Deconstructed species abundance distributions showed that it was highly probable (>0.999) to find a species with estuarine preference in the common component of the low-salinity northern site as compared with the two more southern marine sites, suggesting an important role for

environmental filtering. At each site, species with mismatched environmental preferences and strong dispersal capacities were present in the common component, providing evidence to support mass effects.

Community assembly in the past molluscan community was likely controlled by a combination of environmental filtering and mass effects. Today, diversions of water have led to increased salinities in the estuary and a likely shift to patch dynamics as the dominant paradigm. Restoring the estuarine environment and populations of estuarine species will likely have to overcome high demand for water in the Colorado River basin and the establishment of marine species in the estuary.

Introduction

Community ecology has long focused on the interactions of species with each other and with their physical environments at local scales (Leibold, 1998; Leibold et al., 2004; Logue et al., 2011; Jackson and Blois, 2015). Emergence of the metacommunity concept has generated a new wave of study on the interdependence of local interactions, between and within species and their environments, and processes acting on larger scales to connect local communities (Logue et al., 2011; Heino et al., 2015; Datry et al., 2016). In the metacommunity—a set of local communities linked by dispersal of multiple potentially interacting species (Wilson, 1992)—four paradigms have been proposed to explain community assembly: species sorting (hereafter referred to as environmental filtering to avoid potential confusion given the macroevolutionary connotation of the term “species sorting” in paleontology (Stanley,

1975; see also Lieberman and Vrba, 1995)), mass effects, patch dynamics, and neutrality (Leibold et al., 2004; Logue et al., 2011).

These four paradigms span disparate environmental conditions and include processes acting on local and regional scales (Table 3). 1) Environmental filtering prescribes a heterogeneous environment with species distributions determined by species' differing capacities to cope with environmental conditions and utilize resources (Leibold, 1998; Cottenie et al., 2003). Species' dispersal capacities allow them to reach multiple habitat patches but species only persist in patches where local conditions—biotic and abiotic—enable high fitness, which differentiates environmental filtering from mass effects (Logue et al., 2011). 2) Under the source-sink dynamics of mass effects, species' dispersal capacities are sufficiently high that some species can be found in suboptimal habitat patches; however, such sink populations are only maintained by recurring dispersal from the source population because they are outcompeted locally (Mouquet et al., 2003; Mouquet and Loreau, 2003). 3) Patch dynamics differs from environmental filtering and mass effects in that it assumes all patches of habitat are equivalent and assembly is controlled by colonization-competition trade-offs (Calcagno et al., 2006; Cadotte, 2007). 4) Neutrality, which often serves as a null theory, dictates that all species are ecologically equivalent and distributed to patches via stochastic migration and immigration (Hubbell, 2001; Gravel et al., 2014). Although these paradigms are well defined in theory, experimental and observational studies of natural systems are needed to better understand the frequency with which each paradigm occurs and how processes from multiple paradigms interact (Logue et al., 2011; Heino et al., 2015; Datry et al., 2016).

Differentiating between dominant paradigms can be especially important, as conservation strategies are likely to have varying efficacy depending on which paradigm is dominant (Mouillot, 2007; Logue et al., 2011; Moritz et al., 2013; Heino et al., 2015; Ohira et al., 2015; Mou-Tham et al., 2017). For example, Mouillot (2007) found habitat preservation should be a priority if environmental filtering dominates, whereas maintenance of population densities and habitat heterogeneity are likely more important if mass effects is dominant.

Table 3 Defining characteristics of the four community assembly paradigms.

	Species Equivalence	Patch Heterogeneity	Dispersal Rate	Dominant Mechanism
Environmental filtering	No	Yes	Moderate	Niche differentiation
Mass effects	No	Yes	High	Source-sink dynamics
Patch dynamics	No	No	Moderate	Competition-colonization tradeoff
Neutrality	Yes	Not applicable	All species equivalent	Stochasticity

In order for the theory and principles of community assembly to be most impactful in conservation practice, there is a need for studies on a greater diversity of organisms and in a wider array of habitats, particularly those with diffuse boundaries (e.g., habitats along environmental gradients; Logue et al., 2011). Of the 98 case studies reviewed by Logue et al. (2011), the majority came from lentic freshwater systems ($n=41$, 42%) and terrestrial habitats ($n=29$, 30%). There were relatively few studies of marine habitats ($n=13$, 13%). Bacteria were the most commonly studied organisms ($n=25$, 26%), followed by plants ($n=17$, 17%) and zooplankton ($n=15$,

15%). Fourteen (14%) studies considered zoobenthos, although only seven of those were from marine systems (Logue et al., 2011). The studies reviewed by Logue et al. (2011) also commonly utilized microcosms and mesocosms that mimicked natural systems with well-defined boundaries (e.g., lakes, islands). Studies of habitats with diffuse boundaries (e.g., estuaries, river systems) were considerably underrepresented, leading Logue et al. (2011) to call for more studies on such habitats.

Additionally, Logue et al. (2011) called for novel approaches for differentiating between community assembly paradigms to better test the predictions made by community assembly theory. The species abundance distribution (SAD) and its subsequent deconstruction (Magurran and Henderson, 2003; Ulrich and Zalewski, 2006; Matthews et al., 2014) is one such approach, particularly because it is amenable to application across different timescales. Dozens of models have been proposed to fit SADs (McGill et al., 2007), and this continued scrutiny has revealed complex multimodal distributions (Ugland and Gray, 1982; Magurran and Henderson, 2003; Dornelas and Connolly, 2008; Vergnon et al., 2012; Matthews et al., 2014). Due to this complexity, and the recognition that discrete subsets of the community can independently influence the SAD (e.g., the amalgamation hypothesis; Matthews et al., 2014), the deconstruction approach was developed to further assess the processes structuring communities (Magurran and Henderson, 2003; Ulrich and Zalewski, 2006; Matthews et al., 2014). In the deconstruction approach, species are grouped into subsets based on broadly distinguishable species' characteristics including but not limited to endemic status, dispersal capacity, environmental preference, or commonness in samples (Matthews et al., 2014). The distribution of species in these

subsets can then be considered separately or compared with each other to understand the relationship between species' characteristics and abundances. For example, in a dataset of fish abundances collected over 21 years, Magurran and Henderson (2003) grouped species based on their annual commonness and assigned them ecological preferences. In comparing the distributions of these subsets, Magurran and Henderson found that the unexpected proliferation of rare species in their whole-community SAD, from the entire 21-year study interval, could be explained by the occasional occurrence of many different species that had ventured outside of their preferred habitats (i.e., from marine to estuarine). In a similar manner, the four community assembly paradigms can be differentiated using the whole-community and deconstructed SADs. Here we apply this approach to assess which paradigm dominated community assembly for marine mollusks in the Colorado River estuary (CRE)—prior to upstream dams and water diversions occurred during the 20th century—in order to identify the restoration strategies that are most likely to succeed (e.g., restore habitat; population densities) in this community.

Community assembly in the Colorado River estuary

The CRE molluscan community has changed considerably over the last century due to anthropogenic influence (Kowalewski et al., 2000; Rodriguez et al., 2001a; Cintra-Buenrostro et al., 2005; Smith and Dietl, 2016; Dietl and Smith, 2017). Prior to damming and water diversions along the Colorado River in the twentieth century, annual river discharge of 16×10^9 cubic meters of water (Meko et al., 2007) created a salinity gradient in the CRE (Figure 1; Cintra-Buenrostro et al. 2012).

Isotopic analysis of the clam *Mulinia modesta* (formerly *M. coloradoensis*; see Coan and Valentich-Scott, 2012) from the pre-dam era (i.e., before 1930) showed average

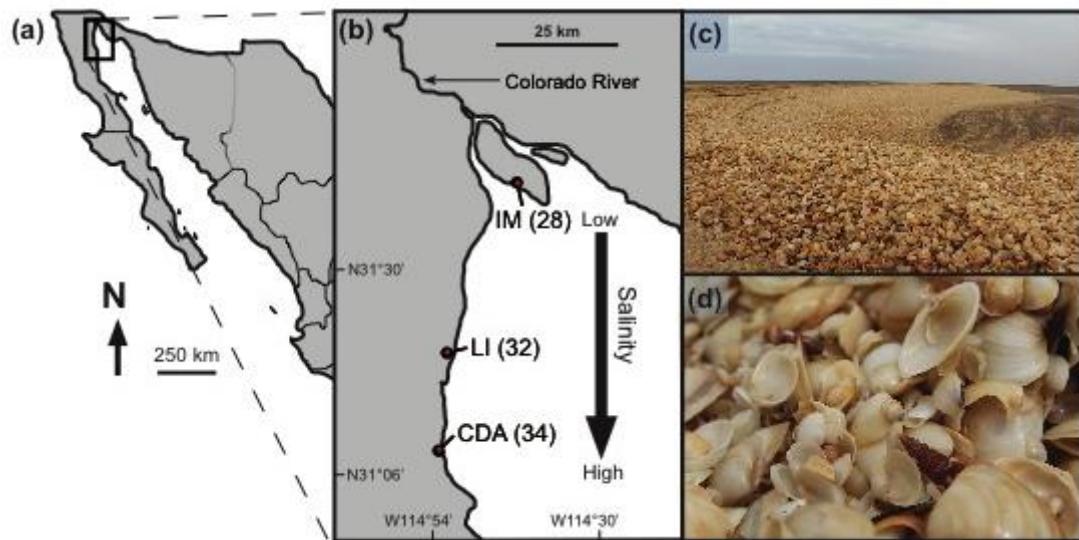


Figure 13 Location of the Colorado River estuary (a) and inset with the three sampling sites and the pre-dam era salinity gradient (b; gray shaded area = land). Actively forming chenier at Isla Montague (c) and close up of the chenier surface (d). Salinity values, in practical salinity units, follow locality abbreviations in parentheses. IM = Isla Montague; LI = Las Isletas; CDA = Campo don Abel.

salinities in the estuary of 28 psu in its river-ward, northernmost portion, 32 psu in the middle, and 34 psu in its sea-ward, southernmost portion (Cintra-Buenrostro et al., 2012). Along the CRE shoreline, trillions of molluscan shells from the pre-dam era have amassed in dune-like assemblages (Kowalewski et al., 2000), called cheniers, which form as wave action pushes shells and sediment from the local tidal flat toward the shoreline (Augustinus, 1989). Using amino acid racemization dating, Kowalewski et al. (1998) found that 83% ($n=40$) of shells in these molluscan death assemblages—the taxonomically identifiable, dead remains encountered in a seabed or landscape

(Kidwell, 2013)—were temporally averaged over the past 100 – 300 years. The sampled CRE molluscan community is thus an average, rather than a snapshot, of the community that existed during that time period, offering a unique temporal perspective. Despite this temporal mixing, taxonomic similarity and rank-order abundance in death assemblages often maintain high fidelity with the living assemblages from which they have formed (Kidwell, 2007, 2013; Olszewski and Kidwell, 2007; Tomašovych and Kidwell, 2010), as is the case in the CRE (Kowalewski et al., 1994, 1998; Dietl and Smith, 2017).

Using SADs and their subsequent deconstruction, we assess which paradigm explained community assembly in the pre-dam era CRE molluscan metacommunity to better understand what type of conservation action might be most effective (e.g., habitat restoration; maintenance of populations). We dismiss the patch dynamics paradigm because the assumption of a homogeneous environment did not hold true in the CRE (i.e., there was a salinity gradient in the pre-dam era; Cintra-Buenrostro et al. 2012). Similarly, we assume neutrality can be dismissed given the well-documented role of abiotic factors in influencing estuarine community membership (e.g., Remane and Schlieper, 1958; Dauvin, 2007; Elliott and Quintino, 2007) and test this assumption by examining the fits of three models (log-series, log-normal, and zero-sum multinomial) to the metacommunity, and to the whole-community SADs of each site. The two remaining paradigms for heterogeneous environments, environmental filtering and mass effects, can be more challenging to differentiate (Mouquet et al., 2003; Leibold et al., 2004; Mouillot, 2007; Logue et al., 2011; Winegardner et al.,

2012; Heino et al., 2015). To do so, species' dispersal capacities and life histories must be considered (Moritz et al., 2009; Okuda et al., 2010; Heino et al., 2015).

Marine mollusks have a variety of reproduction strategies, including direct-developing crawl-away larvae, short-term lecithotrophic larvae, and long-term planktotrophic larvae, which can disperse over a few centimeters, hundreds of meters, or thousands of kilometers, respectively (Thorson, 1950; Grantham et al., 2003; Kinlan and Gaines, 2003). Unfortunately, the reproductive strategies and dispersal capacities of most mollusks remain unstudied (Scheltema, 1984; Grantham et al., 2003; Kinlan and Gaines, 2003). It is possible to determine these factors, however, by examining the youngest portion of a mollusk shell (Thorson, 1950; Ockelmann, 1965; Lutz et al., 1980; Jablonski and Lutz, 1983). Furthermore, it is possible to predict resulting patterns in the distribution of strongly and weakly dispersing species in the SAD deconstruction framework as related to environmental filtering and mass effects. The environmental filtering paradigm acknowledges that species can disperse within the metacommunity, but only with a high enough rate for species to become established if environmental conditions match their preferences (Mouquet et al., 2003; Mouquet and Loreau, 2003). By contrast, dispersal is predicted to be greater under mass effects to the degree that species can disperse and establish populations outside of their environmental preferences (Leibold, 1998; Cottenie et al., 2003). In terms of SAD deconstruction for the CRE, environmental filtering predicts a strong relationship between commonness and preference along the salinity gradient, such that core species only occur in their preferred habitat. To the contrary, if mass effects dominated

community assembly, a weak relationship between commonness and preference is predicted, with core species occurring outside of their preferred habitats.

Methods

Sampling

Samples were taken from the molluscan death assemblages at three sites in the CRE following the north-south salinity gradient that existed before large-scale damming and water diversions in the Colorado River basin began in the 1930s (Figure 13). At each site, five bulk samples were randomly collected from the top 5 – 10 cm of chenier surfaces ($0.25 – 0.50 \text{ m}^2$), which are well-mixed with the subsurface (Kowalewski et al., 1998), at approximately 30 m intervals. Samples ranged in volume from 2 – 10 L. In the lab, all samples were washed and sieved using a 5-mm mesh, identified to the species level, and counted to create SADs. For gastropods, only specimens including the shell apex were counted. Similarly, only bivalves with an intact umbo were counted and, given that bivalves have two elements (i.e., left and right valves), bivalve count totals were halved to estimate their abundance (Kowalewski, 2002). Count data from each sample were subsampled ($n=337$, the smallest average bulk sample size from the three sites) and bootstrapped ($n=1000$) to standardize for sample size using the ‘rrarefy’ function in the R *vegan* package (Oksanen et al., 2015).

Whole-Community SADs

In order to confirm our a priori assumption that the neutral paradigm could be dismissed, three SAD models—Fisher’s log-series (LS), Poisson log-normal (PLN), and metacommunity zero-sum multinomial (ZSM)—were fit to species counts for the entire metacommunity, and each individual site, using the ‘sads’ package (Prado and Miranda, 2014) in R (see Appendix 10). Model fits were compared using the Akaike information criterion with a correction for sample size (AICc). A best fit by the ZSM model would indicate that neutral processes controlled community assembly and a best fit by either LS or PLN would indicate niche-based processes (Hubbell, 2001; Matthews and Whittaker, 2014a). Both LS and PLN were applied because they tend to give the best fit to end members on the spectrum reported for disturbed and equilibrium communities, respectively (May, 1975; Gray and Mirza, 1979; Ugland and Gray, 1982; Matthews and Whittaker, 2014b).

SAD Deconstruction

The SADs for each site were deconstructed by commonness (core or satellite) and environmental preference (estuarine or marine) to determine which niche-based paradigm (environmental filtering or mass effects) best explains community assembly in the molluscan metacommunity. For deconstruction by commonness, core species have previously been defined as those species present in at least 50% of samples and satellite species defined as those present in fewer than 50% of samples (Magurran and Henderson, 2003; Matthews et al., 2014). We employ a modified approach for deconstruction to accommodate the geohistorical data used here. Whereas previous

studies have used contemporaneously collected spatial data (e.g., Matthews et al., 2014) or repeated sampling on an annual basis (e.g., Magurran and Henderson, 2003), our paleocommunity data are temporally averaged over a few hundred years (Kowalewski et al., 1998). As such, it may not be appropriate to consider the concepts of rarity and commonness on an equivalent basis with their conceptualization in the ecological literature (Cobabe and Allmon, 1994; McKinney et al., 1996; Olszewski and Kidwell, 2007; Olszewski, 2012; Kidwell, 2013). By using a 50% threshold for occurrence in samples, the core-satellite approach (*sensu* Magurran and Henderson 2003; Matthews et al. 2014) accounts for spatial variability in species' abundances. In a paleocommunity, particularly in the chenier assemblages used here, individuals in a given sample are condensed from a spatial area that exceeds standard ecological sampling. Through wave action and tidal motion, molluscan remains in the CRE are pushed shoreward—with little movement lateral to the shore—creating an assemblage that is an average of the entire tidal flat community (Augustinus, 1989; Kowalewski et al., 1998; Dietl and Smith, 2017). Thus, we define satellite species as those present in abundances of less than 1% of the total number of individuals at each site (Kidwell, 2013). As the samples ($n=5$) from each site have been standardized ($n=337$; total individuals=1,685), the threshold used here is $n=17$, where $n < 17$ places a species in the satellite component. Given that death assemblages also accumulate rare species in low abundances (i.e., <1%) over timescales that exceed ecological sampling, this scheme has the advantage of consistently categorizing such species as members of the satellite component. As such, paleocommunity data can be leveraged to understand the

broad set of species that potentially interacted in the community during the interval of time-averaging.

Each species was categorized as estuarine or marine based on preferences—considered to be where a species optimizes growth and reproduction with respect to biotic and abiotic constraints—for low (< 34 psu) and high salinity (≥ 34 psu), respectively (see Appendix 11). Preferences were assigned following literature searches using exact species names, but when species-specific data were not available, preferences were assigned based on those of congeners in accordance with best professional judgment (Tweedley et al., 2014; Gillett et al., 2015). After categorization, the association between environmental preference and commonness was assessed using a binomial model with simulation ($n=2000$). From the model simulations, Bayesian probabilities were generated for the likelihood of finding species with respective environmental preferences in the core component at each site relative to each of the other sites (see Appendix 10 for R code).

Results

Whole-Community SADs

The LS, PLN, and ZSM models were fit to the SADs generated from samples of the molluscan death assemblages at the three CRE sites and for the metacommunity (Figure 14). According to AICc, the PLN provided the best fit, followed by LS then ZSM, for the metacommunity SAD (Table 4). ZSM did provide the best fit for the northernmost site; however, the AICc difference from LS was less than 2.0, which indicates an indistinguishable degree of support for the models (Burnham and

Anderson, 2003). For the middle and southern sites, PLN provided the best fit, but as with the northern site, AICc differences were below 2.0. There was no evidence to support ZSM as the best model for the metacommunity.

SAD Deconstruction

SAD deconstruction into core and satellite components resulted in lognormal-like distributions for core taxa and logseries-like distributions for satellite taxa (Figure 3). The core component in the north was primarily composed of species with environmental preferences for estuarine conditions ($n=5$, 83%) and a single species (17%) with marine preferences. Of the three species in the satellite component, one (33%) had estuarine preferences and the remaining two (67%) had marine preferences. At the middle site, marine species made up the majority of the core ($n=6$, 60%) and satellite ($n=13$, 87%) components. Four (40%) estuarine species had core designations and two (13%) had satellite designations. At the southernmost site, species with marine preferences made up the majority of the core component ($n=13$, 87%) and estuarine species ($n=2$, 13%) composed the remainder. The satellite component was composed of three (9%) estuarine species and twenty-nine (91%) marine species (see Appendix S2 for count data). Based on simulations of the binomial model, the likelihood of an estuarine species occurring in the core component from the northern site was high (0.999) compared to the two southern sites. The probability of an estuarine species occurring at the middle site was equally high (0.999) in comparison to the southern site.

Table 4 AICc values for logseries (LS), lognormal (PLN), and zero-sum multinomial (ZSM) models. Bolded values indicate best fit. Multiple bolded values indicate no distinguishable difference between model fits.

	AICc		
	<u>LS</u>	<u>PLN</u>	<u>ZSM</u>
Isla Montague	104.1	107.3	103.4
Las Isletas	217.5	215.7	219.3
Campo don Abel	368.5	367.9	369.5
Metacommunity	474.7	468.6	477.8

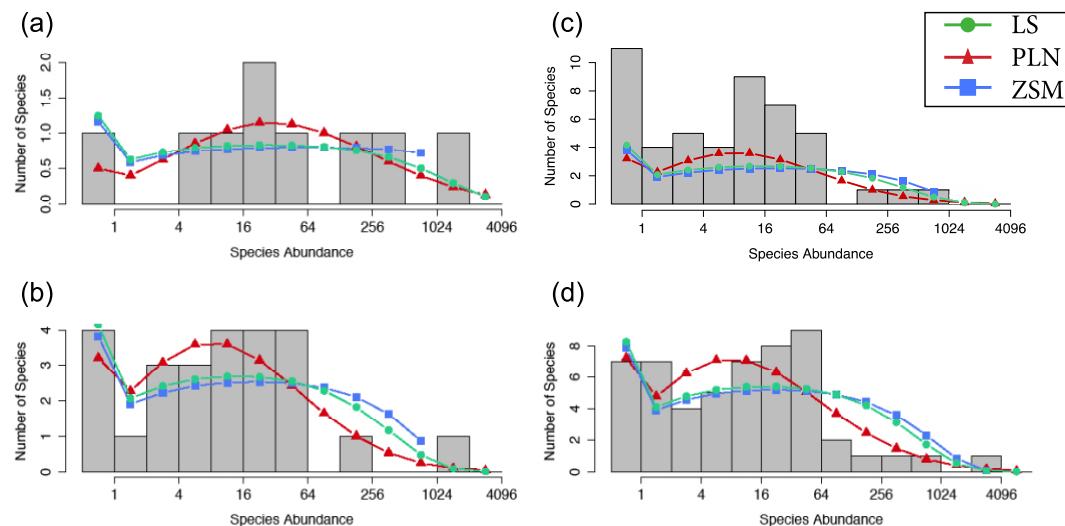


Figure 14 Whole-community species abundance distributions for mollusks from Isla Montague (a), Las Isletas (b), Campo don Abel (c), and the entire metacommunity (d) with fits for the log-series (LS; green circles), log-normal (PLN; red triangles), and zero-sum multinomial (ZSM; blue squares) models.

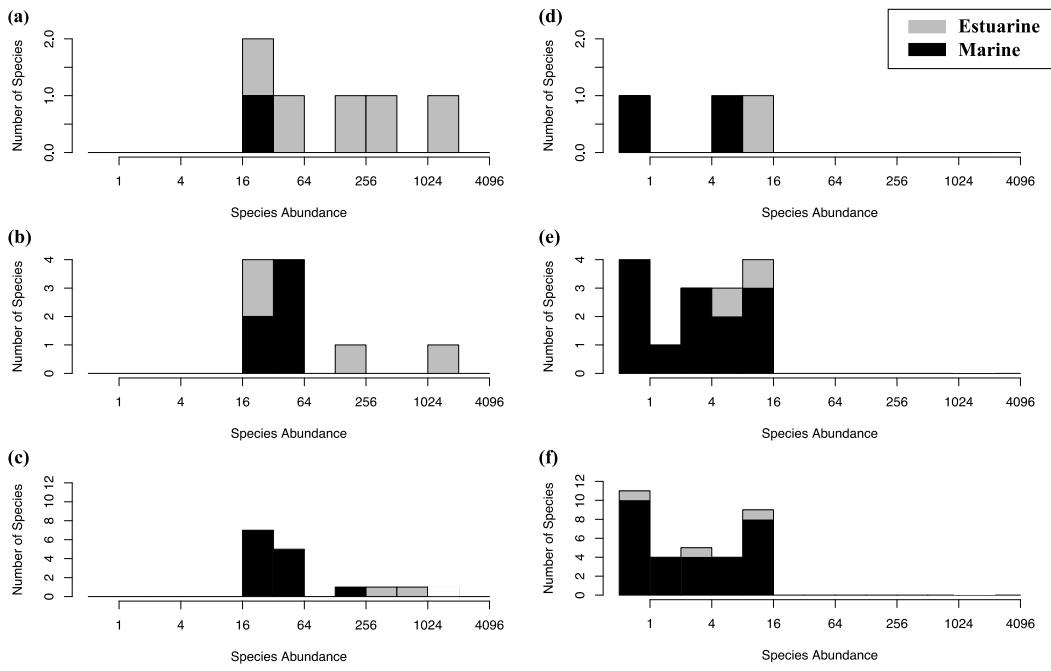


Figure 15 Deconstructed species abundance distributions for mollusks from Isla Montague (a, d), Las Isletas (b, e), and Campo don Abel (c, f). For each site, the core component is on the left (a, b, c) and the satellite component is on the right (d, e, f). Estuarine species are in gray and marine species are in black.

Discussion

Fits of the SAD models to the whole-community data suggest niche processes better explain CRE community assembly than neutral processes. After deconstruction of the SADs to differentiate between environmental filtering and mass effects, there is evidence to support both paradigms. Given that the CRE habitat has become more homogenous over the last century due to increasing salinities associated with reduced freshwater input, the processes governing community dynamics may be different today, which may have implications for future restoration and conservation efforts in the CRE.

Whole-Community SADs

The PLN model was the best-fit model to the metacommunity SAD (Table 4), eliminating neutrality as the dominant community assembly paradigm. Likewise, model fits for the individual sites show no conclusive evidence to support neutrality. Given the time-averaged nature of the chenier assemblages, the lack of support for the ZSM is likely underestimated. Time-averaging—the mixing of ecological signals and materials in a death assemblage over an extended period of time (Kowalewski et al., 1998; Kidwell and Tomasovych, 2013)—often leads to the accumulation of rare species and diminished dominance of any given highly abundant species due to the fluctuation of dominant species over time (Olszewski and Kidwell, 2007; Tomašovych and Kidwell, 2010; Kidwell, 2013). In short, just as predicted by the ZSM model, SADs of time-averaged assemblages tend to have more rare species and more very-common species than predicted by a log-normal model (see Figure 14 where the ZSM is always above the PLN at low and high species counts). SADs from death assemblages are more likely to be best fit by the ZSM model (Tomašovych and Kidwell, 2010). Despite this bias, the neutral theory model (ZSM) is not the best-fit model for the CRE molluscan SADs, giving strong evidence with which to dismiss the neutrality paradigm.

SAD Deconstruction

In the northern CRE, past estuarine conditions were likely harsh enough to influence community assembly. As has been proposed in the “estuarine quality paradox” (Remane and Schlieper, 1958; Dauvin, 2007; Elliott and Quintino, 2007),

harsh estuarine conditions (e.g., low salinity) regularly exclude many species, resulting in naturally low community diversity. Indeed, Dietl and Smith (2017) found the pre-dam era community in the northern CRE was characterized by low richness, which is confirmed here by comparison with the two more southerly sites along the past salinity gradient. Yet, the marine species *C. fluctifraga* (n=19, 1.1%), which was the second most common bivalve, persisted in the core component despite growth rates diminished by as much as 50% during the spring and early summer due to spring floods (Schöne et al., 2003). The *C. fluctifraga* prodissoconch—the initial calcified growth stage in bivalves and an indicator of larval dispersal mode (Ockelmann, 1965)—is small (<150 µm; see Appendix 12) suggesting a planktotrophic larval stage with widely dispersing larvae (Lutz et al., 1980; Jablonski and Lutz, 1983). The persistence of *C. fluctifraga* in the core component and this species' strong dispersal capacity support mass effects even as low diversity at this site suggests an important role of environmental filtering in assembly.

Similarly, the results from the middle site in the CRE support both paradigms. Salinity at the middle site was intermediate with respect to the salinities at the northern and southern sites. As reported by Cintra-Buenrostro et al. (2012), this site was influenced by freshwater input throughout the year, with salinity remaining lower (32 psu) than full marine (>34 psu) and likely dropping below 26 psu during periods of high river flow, such as annual spring floods (Carbajal et al., 1997). As might be expected based on these salinity conditions, estuarine species accounted for 83% of individuals (n=1396). Even so, six of the ten core species had marine preferences (Figure 3) and, interestingly had a mix of strong (e.g., *C. fluctifraga*) and weak (e.g.,

Crepidula onyx) dispersal capacities (see Appendix 12). Thus, at this intermediate site, salinity preferences for both estuarine and marine species could be accommodated, as species with either preference appear to have been capable of maintaining populations. This community-wide “goldilocks zone” may be a common occurrence in studies of systems with diffuse boundaries (Logue et al., 2011; Heino et al., 2015; Datry et al., 2016).

At the fully marine southern site, the most common pre-dam era species, *M. modesta* (n=649, 39%), had estuarine preferences and a small prodissococonch (see Appendix S3). Considering the abundance of *M. modesta*, its strong dispersal capacity, and the considerable role of common species in structuring communities (Gaston, 2010; Connolly et al., 2014), dispersal (i.e., mass effects) undoubtedly played an important role in assembly. Still, the majority of species in the core component had marine preferences (n=13, 87%; Figure 15) and species with estuarine preferences and weak dispersal capacities remained uncommon (e.g., *M. olivaceus*, n=0; *C. californica*, n=10; *Eupleura limata*, n=4). These latter lines of evidence suggest an important role of environmental filtering in assembly.

In summary, across sites along the salinity gradient, 71% (22 of 31) of core species were present in agreement with their environmental preferences and probabilities for the occurrence of species with estuarine preferences in the core component were high in the north relative to the two southern sites. Thus, environmental filtering is seemingly well-supported as the explanatory paradigm for community assembly. Yet, several species (e.g., *C. fluctifraga* in the north, *M. modesta* in the south) occurred in the core component when not predicted to do so

based on environmental preference. In these cases, strong dispersal capacities (i.e. mass effects) likely allowed species to persist in non-optimal environments at relatively high abundances. Considering the interrelated evidence supporting environmental filtering and mass effects, processes of both paradigms likely contributed to community assembly.

This conclusion—a combination of environmental filtering and mass effects—is consistent with previous studies on community assembly in marine systems, limited as they are. Although there have been many more studies of community assembly in the years since the review by Logue et al. (2011), there still exists “a relative deficit of research on marine systems” on this topic (Heino *et al.* 2015, p. 849). Moreover, the majority of studies from marine systems are on rocky intertidal habitats (e.g., (Noda, 2009; Caro et al., 2010; Okuda et al., 2010; Valdivia et al., 2015), leaving a paucity of studies on soft-bottom habitats such as the one studied here. In the rocky intertidal, Okuda et al. (2010) found that environmental filtering processes controlled community assembly for macroalgae and mollusks, but their analysis also showed a complementary role for spatial processes, suggesting similar importance for mass effects (Heino et al., 2015). Others have found that dispersal-related factors (i.e., mass effects) exert considerable influence on marine metacommunity dynamics (Matthiessen et al., 2007; Moritz et al., 2009; Guizien et al., 2014). Although much work remains to be done on marine species’ dispersal capacities, Kinlan and Gaines (2003) reported strong evidence to suggest that marine species tend to disperse over greater distances than terrestrial species, which may increase the incidence of source-sink dynamics (i.e., mass effects) in heterogeneous near-shore marine systems (Heino

et al., 2015). As discussed by Heino et al. (2015) in their review of metacommunity organization, environmental preferences will likely always contribute to marine molluscan community assembly but, as in the present study and in previous experimental (Matthiessen et al., 2007) and observational (Okuda et al., 2010) studies, species' capacities to disperse also commonly contribute.

Conservation implications for shifts in community assembly

Knowledge of the predominant community assembly paradigm can have important implications for ecosystem management and conservation (Mouillot, 2007; Logue et al., 2011; Moritz et al., 2013; Heino et al., 2015; Datry et al., 2016). For example, in a study of coastal fish community conservation, Mouillot (2007) suggested that, if environmental filtering processes dominate, it will be most important to preserve or restore habitat, whereas under mass effects the focus should be on maintaining population densities and heterogeneity among lagoons. With patch dynamics, however, emphasis should be given to individual turn-over and species' fitness (Mouillot, 2007). These areas of conservation importance likely hold beyond fish communities but are less straightforward when habitat changes occur and the processes controlling community assembly change.

Habitat change in the CRE has been driven by extensive damming and water diversions along the Colorado River that have reduced the flow of freshwater in the CRE to no more than a trickle (Rodriguez et al., 2001b; Glenn et al., 2007; Cintra-Buenrostro et al., 2012). In the north, at the former mouth of the river, salinities frequently dropped below 28 psu prior to damming, but now regularly exceed 40 psu

(Carabajal et al., 1997; Carriquiry and Sánchez, 1999; Cintra-Buenrostro et al., 2012).

Populations of species with estuarine preferences, most notably *M. modesta*, have declined dramatically (Kowalewski et al., 2000; Rodriguez et al., 2001a; Cintra-Buenrostro et al., 2005), total bivalve density has dropped from more than 50 to 3 – 17 individuals per square meter (Kowalewski et al., 2000; Avila-Serrano et al., 2006), and community richness and evenness have increased (Dietl and Smith, 2017). At the same time, molluscan species with marine preferences are moving northward, as they are no longer excluded by estuarine conditions (Smith and Dietl, 2016). Abiotic conditions in the CRE have become more homogenous and species composition is following suit. The dominant community assembly paradigm has likely changed.

Under these new conditions, patch dynamics and corresponding competition-colonization tradeoffs likely drive community assembly. Priority effects—the influence of species arrival order and timing on the capacity of other species to join the community (see Fukami, 2015 for a recent review)—may, however, prolong the transition. Priority effects likely influenced the CRE community over a few decades, as molluscan lifespans are commonly a decade or less (e.g., *M. modesta* lifespan averages three years, Rodriguez *et al.* 2001). Indeed, Dietl and Smith (2017) found that *C. fluctifraga* (a marine species) has already displaced *M. modesta* (an estuarine species) as the most common clam at the northernmost CRE site, Isla Montague. Our study thus conservatively constrains this shift in community assembly processes to the 80-year period since widespread water diversion and dam construction began in the Colorado River basin, and strongly suggests that the shift occurred over a shorter time span. Even so, estuarine species have not completely disappeared and, in direct

competition with marine species, continue to occupy space and influence nutrient cycling, albeit to a lesser degree than in the past (Smith et al., 2016; Dietl and Smith, 2017). The new, high salinity (>34 psu) environment should give marine species a competitive advantage, particularly as filtration and growth rates have been shown to be density-dependent in many molluscan species (Wilson, 1990), and may allow them to displace many estuarine species. Estuarine species with high colonization potential (e.g., *M. modesta*) will likely persist, but at considerably lower population sizes.

Public will permitting, restoring freshwater flow to the CRE may once again create the environmental conditions preferred by estuarine species, at least in the northernmost portion of the delta. Under binational agreement Minute 319 between the United States and Mexico (IBWC, 2012), restoration flows of approximately 1% of the historical annual discharge of the Colorado River were released in the spring of 2014 to mimic natural spring floods (Flessa et al., 2013). Of the ~130 million cubic meters of water that were released, 1% of that water reached Isla Montague, our northernmost site (Flessa et al., 2014). In the northern CRE, the restoration flows may have recreated low-salinities, temporarily restoring the habitat to its formerly brackish conditions—a strategy (i.e., habitat restoration) best suited when environmental filtering processes are dominant (Mouillot, 2007). Indirectly, population densities of *M. modesta* also may have rebounded, which is an effective strategy (i.e., maintaining population densities) under mass effects (Mouillot, 2007). Lower salinities (< 30 psu) may improve the reproductive success of *M. modesta* (Rodriguez et al., 2001a), as has been demonstrated experimentally for the congener, *Mulinia lateralis* (Calabrese, 1969). It remains to be seen, however, whether the *M. modesta* population has the

capacity to rebound on its. Nonetheless, increasing habitat heterogeneity by restoring estuarine habitat via the restoration flows is likely a requisite first step. Restoration in the CRE will continue, as detailed in Minute 323 (Section VIII; IBWC, 2017), and it will be imperative to continue monitoring the CRE molluscan community to evaluate the potential effects of the flows (Dietl and Smith, 2017). The flows may lead to an increase in the *M. modesta* population (e.g., restoring *M. modesta* as the most abundant clam in the CRE); however, if marine species have become sufficiently established, priority effects may create an elevated threshold for flow volume and duration. Given the large human demand for water in the Colorado River basin, attaining such a threshold may be a considerable challenge and restoration may not be as simple as just adding water.

Conclusion

In differentiating between the dominant paradigms of community assembly, SADs and their subsequent deconstruction can provide valuable insight. The SAD approach may be particularly valuable because it can be applied to any taxonomic group—regardless of timescale—and make use of a variety of parameters (e.g., dispersal capacity; body size), extending beyond those used here (i.e., commonness, environmental preferences). Applying this approach to mollusks along a salinity gradient, environmental preference (i.e., environmental filtering) and dispersal capacity (i.e., mass effects) combined to explain community assembly during the last 100 – 300 years in the CRE. Mollusks, which have been an understudied group in community assembly, tend to have strong dispersal capacities and often live in habitats

with harsh environmental conditions (e.g., estuaries, intertidal zones), suggesting that this combination of environmental filtering and mass effects may commonly contribute to community assembly for mollusks. Generally, this conclusion is in agreement with observations from previous studies of marine communities, suggesting that environmental filtering and mass effects both likely contribute to the assembly of marine communities. Even so, habitat change can precipitate change to the dominant community assembly paradigm, as likely has occurred in the CRE. In such cases, geohistorical records can provide invaluable pre-disturbance data, which are often unattainable from any other source, to inform conservation practice.

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CHAPTER 5

FOSSIL CLAM SHELLS REVEAL UNINTENDED CARBON CYCLING CONSEQUENCES OF COLORADO RIVER MANAGEMENT³

Abstract

Water management that alters riverine ecosystem processes has strongly influenced deltas and the people who depend on them, but a full accounting of the tradeoffs is still emerging. Utilizing paleoecological data, we document a surprising biogeochemical consequence of water management in the Colorado River Basin. Complete allocation and consumptive use of the river's flow has altered the downstream estuarine ecosystem, including the abundance and composition of the mollusk community, an important component in estuarine carbon cycling. In particular, population declines in the endemic Colorado delta clam, *Mulinia modesta*, from 50 – 125 individuals m⁻² in the pre-dam era to three individuals m⁻² today, have likely resulted in a reduction, on the order of 5900 – 15000 t C yr⁻¹ (4.1 – 10.6 mol C m⁻² yr⁻¹), in the net carbon emissions associated with mollusks. Although this reduction is large within the estuarine system, it is small in comparison to annual global carbon emissions. Nonetheless, this finding highlights the need for further research into the effects of

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dams, diversions, and reservoirs on the biogeochemistry of deltas and estuaries worldwide, underscoring a present need for integrated water and carbon planning.

Introduction

Rivers worldwide have been profoundly modified to maximize the production of a subset of the services they provide, such as hydroelectric power and reliable water for irrigation and municipal use (Nilsson et al., 2005; Vörösmarty et al., 2010). The upstream infrastructure and water diversions required to provide these services can, however, have a pronounced effect on downstream deltas and estuarine ecosystems. With human demands for freshwater remaining high or increasing, deltas and estuaries are poised to experience heightened stress from ocean acidification and sea level rise as the climate changes. These compounded stressors may have wide reaching impacts, including perturbing carbon cycling in river systems (Bauer et al., 2013; Cloern et al., 2016). Yet, our current understanding of the influence of large-scale water management on carbon sequestration and emission hinders the comprehensive evaluation of infrastructure or other water resource planning (Strutt et al., 2008; Shrestha et al., 2011a, 2011b).

The need for research examining the carbon consequences of water management associated with the alterations of biophysical processes in rivers is particularly acute in deltas and their estuaries (Bauer et al., 2013). Carbon emissions from estuaries, which can range from $17 - 46 \text{ mol C m}^{-2} \text{ yr}^{-1}$ (Borges et al., 2005), are significant in regional carbon budgets (Frankignoulle et al., 1998; Borges et al., 2006) and cumulatively can amount to global emissions of $3.4 - 4.5 \times 10^8 \text{ t C year}^{-1}$

(Borges, 2005; Borges et al., 2005). Whereas overall emissions from estuaries are becoming well quantified (Cai, 2011), the individual components of the multifaceted estuarine carbon cycle (Figure 16) merit further study, particularly mollusks.

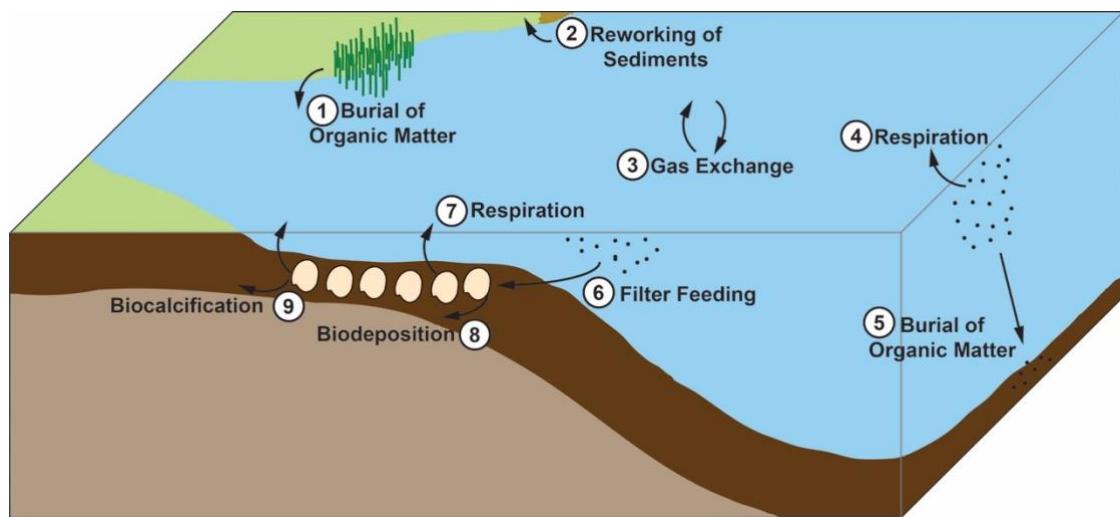


Figure 16 A subset of the processes involved in estuarine carbon cycling. (1) Sequestration of carbon via vegetation (e.g., salt marshes, mangroves) growth, death, and burial; (2) Emission of carbon due to reworking of carbon-rich sediments; (3) Constant gas exchange between ocean and atmosphere; (4) Emission of carbon via respiration by microbes and zooplankton; (5) Sequestration of carbon via burial of deceased plankton; (6) Filter feeding by bivalves; (7) Carbon emission via bivalve respiration; (8) Carbon sequestration via biodeposition; (9) Carbon sequestration and emission via biocalcification.

Mollusks are a vital element of the tidal and sub-tidal benthic fauna of estuaries, collectively emitting $2 - 20 \text{ mol C yr}^{-1}$ (Chauvaud et al., 2003; Martin et al., 2007; Mistri and Munari, 2012) and playing a large role in the pelagic-benthic cycling of nutrients (e.g., carbon, nitrogen, phosphorus; Newell, 2004; Nizzoli et al., 2006; Petersen et al., 2008; Filgueira et al., 2015). In particular, bivalve mollusks (commonly, “clams”) can be found locally in densities in excess of 1000 individuals meter⁻² (Virnstein, 1977; Sikora and Sikora, 1982) and can contribute significantly to

estuarine carbon emissions via respiration and biogenic calcification (i.e., shell formation). Although carbon sequestration exceeds carbon emission during shell formation, the amount of carbon dioxide released via respiration typically exceeds the amount of carbon that is sequestered, resulting in net carbon emissions (Chauvaud et al., 2003; Martin et al., 2007; Mistri and Munari, 2012; Munari et al., 2013). It is well documented that water management can affect molluscan populations (Kowalewski et al., 2000; Rodriguez et al., 2001; Cloern et al., 2016), however, to the best of our knowledge, the carbon implications of these effects have never been assessed.

The paleoecological record on the Colorado River estuary (CRE; Figure 17) offers a unique means to conduct such an analysis. Prior to damming and diversions in the 1930s, natural annual flows ranged between $1.6 \times 10^9 \text{ m}^3$ and $1.8 \times 10^9 \text{ m}^3$ at Lee's Ferry in northern Arizona (Meko et al., 2007) but the river now fails to reach the sea in most years (with the exception of the recent environmental pulse flow under the groundbreaking binational Minute 319 agreement; (Flessa et al., 2013). The lack of Colorado River water has led to substantial declines in clam (Kowalewski et al., 2000), shrimp (Galindo-Bect et al., 2000), and fish (Rowell et al., 2005) populations, in addition to reduction in estuarine, riparian, and wetland vegetation (Glenn et al., 2013). Salt marshes, wetlands and riparian forests now cover a small fraction of their former area (Zamora-Arroyo et al., 2005; Zamora-Arroyo and Flessa, 2009) and the once brackish estuary is now saltier than the sea (Carabajal et al., 1997; Carriquiry and Sánchez, 1999).

Very few environmental data were collected before the main period of dam construction (1900-1965) on the Colorado River. However, paleoecological data from

cheniers—beach ridges composed almost exclusively of molluscan remains (Thompson, 1968; Lluch-Cota et al., 2007)—permit estimates of the size and density of the pre-dam (prior to 1930) molluscan community, particularly the clam, *Mulinia*

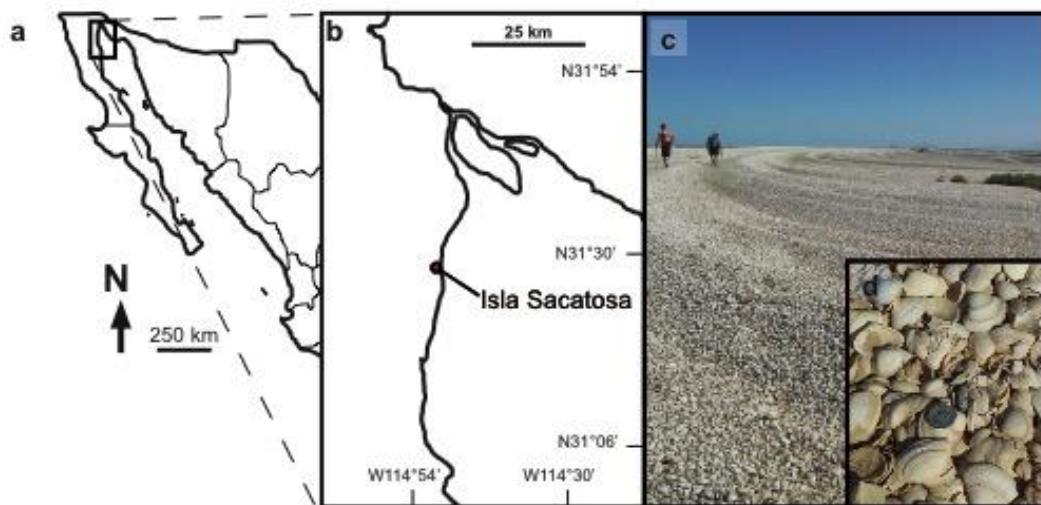


Figure 17 Cheniers in the Colorado River delta. (a) Location of delta in Mexico. (b) Colorado River delta locality from Kowalewski et al. (1994). (c) A chenier in the Colorado River delta at a locality south of Isla Sacatosa. (d) Close-up of *Mulinia modesta*; coin, 0.24 cm in diameter.

modesta, (Kowalewski et al., 2000; Lluch-Cota et al., 2007; Glenn et al., 2013). Cheniers of three ages are present, two that formed between 90 – 1,500 and 2000 – 5,000 years ago, and a third that has been actively forming over the past 90 years (Kowalewski et al., 1994). Dated shells from these cheniers indicate that *M. modesta* accounted for as much as 95% of the individuals during the pre-dam era and occurred at densities that were likely well in excess of 50 individuals m⁻² (Kowalewski et al., 2000). In contrast, current molluscan densities of 3 – 17 individuals m⁻² (Avila-Serrano et al., 2006) indicate the scope of the ecological change associated with river management (Kowalewski et al., 2000; Rodriguez et al., 2001; Cintra-Buenrostro et

al., 2005). Accordingly, we combined evidence of pre-dam conditions from cheniers with data from contemporary mollusk community surveys to investigate how reduced clam density following upstream river diversion altered carbon sequestration and emissions (in terms of CO₂) in the estuary of the CRE.

Methods

Clam Density

We established estimates for the density of clams living on the CRE tidal flats during the pre-dam era and the present-day based on the work of Kowalewski et al. (2000) and Avila-Serrano, et al. (2006). Kowalewski et al. (2000) estimated pre-dam clam density for the 90 – 1,500 year old chenier by combining bulk samples from the molluscan assemblage, estimates of the total area of shell deposits, and an average chenier thickness (Table 3). They estimated an average density of 87,500 clams m⁻³, which translates to approximately 2.1×10^{12} total clams in the chenier. Amino acid racemization confirmed that 98% (n= 125) of the shells in the chenier dated from the period C.E. 950 – 1950. Based on estimates of the pre-dam tidal flat area (Table 3) and an average ontogenetic age of three years, Kowalewski et al. (2000) then calculated an average clam density of approximately 50 individuals m⁻² during this period. This value likely represents a conservative estimate of clam density given that various taphonomic processes (e.g. shell dissolution, abrasion, fragmentation, etc.) remove shell material after death (Kowalewski et al., 1994, 1998). Based on the age distribution of dated shells and accounting for shell removal, Kowalewski et al. (2000) proposed that the total number of clams alive during C.E. 950 – 1950 may have

exceeded 5×10^{12} , or a constant standing density of 125 individuals m^{-2} across the entire Colorado River delta tidal flat. This estimate remains highly conservative, however, because, for practical reasons, Kowalewski *et al.* (2000) did not consider individuals smaller than the 12.5 mm mesh size that they used to sieve samples. Indeed, surveys of the living community suggest that large individuals (>12.5 mm) may compose the majority of biomass yet represent only 20% of individuals in the community (Kowalewski et al., 2000). Thus, we calculated changes in carbon based on pre-dam densities of 50 and 125 individuals m^{-2} in order to estimate a conservative range of values.

Surveys of the contemporary tidal flat molluscan community along seven transects throughout the Colorado River delta suggest an average density of approximately 17 individuals m^{-2} (Kowalewski et al., 2000; Avila-Serrano et al., 2006). This estimate includes mollusks of all sizes, however, when only considering clams greater than 12.5-mm, density drops to three individuals m^{-2} (Kowalewski et al., 2000). We based present-day values on this latter estimate for consistency with the pre-dam data.

Carbon storage and emission

Using these pre-dam and present-day estimates of clam density, we then calculated annual carbon sequestration and production from biogenic calcification and carbon emission due to respiration. Annual carbon sequestration was calculated based on standing clam density and one-third average shell dry mass (assuming constant growth over a clam's three-year lifespan for ease of calculation; Table 3), with mass

Table 3 Parameter estimates and assumptions for carbon calculations

Parameter	Estimate	Source
Chenier Area	$5.96 \times 10^6 \text{ m}^2$	Kowalewski et al., 2000
Chenier Thickness	4 m	Kowalewski et al., 2000
Chenier Volume	$2.4 \times 10^7 \text{ m}^3$	Kowalewski et al., 2000
Clams by Volume in Cheniers	$87,500 \text{ m}^{-3}$	Kowalewski et al., 2000
Tidal Flat Area	$1.2 \times 10^8 \text{ m}^2$	Kowalewski et al., 2000
Pre-dam Clam Density	$50 - 125 \text{ ind/m}^2$	Kowalewski et al., 2000
Modern Clam Density	$3 - 17 \text{ ind/m}^2$	Kowalewski et al., 2000; Avila-Serrano et al., 2006
Clam Dry Mass	$11.13 \pm 8.3 \text{ g/ind}$	Measured
Pre-dam Salinity (North)	22 – 32 psu	Cintra-Buenrostro et al., 2012
Pre-dam Salinity (South)	30 – 38 psu	Cintra-Buenrostro et al., 2012
Modern Salinity	35 – 42 psu	Dettman et al., 2004
Dry Tissue Weight	1.36 g/ind	Velasco and Navarro, 2003
Dry Tissue to AFDW	$1 \text{ g DT} = 0.81 \text{ g AFDW}$	Rumohr et al., 1987
AFDW Gram to Kilocalorie	$1 \text{ g AFDW} = 5.492 \text{ kcal}$	Cummins and Wuycheck, 1971
Kilocalorie to grams Carbon	$11.4 \text{ kcal} = 1 \text{ g C}$	Chauvaud et al., 2003

corrected to account for the approximately 5% of compounds other than calcium carbonate in clam shells (Gouletquer and Wolowicz, 1989).

$$\text{Calcium Carbonate (g/m}^2\text{)} = \text{Clam Density (clams/m}^2\text{)} * [(\text{Shell Dry Mass (g/clam)} * 0.95)/3]$$

We determined average shell dry mass ($11.13 \pm 8.3 \text{ g/ind}$) by taking the mass of 100 specimens of *M. modesta*, which composed as much as 95% of the molluscan community in the pre-dam era (Kowalewski et al., 1994; Rodriguez et al., 2001). The *M. modesta* specimens were randomly selected from a bulk sample (Kowalewski, 2002) that was sieved with a 12.5 mm screen to ensure comparability with the data

reported by Kowalewski et al. (2000). We estimated grams of carbon per square meter by adjusting for the atomic weight of calcium carbonate:

$$\text{Carbon (g/m}^2\text{)} = 0.12 * \text{Calcium Carbonate (g/m}^2\text{)}$$

We then multiplied g C m⁻² by the total area of the tidal flat to provide values of annual average sequestration (Table 3).

We calculated the production of carbon due to biogenic calcification according to the ratio of released (CO₂) to precipitated (CaCO₃) carbon (ψ ; 41). Carbon emission to the atmosphere during biogenic calcification is buffered by water chemistry, with the exchange rate influenced by temperature and salinity. Warmer temperatures and greater salinities reduce ψ , decreasing the emission of CO₂ to the atmosphere relative to the precipitation of carbonate (i.e., fresh, cold water leads to the least precipitation). Seawater temperature data are available for the present-day and vary seasonally from 5 – 40° C (Goodwin et al., 2001; Ramirez-Leon, 2015), but data from the pre-dam era are limited to a handful of data points at 18 – 20° C, collected by the U.S. Fish Commission steamer *Albatross* in March 1889 (Townsend, 1901). Due to this limitation on temperature data, we used the univariate ψ equation for salinity, which does not include temperature (i.e., assumes constant temperature):

$$\psi = 0.949 - (7.9 \times 10^{-3} * S)$$

where ψ is the ratio of released : precipitated carbon, and S is salinity in practical salinity units (psu), and $p\text{CO}_2 = 350 \mu\text{atm}^4$ (Frankignoulle et al., 1994; Chauvaud et al., 2003; Mistri and Munari, 2012; Munari et al., 2013).

Salinity in the CRE has increased following the construction of dams throughout the basin (Carbajal et al., 1997; Rodriguez et al., 2001). Today, salinities range from 35 – 42 psu (Dettman et al., 2004), though periodic flow releases (at significantly lower volumes than occurred historically) have occasionally reduced salinities to 29 – 36 psu (Lavin and Sánchez, 1999; Dettman et al., 2004). We therefore assumed a value of 38.5 psu for the present. Isotopic data from the shells of *M. modesta* suggest individuals near the mouth of the river grew under salinities of 22 – 33 psu whereas individuals further south experienced salinities of 30 – 38 psu (Cintra-Buenrostro et al., 2012). We used the mean value from the isotopic data, 30 psu, which is in the range reported during more recent flows, to calculate changes in carbon emissions.

Finally, carbon emitted due to respiration was calculated using the relationship established by Schwinghamer et al. (1986):

$$\text{Log}_{10}R = 0.367 + 0.993 * \log_{10}P$$

⁴ 350 μatm was used by Frankignoulle et al. (1994) to establish the ϕ equation and is maintained here. Frankignoulle et al. (1994) reported an increase in ϕ as $p\text{CO}_2$ increases, resulting in positive feedback. Consequently, ϕ is higher today than it was in the past, but 350 μatm remains an appropriate estimate for the entire post-dam era (1930 – present). In the pre-dam era, ϕ was likely lower, however, a decrease to 290 μatm (an estimate for the pre-industrial era; Frankignoulle et al., 1994) results in only a small change (0.04) in ψ . Thus, given the small difference and because the pre-dam era also encompassed higher $p\text{CO}_2$ during the industrial era, 350 μatm was also used for pre-dam era calculations.

where R and P are respiration and biomass production ($\text{kcal m}^{-2} \text{ yr}^{-1}$), respectively. We applied the conversion factor of $5.492 \text{ kcal} = 1 \text{ g ash-free dry mass (AFDM)}$ to estimate P (Cummins and Wuycheck, 1971) and estimated carbon emission from R as $11.4 \text{ kcal} = 1 \text{ g C}$ (Chauvaud et al., 2003). Live *M. modesta* were not available to determine AFDW, however, dry tissue weights of $1.36 \text{ g individual}^{-1}$ have been reported in the literature for the closely related and morphologically similar *Mulinia edulis* (Velasco and Navarro, 2003) and can be converted to AFDW-equivalent using the conversion factor of $1 \text{ g dry tissue weight} = 0.81 \text{ g AFDW}$ (Rumohr et al., 1987). Thus, we use a value of 1.1 g AFDW in our calculations.

Results

Both sequestration, via biogenic calcification, and emission, via respiration and calcification, have fallen sharply with the alteration of the CRE estuarine ecosystem. Estimated sequestration from current clam populations is $0.1 \text{ mol C m}^{-2} \text{ yr}^{-1}$, whereas pre-dam abundances imply sequestration of 1.8 to $4.4 \text{ mol C m}^{-2} \text{ yr}^{-1}$ (Table 4, at low and high densities, respectively). Atmospheric emissions due to calcification have also declined by roughly an order of magnitude from 1.3 to $3.1 \text{ mol C m}^{-2} \text{ yr}^{-1}$ (at low and high pre-dam densities, respectively) to $0.07 \text{ mol C m}^{-2} \text{ yr}^{-1}$. Similarly, historic emissions from respiration ranging from 4.9 to $12.2 \text{ mol C m}^{-2} \text{ yr}^{-1}$ (at low and high densities, respectively) have declined to $0.3 \text{ mol C m}^{-2} \text{ yr}^{-1}$. As a consequence, net carbon emissions have decreased from a range of 4.4 to $10.9 \text{ mol C m}^{-2} \text{ yr}^{-1}$ to $0.26 \text{ mol C m}^{-2} \text{ yr}^{-1}$. This corresponds to a cumulative annual reduction in tidal flat carbon emissions ranging from 5.9×10^3 to $15.0 \times 10^3 \text{ t}$.

Table 4 Estimated carbon sequestration and emission for the pre-dam and modern eras. Pre-dam low (50 ind m^{-1}) and high (125 ind m^{-1}) refer to the number of individuals per square meter inferred from chenier deposits (Kowalewski et al., 2000). Emissions via calcification were estimated at salinities of 30 psu and 38.5 psu for the pre-dam and modern eras, respectively. Emissions from respiration were estimated based on an ash-free dry mass of 1.1 g ind^{-1} .

				$\Delta\text{Carbon (low, high)}$	
	Pre-dam low (mol C $\text{m}^{-2} \text{ yr}^{-1}$)	Pre-dam high (mol C $\text{m}^{-2} \text{ yr}^{-1}$)	Modern (mol C $\text{m}^{-2} \text{ yr}^{-1}$)	mol C $\text{m}^{-2} \text{ yr}^{-1}$	t C yr^{-1}
Sequestration via Calcification	1.8	4.4	0.11	1.7, 4.3	2400, 6200
Emission via Calcification	1.3	3.1	0.068	1.2, 3.0	1700, 4400
Emission via Respiration	4.9	12.2	0.3	4.6, 11.9	6600, 17000
Net Emission	4.4	10.9	0.26	4.1, 10.6	5900, 15200

Discussion

The reduction in carbon emissions, by $4.1 - 10.6 \text{ mol C m}^{-2} \text{ yr}^{-1}$, due to the decline of *M. modesta* populations in the Colorado River delta likely corresponds to a large proportional decline in carbon emissions from the estuary as a whole. Borges *et al.* (2005) estimated for estuaries from low latitudes ($0 - 30^\circ$) and high latitudes ($30 -$

60°) that carbon emissions were 17 and 46 mol m⁻² yr⁻¹, respectively. The Colorado River delta is located at approximately 31° N, suggesting that the carbon reductions calculated here represent a reduction of roughly 9 – 23% for the entire estuary. The estimates from Borges *et al.* (2005) may, however, overestimate estuarine emissions due to the abundance (69%; n=16) of high *p*CO₂ European river systems used to make the estimates (Laruelle *et al.*, 2010; Cai, 2011; Chen *et al.*, 2013). In contrast, emissions from several ‘high latitude’ estuaries in the United States were reported to be considerably lower: 15 – 36 mol C m⁻² yr⁻¹ (Jiang *et al.*, 2008; Cai, 2011). Thus, the reductions reported here might correspond to a decline of up to 70% for annual estuary carbon emissions. This considerable change for the estuary has the potential to significantly alter the CRE ecosystem (Newell, 2004; Kristensen *et al.*, 2014) and influence economically important local mariculture (Jiang *et al.*, 2014). Despite these implications, the conveyance, storage, and emission of carbon by rivers—under natural or human-altered conditions—has only recently factored prominently into assessments of the tradeoffs that accompany decisions to store water in reservoirs, to divert it for agricultural and municipal use, or to use it for hydroelectric power generation (Brown *et al.*, 2009; Kareiva, 2012; Auerbach *et al.*, 2014). Even so, these decisions certainly imply different outcomes for the carbon footprint associated with the managed river network (Shrestha *et al.*, 2011b).

Our calculations were constrained in part by the uncertainties inherent to using paleoecological data, however, we most likely underestimated the difference in carbon emissions before and after extensive river diversion. The largest uncertainty in our analyses was the estimate of clam density prior to extensive water diversions. Many

processes transport (e.g., wave action, currents) and degrade (e.g., fragmentation, dissolution⁵) the remains of organisms after death (Kowalewski et al., 1994), and the shells preserved in cheniers provide a conservative, lower bound on original density. Additional uncertainty was due to the absence of precise estimates for *M. modesta* AFDM. Despite being congeneric, minor differences in shell morphology between *M. modesta* and *M. edulis* may have introduced minor errors into our calculations. Notwithstanding these considerations, our estimates for pre-dam carbon emission and sequestration are comparable to values reported for other calcifying organisms such as clams (Chauvaud et al., 2003; Mistri and Munari, 2012), corals (Ware et al., 1992), barnacles (Golléty et al., 2008), and brittle stars (Migne et al., 1998; Table 5). These studies support the validity of our parameter estimates and strengthen the conclusion that carbon emissions from the molluscan community in the estuary of the Colorado River delta have dropped precipitously following the complete appropriation of the river's flow.

Table 5 Carbon sequestration and emission for other calcifying systems in moles of carbon per square meter per year.

Species	Sequestration via Calcification	Emission via Calcification	Emission via Respiration	Source
<i>Potamocorbula amurensis</i>	2.2	1.5	3.1	Chauvaud et al., 2003
	8.2	5.6	22.7	Mistri and

⁵ The process of dissolution releases carbon dioxide and contributes to carbon cycling. Because cheniers are subaerial accumulations, however, they are not affected by the same set of destructive processes as assemblages in other marine environments (Kowalewski et al., 1994). Thus, shell dissolution via seawater was likely limited. The dissolution that did occur on the tidal flat would have effectively reduced the amount of carbon sequestered in clam shells, resulting in greater net emissions proportionate to total clam abundance in the pre- and post-dam eras.

<i>philippinarum</i>				Munari, 2012
<i>Mytilus galloprovincialis</i>	136.6	86.8	187.8	Munari et al., 2013
Barnacles	4.8 – 18.0	3.4 – 12.7	3.9 – 14.1	Golley et al., 2008
Brittle Stars	6.8	4.8	-	Migne et al., 1998
Corals	15.0	12.0	-	Ware et al., 1991

Whereas the reduction in carbon emissions is likely a significant portion of the pre-dam era estuary emissions, the mass is small relative to overall carbon emissions resulting from water management in the southwestern United States. For instance, the United States Bureau of Reclamation utilizes a 24.3% share of power from the coal-fired Navajo Generating Station to lift Colorado River water to Phoenix and Tucson through the Central Arizona Project, emitting 1.1×10^6 t ($\sim 9.2 \times 10^{10}$ mol) of carbon annually (<http://ghgdata.epa.gov/ghgp/main.do#>). Similarly, Shrestha *et al.* (2011a) estimated that 1.4×10^5 t ($\sim 1.2 \times 10^{10}$ mol) of carbon are emitted annually as a consequence of conveyance of Colorado River water to the Las Vegas Valley. By comparison, the reduced carbon emissions at the delta resulting from diverted flow are vastly outweighed by the carbon emissions required to divert that flow.

The estuary emissions reduction may not be significant compared to other carbon emissions related to water management in the Colorado River system, however, extrapolating to a global scale, the mass of reduced carbon emissions becomes much larger. An overview of the world's largest river systems revealed that 172 out of 292 have been diverted by dams and water management (Nilsson *et al.*, 2005). Assuming the conditions in the Colorado River system are representative of the average large river system, then global reductions in carbon emissions associated with molluscan populations are on the magnitude of 1.0×10^6 to 2.6×10^6 t C year $^{-1}$, using

the low and high estimates reported here. Estimates such as these are often prone to a large degree of uncertainty ($\pm 50\%$) given the tenuous nature of the assumptions behind them (Woodwell et al., 1973; Borges et al., 2006). Keeping this in mind, the hypothetical reduction in global carbon emissions is at most on the scale of a large power plant (i.e., Navajo Generating Station).

Although modest in comparison to the present-day emissions resulting from river management, the change that we document nonetheless illustrates the need to advance and refine the science to support better accounting of the carbon budgets associated with rivers and water management systems (Shrestha et al., 2011a, 2011b; Frijns, 2012). Carbon emission from clams is one of many components that contribute to a river's total carbon footprint (Figure 16). The complexity of carbon cycling in rivers and estuaries reflects the diverse organisms that inhabit the interwoven components of these systems and understanding these connections will be critical to well-informed planning and policymaking under an uncertain future. For instance, as climate change increases temperatures and the frequency, duration, and severity of drought in the southwestern United States (US Department of Interior, 2011; Dawadi and Ahmad, 2012), integrated management of water, energy, and ecosystem services is essential. The unintended reduction in net carbon emissions following the decline of mollusk populations in the Colorado River delta further demonstrates the need to seek solutions to pressing global challenges that maximize ecosystem services while maintaining ecosystem function as new social priorities emerge or new scientific insight is gained (Doyle, 2012; Auerbach, 2013; Doyle, 2013).

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APPENDICES

Appendix 1: Museum Collections

Museum collections from the Santa Barbara Museum of Natural History, Natural History Museum of Los Angeles County, California Academy of Sciences, and National Museum of Natural History were surveyed to check for pre-dam era *Notocochlis chemnitzii* specimens from the Colorado River estuary (CRE). We chose the three former museums due to their large size and proximity to the CRE, making them the most likely museums to hold pre-dam CRE collections. We included the National Museum of Natural History because it holds the collections from the northern Gulf of California used by Dall (1890; 1891; 1894) to describe the regional molluscan fauna and document new species such as *Mulinia coloradoensis* (although this species has since been synonymized with *M. modesta* by Coan and Valentich-Scott, 2012). First, we executed searches of the available online databases for each of the respective museums. Second, because it is common for collections to exist that have not yet been digitized in a searchable format, we contacted curators at each of the museums to obtain information on these undigitized collections. We asked curators to identify the presence of *N. chemnitzii* from the CRE prior to the 1930s and inquired about the existence of any collections whatsoever from the CRE during the pre-dam era. The availability of material at the museums was variable (Appendix Table 1), however, no pre-dam era *N. chemnitzii* from the CRE were found.

Appendix Table 1 Holdings of Colorado River delta collections at museums in the United States likely to have pre-dam era collections.

Museum	Collections Information
Santa Barbara Museum of Natural History	<ul style="list-style-type: none"> • No pre-dam CRE collections • Pre-dam <i>N. chemnitzii</i> from southern Gulf of California
Natural History Museum of Los Angeles County	<ul style="list-style-type: none"> • No pre-dam CRE collections
California Academy of Sciences	<ul style="list-style-type: none"> • Pre-dam CRE collections exist but do not contain <i>N. chemnitzii</i> • Pre-dam <i>N. chemnitzii</i> from southern Gulf of California
National Museum of Natural History	<ul style="list-style-type: none"> • Pre-dam CRE collections exist, namely those from Dall (1890; 1891; 1894) • No pre-dam CRE <i>N. chemnitzii</i>

Appendix 2: Negative Evidence

All of Kidwell's (2013) alternatives to explain the absence of a rare species in the death assemblage when it is found in the live assemblage are based on absence data, or, negative evidence. In our case, we argue that a lack of *N. chemnitzii* body fossils, or related trace fossils (e.g., edge drill holes), in pre-dam samples suggests that *N. chemnitzii* did not live in the CRE during the pre-dam era. Negative evidence is often dismissed because it is considered inferior to positive evidence. This criticism of negative evidence may seem to undermine our conclusion that *N. chemnitzii* recently expanded its range to the CRE, however, negative evidence can be powerful and compelling when correctly interpreted (Heussen et al., 2011; Macagno and Walton, 2011).

Negative evidence is considered to be of little use because it depends entirely upon the completeness of the negated factors (Macagno and Walton, 2011). Under the

principle of “negation as failure” (Clark, 1978), to show that “Y” does not exist, one must search for proof of “Y” and can only conclude that “Y” does not exist after exhaustively considering every avenue. We must question then, “Did we exhaustively search the cheniers and tidal flat?” The answer to this question is, of course, no. We did not pick up a trillion shells to ensure that each one of them was not *N. chemnitzii*. We are, however, confident that our sampling effort, which recovered approximately 4,000 body fossil specimens in nearly 100 distinct samples, adequately satisfied the “negation as failure” principle.

Multiple lines of evidence, in the form of body fossils, trace fossils, and in the recovery of specimens of *N. chemnitzii* in cheniers from the post-dam construction era (hereafter post-dam), increase our confidence. Consider the absence of body fossils in pre-dam samples: as many as four different collectors target sampled the death assemblage at each locality. During sampling, tens of thousands of shells were visually inspected and thousands were collected. Under the exact same collecting protocol, *N. chemnitzii* were found in post-dam samples, and, during our sampling we encountered many rare gastropod species as would be expected with the target-sampling method. The occurrence of these rare taxa suggests that if *N. chemnitzii* had been present we should have at least encountered a single individual, especially given the low taphonomic loss potential of the size range of shells we targeted and the propensity of time-averaged death assemblages to capture rare species (Kidwell, 2013).

Appendix 3: Biological Limitations

Historically, *N. chemnitzii* had a range extending throughout much of the Gulf of California and as far South as Peru (Keen, 1971) and, based on our findings, in the decades since the Colorado River was diverted has extended its range to the CRE. Evidence from shell middens and fossil deposits confirms a long history for *N. chemnitzii* in the Gulf of California. Archaeological middens from the past several millennia are abundant along the Gulf of California's coasts (Foster et al., 2012) and *N. chemnitzii* has been reported in middens as far north as Bahia de los Angeles (Figure 1; Laylander et al., 2013). Similarly, Late Pleistocene fossil deposits at Puerto Libertad contain numerous *N. chemnitzii* and abundant drillholes are evidence of their prevalence in the benthic community as a predator (Stump, 1975). Despite its extensive range and long history in the Gulf of California, *N. chemnitzii* appears to have been unable to establish a population in the delta region until recently. We consider five alternatives for the absence of *N. chemnitzii* in the pre-dam cheniers: (1) lack of suitable prey; (2) limited dispersal ability; (3) physiological sensitivity to cooler pre-dam water temperatures, (4) substrate preference; and, (5) lack of physiological tolerance of low salinities.

Prey Availability

Notocochlis chemnitzii may have been unable to establish a population in the CRE if suitable prey species were not present. It has been estimated using pre-dam shell accumulations, however, that *M. modesta* lived at densities in excess of 50-individuals/m² (Kowalewski et al., 2000). This bivalve was not only highly abundant

but also an energetically favorable prey item, due to its thin shell and high biomass, and a preferred prey resource for the naticid *N. reclusiana* (Cintra-Buenrostro et al., 2005). Naticids do not always prey upon the most abundant species (Kitchell et al., 1981); however, it seems likely that *N. chemnitzii* would have preyed on *M. modesta* given its favorable cost-benefit ratio (high energetic returns per unit time of foraging). Furthermore, *N. chemnitzii* commonly preyed on *Chione*, *Tellina*, and *Lucina* in the Late Pleistocene deposits of the Gulf of California (Stump, 1975) and should have been more than capable of consuming the thin-shelled *M. modesta*. Thus, the absence of suitable prey does not explain the past limitation on *N. chemnitzii*'s distribution in the CRE.

Dispersal

The emergent form of naticid larvae when they hatch from an egg collar and disperse is either a planktonic veliger or crawl-away juvenile (Scheltema and Williams, 1983; Pastorino et al., 2009). This type of life-history information is available for many species (Scheltema and Williams, 1983); to the best of our knowledge, however, we do not know which type of larvae *N. chemnitzii* produces. Complicating the matter is the fact that congeners exhibit both planktonic and crawl-away emergent forms (Pastrino et al., 2009). Despite this uncertainty, we are confident that pre-dam era *N. chemnitzii* distribution was not limited to a southern range by a lack of dispersal ability.

Assuming *N. chemnitzii* disperses in the plankton, a previously limited range would require a difference in pre- and post-dam era circulation patterns in the Gulf of

California. In the pre-dam era, freshwater from the Colorado River moved predominantly along the western coast of the northern Gulf of California and influenced this coastline at least 65 kilometers south of the CRE (Rodriguez et al., 2001). Outside of the Colorado River's influence, however, circulation patterns in the Gulf of California have changed very little since the diversion of the Colorado River. In the pre-dam era and continuing today, there have been currents moving from the southern regions to the CRE (Carbajal et al., 1997). Additionally, in the northern Gulf of California, a basin-wide gyre circulates water across the entire region (Palacios-Hernandez et al., 2002). In the past, this pattern of circulation should have brought *N. chemnitzii* planktonic larvae to the CRE, although, they may not have found suitable conditions for successful recruitment. It seems unlikely that the absence of *N. chemnitzii* in the pre-dam era can be explained by limited planktonic dispersal.

If we assume that *N. chemnitzii* disperse via crawl-away juveniles, it remains that dispersal potential cannot explain their absence from the CRE. In this case, the only obstacle to *N. chemnitzii* dispersal would be the time needed to traverse the distance to the CRE from their southern range. We know, however, that *N. chemnitzii* have been present in the Gulf of California since at least the Pleistocene (Stump, 1975), and should have had ample time to reach the CRE. As with planktonic dispersal, it seems likely that if *N. chemnitzii* disperse with crawl-away juveniles, dispersal potential itself should not have been the limiting factor. Instead, it seems likely that the conditions encountered by juveniles in the CRE may have been unfavorable to *N. chemnitzii*.

Temperature Sensitivity

Drilling gastropod predators, including naticids, are often sensitive to water temperature (Anderson, 1992; Bertness, 1999). A difference in pre- and post-dam era water temperature could therefore potentially explain the absence of *N. chemnitzii* in the pre-dam cheniers. Today, water temperature in the CRE fluctuates around seasonal means of 15-31° C (Thompson, 1968), although extremes in excess of 5° C and 40° C do occur (Goodwin et al., 2001). Our understanding of water temperature in the pre-dam era, when the Colorado River was flowing unimpeded, is restricted to data from the pre-dam U.S. Fish Commission’s “Albatross” research cruise in 1889 (Townsend, 1901). In March 1889, surface water temperature in the CRE was measured as 20° C (Townsend, 1901) which is consistent with the surface temperature of 20.25° C reported during the same time of year in 1996 when no freshwater was flowing into the CRE (Lavin and Sanchez, 1999). Together these data suggest that water temperature has not changed appreciably since the diversion of the Colorado River, likely due to the bathymetry of the northern Gulf of California.

The CRE is positioned on a broad shallow shelf in the northern Gulf of California and experiences warmer water temperatures than the offshore Gulf of California throughout much of the year (Paden et al., 1991). Available data collected in 1889 and 1996 show this trend—water temperature in both cases was at least 1° C warmer in the CRE than surrounding northern Gulf of California (Townsend, 1901; Lavin and Sanchez, 1999)—suggesting that water temperature in the CRE should have been amenable to *N. chemnitzii* in the pre-dam era during most of the year. The water temperature trend does, however, reverse during the cold winter months when the

shallow waters become heavily influenced by cold air temperatures (Paden et al., 1991; Lavin and Sanchez, 1999). It is these cold winter water temperatures that may have excluded *N. chemnitzii* from the CRE in the past. In the winter months today, however, water temperature in the estuary drops to ~5° C (Goodwin et al., 2001) and this likely is not a large deviation from past winter low water temperatures.

Using satellite infrared images, Lavin et al. (2003) found that water temperatures in the Gulf of California increased by ~1° C between 1984 and 2000 (see also Lluch-Cota et al., 2010). These data suggest that winter low water temperatures may have been colder in the past and may have excluded *N. chemnitzii* from the CRE. Although warming may have occurred in the Gulf of California, a 1° C change (increasing winter lows from 4° C to 5° C) in water temperature is unlikely to explain the absence of *N. chemnitzii* given that daily water temperatures can fluctuate by more than 10° C. Furthermore, observations of a rare Colorado River discharge event in 1993, similar to flow conditions of the pre-dam era, suggested that freshwater entering the CRE was warmer than Gulf of California waters (Lavin and Sanchez, 1999), which would have counterbalanced the potentially colder winter low water temperatures. A change in water temperature is not likely to explain the absence of *N. chemnitzii* from the pre-dam era CRE.

Substrate Preference

Benthic predators tend to be sensitive to substrate type because it can impact their foraging effectiveness and survivorship (Stump, 1975; Seitz et al., 2001 and references therein; Chattopadhyay et al., 2014). If in the pre-dam era, the dominant

substrate type was unsuitable for *N. chemnitzii*, it may have prevented *N. chemnitzii* from establishing a viable population after dispersing to the area. In the CRE today, substrate is highly variable moving both parallel and perpendicular to the shoreline, creating a mosaic of sand- and mud-dominated patches (Thompson, 1968; pers. obs.).

The Colorado River once delivered over 10^8 metric tons of sediment to the CRE each year and the resulting tidal flat may have looked dramatically different (Thompson, 1968). Mineralogical analysis by Thompson (1968) found that the Colorado River was the primary source of fine grain sediment, and that 80% of the river's sediment load was composed of suspended silt and clay (Thompson, 1968). Today, with no Colorado River input, very little fine-grained sediment reaches the CRE and, during each tidal cycle, muds and silts are resuspended and subsequently removed to deeper waters (Thompson, 1968; Carriquiry and Sanchez, 1999). Coarser sediments (i.e., sands) have become more prevalent today than in the past and a sedimentological mosaic has been created. This difference may have had an inhibitory effect on successful *N. chemnitzii* recruitment, however, in the absence of experiments with live *N. chemnitzii*, we can only speculate that unfavorable substrate may have limited *N. chemnitzii* to a more southerly range in the pre-dam era.

Salinity Sensitivity

Salinity in the CRE has increased dramatically since the diversion of the Colorado River. In the pre-dam era CRE, salinities frequently dropped below 30 psu, whereas today salinities regularly exceed 40 psu (Carabajal et al., 1997; Carriquiry and Sanchez, 1999). Just as with sediment grain-size, naticids exhibit variable sensitivity

to salinity (Anderson, 1992; Chattopadhyay et al., 2014). Thus *N. chemnitzii* may have been excluded from successfully dispersing to the CRE by previously brackish salinities. Unfortunately, as with substrate, experimental studies on *N. chemnitzii* do not exist to estimate its salinity preferences. Separate from or synergistically with the change in substrate, reduced salinity likely played a key role in the exclusion of *N. chemnitzii* from the CRE. Confirming experimentally that *N. chemnitzii* is sensitive to muddy substrate and brackish water conditions would provide an independent line of evidence supporting our interpretation that the diversion of the Colorado River was the main driver in permitting *N. chemnitzii* to expand its range into the CRE.

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Appendix 4: Subsampling of the Colorado River estuary molluscan community

Subsampling was conducted when counts for a given species exceeded 150 specimens in a sample. Prior to subsampling, samples were sorted by species and counted. Subsampling was conducted by gently mixing specimens of the species of interest in a tray until specimens were distributed randomly according to size. The tray was then divided into four sections and one section was randomly chosen for measurement. This process was repeated if the subsample still exceeded 150 specimens. Only subsampled specimens were used to determine counts of drilled and undrilled specimens and only these specimens were measured to evaluate the potential

for size bias in predator selection of prey. Five species were subsampled: *Mulinia modesta*, *Nassarius moestus*, *Cerithideopsis californica*, *Anomia peruviana*, and *Melampus olivaceus* (Appendix Table 2). Of these species, three (*Cerithideopsis californica*, *Anomia peruviana*, and *Melampus olivaceus*) were not drilled by the naticid predator.

Using the subsamples described above, we estimate the drilling frequency of the full data set of *Mulinia modesta* at all three sites and *Nassarius moestus* at Isla Montague and Las Isletas. The full data set is assumed to be a finite population of size N with drilling frequency DF, which is estimated from a random subsample of n specimens where $n < N$. The estimate of DF using the subsample has a confidence interval around the true DF in the population: $(df - z^* \sqrt{c * df * (1-df)/n}, df + z^* \sqrt{c * df * (1-df)/n})$, where z is a z-score, df is the drilling frequency for the subsample, and $c = (N-n)/(n-1)$ is a finite population correction factor. In all cases, the confidence intervals were small, demonstrating little effect of subsampling on estimated drilling frequencies (Appendix Table 3). These results agree with previous reports in the literature that 25–30 individuals can provide accurate estimates of drilling frequencies (Kowalewski, 2002).

Appendix Table 2 Counts of individuals from complete samples (raw counts) and subsamples.

	Isla Montague		Las Isletas		Campo don Abel	
	Raw Count	Subsample	Raw Count	Subsample	Raw Count	Subsample
<i>Mulinia modesta</i>	4652	194	3962	245	627	251
<i>Nassarius moestus</i>	692	281	539	311	241	241
<i>Cerithideopsis californica</i>	1402	297	11	11	9	9
<i>Melampus olivaceus</i>	182	105	0	0	0	0
<i>Anomia peruviana</i>	0	0	165	95	1	1

Appendix Table 3 Confidence intervals (95% CI) on drilling frequencies (*df*) for subsampled species.

	Isla Montague		Las Isletas		Campo don Abel	
	<i>df</i>	95% CI	<i>df</i>	95% CI	<i>df</i>	95% CI
<i>Mulinia modesta</i>	0.129	±0.024	0.184	±0.024	0.179	±0.019
<i>Nassarius moestus</i>	0.025	±0.007	0.077	±0.010	-	-

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Appendix 5: Estimation of *Neverita reclusiana* population size in the Colorado River estuary

The pre- and post-dam population size of *N. reclusiana* was estimated based on the biomass of clams available as a prey resource. Just as estimating population sizes of living organisms requires several assumptions to be made (e.g., all species in a community are equally likely to be sampled; samples are representative of the entire habitat area; sampling reflects population distributions in size, age, etc.; sampling does not impact community dynamics (Heyer et al., 1994; Kraeuter and Castagna, 2001)), there are additional assumptions underlying the estimation of population size from death assemblages (e.g., time-averaging of multiple generations; preservational bias). Pre-dam estimates were made solely with respect to the *Mulinia modesta* population—assuming that, as this species composed up to 95% of the community, estimates based on this species reasonably approximate the entire community—and an estimated density of 50 ind./m² over a tidal flat area of 1.2 x 10⁸ m² (Kowalewski et al., 2000). To arrive at this density, Kowalewski et al. (Kowalewski et al., 2000) estimated the

areal extent of the cheniers and the average depth of the chenier accumulations. Subsequently, they determined an average density of complete *M. modesta* larger than 12.5 mm in the cheniers. Based on estimates of time-averaging in the cheniers (Kowalewski et al., 1998), they determined that the *M. modesta* shells originated over a 1,000-year period and, using published estimates for average *M. modesta* lifespan (three years; Rodriguez et al., 2001), approximated the number of generations represented in the cheniers to be 333. Using these estimates, Kowalewski et al. (Kowalewski et al., 2000) estimated that the density of *M. modesta* was 50 ind./m² in the pre-dam era. They also noted that their estimate was likely a conservative one, as approximately 60% of *M. modesta* individuals were broken and therefore not included in their analysis.

Post-dam estimates were derived from transect surveys of the living community. In the transects, clam—predominantly *C. fluctifraga* and *M. modesta* (Kowalewski et al., 2000; Dietl and Smith, 2017)—densities were three ind./m². Accordingly, biomass was calculated for scenarios with all *M. modesta* and all *Chionista fluctifraga* to provide the minimum and maximum size of the *N. reclusiana* population that could be supported. We use a clam size of 25 mm in shell length to estimate biomass and the conversion factors listed in Appendix Table 4. These calculations yielded an estimate of 3.09 kilojoules/ind. for *M. modesta* and 3.31 kilojoules/ind. for *C. fluctifraga* and are based on size-energy relationships derived from the phylogenetically closely related species, *Mulinia lateralis* (Walker and Tenore, 1984) and *Mercenaria mercenaria* (Nakaoka, 2000), respectively. Given that *C. fluctifraga* has a greater energetic content, fewer *C. fluctifraga* are required to

sustain an individual naticid and a prey population of *C. fluctifraga* could be expected to support a larger *N. reclusiana* population than if the prey population was composed entirely of *M. modesta* (Appendix Table 5). On a diet composed entirely of *M. modesta*, a small (~25 mm in maximum diameter) and large (~39 mm in maximum diameter) naticid must consume 71 – 125 ind./yr², respectively, compared to 66 – 116 ind./yr² for a diet entirely composed of *C. fluctifraga*.

Appendix Table 4 Parameters and estimates for calculating *Neverita reclusiana* population size in the Colorado River estuary.

parameters and conversions	estimate	source
tidal flat area	1.2 x 10 ⁸ m ²	Kowalewski et al. (Kowalewski et al., 2000)
pre-dam clam density	50 ind. m ⁻²	Kowalewski et al. (Kowalewski et al., 2000)
post-dam clam density	3 ind. m ⁻²	Kowalewski et al. (Kowalewski et al., 2000)
clam shell length to dry weight (<i>Mulinia lateralis</i>)	DW (g) = 0.01095*(shell length cm) ^{2.968}	Walker and Tenore (Walker and Tenore, 1984)
clam shell length to dry weight (<i>Mercenaria mercenaria</i>)	DW (g) = 0.0000812*(shell length mm) ^{2.39}	Nakaoka (Nakaoka, 2000)
dry weight to AFDM	1 g DW = 0.81 g AFDM	Rumohr et al. (Rumohr et al., 1987)
AFDM to kilocalorie	1 g AFDM = 5.492 kcal	Cummins and Wuycheck (Cummins and Wuycheck, 1971)
kilocalorie to kilojoule	1 kcal = 4.184 kj	Edwards and Huebner (Edwards and Huebner, 1977)
large naticid energy need	385 kj	Edwards and Huebner (Edwards and Huebner, 1977)
small naticid energy need	218 kj	Edwards and Huebner (Edwards and Huebner, 1977)

Appendix Table 5 Estimates of *Neverita reclusiana* population size in the pre- and post-dam Colorado River estuary.

bivalve density	small naticid		large naticid	
	population	density	population	density
50 <i>M. modesta</i> /m ²	8.5 x 10 ⁷ ind.	0.7 ind/m ²	4.8 x 10 ⁷ ind.	0.4 ind/m ²
3 <i>M. modesta</i> / m ²	5.1 x 10 ⁶ ind.	0.04 ind/m ²	2.9 x 10 ⁶ ind.	0.02 ind/m ²
3 <i>C. fluctifraga</i> / m ²	5.5 x 10 ⁶ ind.	0.05 ind/m ²	3.1 x 10 ⁶ ind.	0.03 ind/m ²

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Appendix 6: Supplemental analyses of *Neverita reclusiana* preference in the pre-dam era Colorado River estuary

Neverita reclusiana exhibited prey preferences at each of the three localities in the pre-dam era CRE and they were not limited to *Mulinia modesta*. As discussed in the main text, these preferences were variable between localities and the preference for *M. modesta* diminished moving southward in the estuary. The complete results of the analysis for the subset of data including only species drilled by *N. reclusiana* are presented in Appendix Table 6. The section that follows Appendix Table 6 examines the effects of a supplementary analysis utilizing data for the whole community. As discussed below, this analysis confirms that *N. reclusiana* preferences were inclusive of more species than just *M. modesta*.

Appendix Table 6 Results of the analysis for the subset of species that were drilled by *Neverita reclusiana* at one or more of the localities.

Site	Taxon	Neutral	Manly's alpha	95% Credibility Interval	Probability alpha > neutral	Probability alpha < neutral	Probability <i>Mulinia</i> alpha is greater	# drilled valves	# individuals
Isla Montague	<i>Felaniella sericata</i>	0.111	0.386	0.027 - 0.796	0.872	0.128	0.302	1	2
	<i>Eupleura limata</i>	0.111	0.209	0.059 - 0.426	0.830	0.170	0.477	16	121
	<i>Mulinia modesta</i>	0.111	0.205	0.060 - 0.413	0.827	0.173	0.000	25	194
	<i>Chionopsis gnidia</i>	0.111	0.049	0.000 - 0.429	0.137	0.863	0.897	0	1
	<i>Chionista fluctifraga</i>	0.111	0.041	0.001 - 0.154	0.068	0.932	0.991	1	41
	<i>Chionopsis pulicaria</i>	0.111	0.040	0.000 - 0.362	0.117	0.883	0.916	0	2
	<i>Nassarius moestus</i>	0.111	0.040	0.009 - 0.099	0.012	0.988	1.000	7	281
	<i>Cosmioconcha palmeri</i>	0.111	0.022	0.000 - 0.202	0.062	0.938	0.963	0	6
	<i>Neverita reclusiana</i>	0.111	0.008	0.000 - 0.077	0.013	0.987	0.996	0	17
Las Isletas	<i>Chionopsis gnidia</i>	0.077	0.239	0.147 - 0.331	1.000	0.000	0.000	56	103
	<i>Lamelliconcha concinnus</i>	0.077	0.137	0.032 - 0.298	0.794	0.206	0.242	3	9
	<i>Eupleura limata</i>	0.077	0.123	0.071 - 0.182	0.957	0.043	0.038	33	118
	<i>Abra palmeri</i>	0.077	0.123	0.004 - 0.367	0.602	0.398	0.426	1	3
	<i>Cosmioconcha palmeri</i>	0.077	0.106	0.046 - 0.186	0.780	0.220	0.257	9	37
	<i>Mulinia modesta</i>	0.077	0.081	0.048 - 0.119	0.571	0.429	0.000	45	245
	<i>Chionista fluctifraga</i>	0.077	0.067	0.032 - 0.113	0.293	0.707	0.739	13	85
	<i>Neverita reclusiana</i>	0.077	0.038	0.017 - 0.066	0.005	0.995	0.994	11	129
	<i>Nassarius moestus</i>	0.077	0.034	0.019 - 0.054	0.000	1.000	1.000	24	311
	<i>Felaniella sericata</i>	0.077	0.026	0.000 - 0.233	0.103	0.897	0.894	0	1
	<i>Semele</i> spp.	0.077	0.010	0.000 - 0.099	0.037	0.963	0.961	0	3
	<i>Tellina hiberna</i>	0.077	0.010	0.000 - 0.036	0.000	1.000	1.000	1	47
	<i>Turridae</i> spp.	0.077	0.007	0.000 - 0.068	0.020	0.980	0.978	0	5
Campo don Abel	<i>Kylix</i> sp. 1	0.056	0.150	0.003 - 0.442	0.738	0.262	0.192	1	1
	<i>Chionopsis gnidia</i>	0.056	0.099	0.054 - 0.156	0.969	0.031	0.000	25	49
	<i>Semele</i> spp.	0.056	0.085	0.024 - 0.182	0.738	0.262	0.078	4	9
	<i>Lamelliconcha concinnus</i>	0.056	0.085	0.024 - 0.182	0.737	0.263	0.078	4	9
	<i>Acorylus rickettsi</i>	0.056	0.075	0.010 - 0.198	0.583	0.417	0.220	2	5
	<i>Cosmioconcha palmeri</i>	0.056	0.064	0.009 - 0.169	0.495	0.505	0.275	2	6
	<i>Chionopsis pulicaria</i>	0.056	0.062	0.007 - 0.168	0.476	0.524	0.293	2	6
	<i>Nassarius moestus</i>	0.056	0.059	0.035 - 0.088	0.577	0.423	0.002	73	241
	<i>Chionista fluctifraga</i>	0.056	0.054	0.014 - 0.121	0.414	0.586	0.255	4	14
	<i>Eupleura limata</i>	0.056	0.047	0.002 - 0.159	0.319	0.681	0.493	1	4
	<i>Mulinia modesta</i>	0.056	0.035	0.020 - 0.054	0.017	0.983	0.000	45	251
	<i>Veneridae</i> sp. 1	0.056	0.034	0.001 - 0.115	0.193	0.807	0.618	1	6
	<i>Turridae</i> spp.	0.056	0.032	0.001 - 0.113	0.178	0.822	0.643	1	6
	<i>Neverita reclusiana</i>	0.056	0.032	0.004 - 0.090	0.139	0.861	0.627	2	12
	<i>Donax californicus</i>	0.056	0.030	0.016 - 0.048	0.006	0.994	0.737	27	175
	<i>Diplodonta soror</i>	0.056	0.025	0.003 - 0.068	0.058	0.942	0.764	2	16
	<i>Sphenia gulfensis</i>	0.056	0.021	0.003 - 0.058	0.031	0.969	0.836	2	19
	<i>Tellina hiberna</i>	0.056	0.012	0.002 - 0.030	0.000	1.000	0.990	3	49

Whole Community

The first supplementary analysis we preformed was on the whole community—all species found in the bulk samples at each site. This analysis used lower null thresholds for each site, resulting from the addition of non-prey species, and

is less conservative than the analysis presented in the main text, where only species that were preyed upon were included in the analysis. This whole community analysis showed more inclusivity of species in the preferred group due to the reduced null thresholds and confirmed our conclusion that multiple prey species were preferred by *N. reclusiana*, perhaps even more species than observed in the original analysis.

For instance, the whole community results from Isla Montague showed a high probability of preference for *Felaniella sericata*, *M. modesta*, and *Eupleura limata* (Appendix Table 7). A minor difference in the whole-community result, as compared to the results presented in the main text, is the higher probability that *M. modesta* was more preferred than *E. limata*, even as both species were highly preferred by *N. reclusiana*.

Appendix Table 7 Predator preference at Isla Montague with all drilled and undrilled species.

Taxon	Neutral	Manly's alpha	95% Credibility Interval		Probability alpha > neutral	Probability alpha < neutral	Probability <i>Mulinia</i> alpha is greater	# drilled valves	# individuals
<i>Felaniella sericata</i>	0.062	0.362	0.019	0.784	0.914	0.086	0.323	1	2
<i>Eupleura limata</i>	0.062	0.202	0.055	0.418	0.960	0.040	0.480	16	121
<i>Mulinia modesta</i>	0.062	0.198	0.055	0.410	0.960	0.040	0.000	25	194
<i>Nassarius moestus</i>	0.062	0.039	0.008	0.097	0.146	0.854	1.000	7	281
<i>Chionista fluctifraga</i>	0.062	0.037	0.001	0.148	0.185	0.815	0.992	1	41
<i>Crepidula</i> sp. 1	0.062	0.030	0.000	0.322	0.120	0.880	0.933	0	1
<i>Chionopsis gnidia</i>	0.062	0.028	0.000	0.328	0.105	0.895	0.941	0	1
<i>Solenosteira capitanea</i>	0.062	0.023	0.000	0.289	0.089	0.911	0.948	0	1
<i>Epitonium</i> sp. 1	0.062	0.021	0.000	0.246	0.089	0.911	0.955	0	2
<i>Chionopsis pulicaria</i>	0.062	0.019	0.000	0.225	0.080	0.920	0.959	0	2
<i>Cumingia pacifica</i>	0.062	0.019	0.000	0.222	0.082	0.918	0.960	0	2
<i>Cosmioconcha palmeri</i>	0.062	0.011	0.000	0.124	0.053	0.947	0.983	0	6
<i>Tagelus affinis</i>	0.062	0.005	0.000	0.058	0.022	0.978	0.997	0	17
<i>Neverita reclusiana</i>	0.062	0.004	0.000	0.048	0.018	0.982	0.997	0	17
<i>Melampus olivaceus</i>	0.062	0.001	0.000	0.011	0.000	1.000	1.000	0	105
<i>Cerithideopsis californica</i>	0.062	0.000	0.000	0.003	0.000	1.000	1.000	0	297

Moving to the middle locality along the past salinity gradient, Las Isletas, several more species were preferred by *N. reclusiana* in the whole community analysis than in the main text results (Appendix Table 8). Eight species, in addition to *M. modesta*, were preferred, compared to three in the main analysis. This difference is due to the addition of many more species in the analysis, which reduced the null threshold from 0.091 when considering only species that were drilled to 0.029 when including all species in the community. Regardless, with respect to the hypothesis that species other than *M. modesta* were preferred, the conclusions drawn from the results of these analyses are the same: *N. reclusiana* preferred several species and was likely able to switch prey species after the decline in the *M. modesta* population. Unlike the results from Isla Montague, the whole-community results from Las Isletas also showed low probabilities for *M. modesta* being more greatly preferred than several other species in the community.

Appendix Table 8 Predator preference at Las Isletas with all drilled and undrilled species.

Taxon	Neutral	Manly's alpha	95% Credibility Interval		Probability alpha > neutral	Probability alpha < neutral	Probability <i>Mulinia</i> alpha is greater	# drilled valves	# individuals
<i>Chionopsis gnidia</i>	0.029	0.226	0.133	0.320	1.000	0.000	0.000	56	103
<i>Lamelliconcha concinnus</i>	0.029	0.126	0.027	0.277	0.972	0.028	0.259	3	9
<i>Eupleura limata</i>	0.029	0.116	0.065	0.176	1.000	0.000	0.036	33	118
<i>Abra palmeri</i>	0.029	0.112	0.004	0.339	0.815	0.185	0.445	1	3
<i>Cosmioconcha palmeri</i>	0.029	0.099	0.042	0.177	0.997	0.003	0.266	9	37
<i>Mulinia modesta</i>	0.029	0.077	0.044	0.114	0.999	0.001	0.000	45	245
<i>Chionista fluctifraga</i>	0.029	0.063	0.030	0.109	0.981	0.019	0.743	13	85
<i>Neverita reclusiana</i>	0.029	0.036	0.016	0.064	0.685	0.315	0.994	11	129
<i>Nassarius moestus</i>	0.029	0.032	0.017	0.051	0.641	0.359	1.000	24	311
<i>Felaniella sericata</i>	0.029	0.016	0.000	0.173	0.124	0.876	0.930	0	1
Terebridae sp. 1	0.029	0.010	0.000	0.121	0.071	0.929	0.961	0	1
<i>Tellina hiberna</i>	0.029	0.009	0.000	0.033	0.041	0.959	1.000	1	47
<i>Turritella leucostoma</i>	0.029	0.009	0.000	0.126	0.064	0.936	0.960	0	1
<i>Adrana penascoensis</i>	0.029	0.008	0.000	0.104	0.067	0.933	0.963	0	1
<i>Knefastia funiculata</i>	0.029	0.008	0.000	0.086	0.070	0.930	0.968	0	2
<i>Trachycardium procerum</i>	0.029	0.008	0.000	0.091	0.072	0.928	0.966	0	2
<i>Cyclinella saccata</i>	0.029	0.006	0.000	0.065	0.048	0.952	0.977	0	1
<i>Psammotreta aurora</i>	0.029	0.006	0.000	0.076	0.054	0.946	0.974	0	2
<i>Dallocardia senticosum</i>	0.029	0.005	0.000	0.061	0.055	0.945	0.980	0	4
<i>Cryptomya californica</i>	0.029	0.004	0.000	0.042	0.037	0.963	0.987	0	5
<i>Notocochlis chemnitizii</i>	0.029	0.004	0.000	0.042	0.034	0.966	0.986	0	3
<i>Semele</i> spp.	0.029	0.004	0.000	0.047	0.039	0.961	0.984	0	3
<i>Ostrea</i> sp. 1	0.029	0.003	0.000	0.029	0.025	0.975	0.994	0	5
Turridae spp.	0.029	0.003	0.000	0.030	0.026	0.974	0.993	0	5
<i>Crepidula</i> sp. 2	0.029	0.002	0.000	0.022	0.020	0.980	0.994	0	5
<i>Tampaella meropsis</i>	0.029	0.002	0.000	0.024	0.022	0.978	0.992	0	4
<i>Calypteraea mamillaris</i>	0.029	0.001	0.000	0.014	0.008	0.992	0.999	0	20
<i>Cerithideopsis californica</i>	0.029	0.001	0.000	0.012	0.009	0.991	0.999	0	11
<i>Crucibulum spinosum</i>	0.029	0.001	0.000	0.014	0.011	0.989	0.998	0	12
<i>Solenosteira capitanea</i>	0.029	0.001	0.000	0.008	0.003	0.997	1.000	0	26
<i>Tagelus affinis</i>	0.029	0.001	0.000	0.011	0.005	0.995	1.000	0	18
<i>Anomia peruviana</i>	0.029	0.000	0.000	0.002	0.000	1.000	1.000	0	95
<i>Argopecten</i> sp. 1	0.029	0.000	0.000	0.006	0.001	0.999	1.000	0	48
<i>Crepidula</i> sp. 1	0.029	0.000	0.000	0.006	0.001	0.999	1.000	0	36
<i>Cumingia pacifica</i>	0.029	0.000	0.000	0.004	0.000	1.000	1.000	0	50

And finally, analysis of the whole-community from the southernmost site, Campo don Abel, resulted in a similar pattern as observed at Las Isletas. More species, including *M. modesta*, were categorized as preferred but likely as an artifact of the inclusion of substantially more species in the analysis (Appendix Table 9). Sixteen species were included in the main text analysis for Campo don Abel compared to 43 for the whole community analysis. Still, the conclusions from the two analyses are largely the same: *M. modesta* was not the only prey species to be preferred by *N. reclusiana*.

Appendix Table 9 Predator preference at Campo don Abel with all drilled and undrilled species.

Taxon	Neutral	Manly's alpha	95% Credibility Interval	Probability alpha > neutral	Probability alpha < neutral	Probability <i>Mulinia</i> alpha is greater	# drilled valves	# individuals
<i>Kylix</i> sp. 1	0.023	0.129	0.005 0.391	0.874	0.126	0.195	1	1
<i>Chionopsis gnidia</i>	0.023	0.094	0.050 0.150	1.000	0.000	0.000	25	49
<i>Lamelliconcha concinnus</i>	0.023	0.079	0.021 0.171	0.968	0.032	0.085	4	9
<i>Semele</i> spp.	0.023	0.079	0.021 0.172	0.965	0.035	0.092	4	9
<i>Acorylus rickettsi</i>	0.023	0.068	0.009 0.182	0.862	0.138	0.241	2	5
<i>Cosmoconcha palmeri</i>	0.023	0.059	0.009 0.158	0.834	0.166	0.284	2	6
<i>Chionopsis pulicaria</i>	0.023	0.058	0.007 0.157	0.806	0.194	0.311	2	6
<i>Nassarius moestus</i>	0.023	0.056	0.033 0.084	0.999	0.001	0.003	73	241
<i>Chionista fluctifraga</i>	0.023	0.052	0.013 0.116	0.883	0.117	0.251	4	14
<i>Eupleura limata</i>	0.023	0.042	0.001 0.147	0.585	0.415	0.529	1	4
<i>Mulinia modesta</i>	0.023	0.033	0.019 0.052	0.892	0.108	0.000	45	251
<i>Neverita reclusiana</i>	0.023	0.030	0.004 0.084	0.540	0.460	0.632	2	12
Turridae spp.	0.023	0.029	0.001 0.104	0.453	0.547	0.662	1	6
Veneridae sp. 1	0.023	0.029	0.001 0.107	0.457	0.543	0.663	1	6
<i>Donax californicus</i>	0.023	0.028	0.015 0.046	0.728	0.272	0.739	27	175
<i>Diplodonta soror</i>	0.023	0.022	0.002 0.064	0.380	0.620	0.781	2	16
<i>Sphenia gulensis</i>	0.023	0.019	0.002 0.054	0.290	0.710	0.851	2	19
<i>Tellina hiberna</i>	0.023	0.011	0.002 0.028	0.058	0.942	0.989	3	49
<i>Abra palmeri</i>	0.023	0.009	0.000 0.101	0.098	0.902	0.921	0	1
<i>Anomia peruviana</i>	0.023	0.009	0.000 0.108	0.087	0.913	0.927	0	1
<i>Nassarius guaymasensis</i>	0.023	0.009	0.000 0.101	0.086	0.914	0.926	0	1
<i>Marginella</i> sp. 1	0.023	0.007	0.000 0.079	0.075	0.925	0.938	0	1
<i>Calliostoma palmeri</i>	0.023	0.006	0.000 0.076	0.070	0.930	0.943	0	1
<i>Limaria orbini</i>	0.023	0.006	0.000 0.071	0.058	0.942	0.951	0	1
<i>Solenosteira capitanea</i>	0.023	0.006	0.000 0.071	0.063	0.937	0.947	0	1
<i>Solen gemmelli</i>	0.023	0.005	0.000 0.050	0.044	0.956	0.963	0	1
<i>Tampaella meropsis</i>	0.023	0.005	0.000 0.062	0.055	0.945	0.954	0	1
Terebridae sp. 1	0.023	0.004	0.000 0.053	0.044	0.956	0.962	0	1
<i>Crepidula</i> sp. 1	0.023	0.003	0.000 0.042	0.041	0.959	0.967	0	2
<i>Crepidula</i> sp. 2	0.023	0.002	0.000 0.021	0.021	0.979	0.985	0	5
<i>Nuculana marella</i>	0.023	0.002	0.000 0.025	0.027	0.973	0.981	0	3
<i>Trachycardium procerum</i>	0.023	0.002	0.000 0.024	0.027	0.973	0.982	0	5
<i>Argopecten</i> sp. 1	0.023	0.001	0.000 0.014	0.014	0.986	0.992	0	6
<i>Cavilinga lingualis</i>	0.023	0.001	0.000 0.010	0.008	0.992	0.996	0	9
<i>Cerithideopsis californica</i>	0.023	0.001	0.000 0.016	0.014	0.986	0.994	0	9
<i>Dallockardiua senticosum</i>	0.023	0.001	0.000 0.011	0.012	0.988	0.993	0	5
<i>Olivella</i> sp. 1	0.023	0.001	0.000 0.008	0.004	0.996	0.998	0	12
<i>Saccula acrita</i>	0.023	0.001	0.000 0.006	0.006	0.994	0.997	0	7
<i>Strigilla cicercula</i>	0.023	0.001	0.000 0.011	0.008	0.992	0.996	0	9
<i>Calypteraea mammilaris</i>	0.023	0.000	0.000 0.004	0.001	0.999	1.000	0	25
<i>Crucibulum spinosum</i>	0.023	0.000	0.000 0.005	0.001	0.999	1.000	0	18
<i>Ostrea</i> sp. 1	0.023	0.000	0.000 0.003	0.003	0.997	0.999	0	11
<i>Semelina capbellorum</i>	0.023	0.000	0.000 0.004	0.001	0.999	1.000	0	18

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Appendix 7: Assessment of alternative explanations for north-south changes to predator preferences in the Colorado River estuary

Several factors might explain the reduction in *Neverita reclusiana* preference for *Mulinia modesta*, and increased preference for alternative prey species, from north to south in the Colorado River estuary (CRE). Two can be readily dismissed (i.e., transportation bias and *M. modesta* relative abundance); however, four others require more extensive analysis.

Transportation bias (Lever et al., 1964; Olszewski and Kidwell, 2007) could be an important explanatory factor if: (i) there was north-south variability in formation of the shell assemblages such that certain species were more likely to be omitted or included, or (ii) drilled and undrilled shells were transported differently. Neither is likely, however, given the process of chenier formation at the three sites. When cheniers form—often on scales of years or decades—tidal and wave action push large clasts towards the shoreline. Subsequently, longshore currents and resuspension of fine-grain sediments lead to the removal of small clasts (Augustinus, 1989). Whereas drill holes may influence the overall hydrodynamic behavior of a shell (Lever et al., 1964), the shell itself is still sufficiently large that it will remain in the chenier.

Likewise, although there are between-species differences in shell morphology that may make the shells of some species more hydrodynamically stable than others, the process of chenier formation moves *all* large clasts toward the shoreline and, given that the processes act over extended periods of time, between-species differences do not impact the outcome.

Differences in *M. modesta* relative abundance can similarly be dismissed. The reduction in preference for *M. modesta* corresponds to the reduction in *M. modesta* relative abundance in the CRE. Thus, it might be tempting to assume a causal relationship between the two variables. Such an argument is readily dismissed, however, as relative abundance is accounted for in the calculation of alpha. That is, alpha values are normalized such that they can be interpreted as the likelihood a predator would consume a given prey species in the event all prey species were present in equal abundances (Chesson, 1983). *Mulinia modesta* relative abundance did decrease north to south (Rodriguez et al., 2001), but those changes have been accounted for in the analysis.

The remaining four alternative explanations require subsequent data collection or analysis in order to be dismissed. Therefore, each is given its own section below: taphonomic bias, body-size bias, durophagous predation, and multiple drilling predators. None of these alternatives provide feasible explanations for the north-south increase in predation intensity in the CRE.

A7.1 Assessing common species to evaluate potential for taphonomic bias

In this analysis, we considered only species found at all three of the localities ($n=10$), thereby constraining the effects of taphonomic bias, which may be an important explanatory factor if there was an interaction between species richness and preservation potential. Additionally, by using a consistent number of prey species the null alpha value was equivalent at all localities, facilitating a direct comparison of preferences between localities. To do so, we fitted two models, one where Manly's alpha was allowed to vary by locality and a second where the alpha was held constant across localities. The performance of these models was then compared using Deviance Information Criterion (DIC; (Spiegelhalter et al., 2002)).

The models were derived from the multinomial distribution on predation counts $r = r_1, \dots, r_m$, where m is the number of taxa, for the likelihood of Manly's alpha:

$$f(r; \alpha, n) = \frac{r!}{r_1! \cdots r_m!} \prod_{i=1}^m \left(\frac{\alpha_i n_i}{\sum_{j=1}^m \alpha_j n_j} \right)^{r_i}$$

where $r = r_1 + \dots + r_m$, n_i are the taxon counts, and $\alpha = \alpha_1, \dots, \alpha_m$ where each $\alpha_i \geq 0$ and $\alpha = \alpha_1 + \dots + \alpha_m = 1$. The Bayesian model we used for Manly's alpha assumes a Dirichlet prior for α : $\alpha \sim \text{Dir}(qw)$. Parameter $q = q_1, \dots, q_m$ has a $\text{Dir}(1/m, \dots, 1/m)$ prior and parameter w , which captures the variance of α as a $\text{Gamma}(0.001, 0.001)$ prior (Fordyce et al., 2011). Using this distribution, the common alpha model was derived as:

$$g(\alpha; r_{IM}, r_{LI}, r_{CDA}, n_{IM}, n_{LI}, n_{CDA}) \\ \propto f(r_{IM}; \alpha, n_{IM}) f(r_{LI}; \alpha, n_{LI}) f(r_{CDA}; \alpha, n_{CDA}) \text{Dir}(\alpha; qw)$$

and the different alpha model as:

$$\begin{aligned}
 & h(\alpha_{IM}, \alpha_{LI}, \alpha_{CDA}; r_{IM}, r_{LI}, r_{CDA}, n_{IM}, n_{LI}, n_{CDA}) \\
 & \propto f(r_{IM}; \alpha_{IM}, n_{IM})f(r_{LI}; \alpha_{LI}, n_{LI})f(r_{CDA}; \alpha_{CDA}, n_{CDA})\text{Dir}(\alpha_{IM}; qw)\text{Dir}(\alpha_{LI}; qw)\text{Dir}(\alpha_{CDA}; qw)
 \end{aligned}$$

DIC was 141.3 for the common alpha model and 98.2 for the different alpha model. The smaller DIC value indicates more support for the different alpha model and, given that the DIC difference is greater than 10, there is strong support to conclude preferences were different among localities. Examination of the calculated alpha values for all three localities when the species were held constant confirms this conclusion (S4 table 1). Furthermore, the results of this analysis confirm that *M. modesta* was not the only species preferred by *N. reclusiana*.

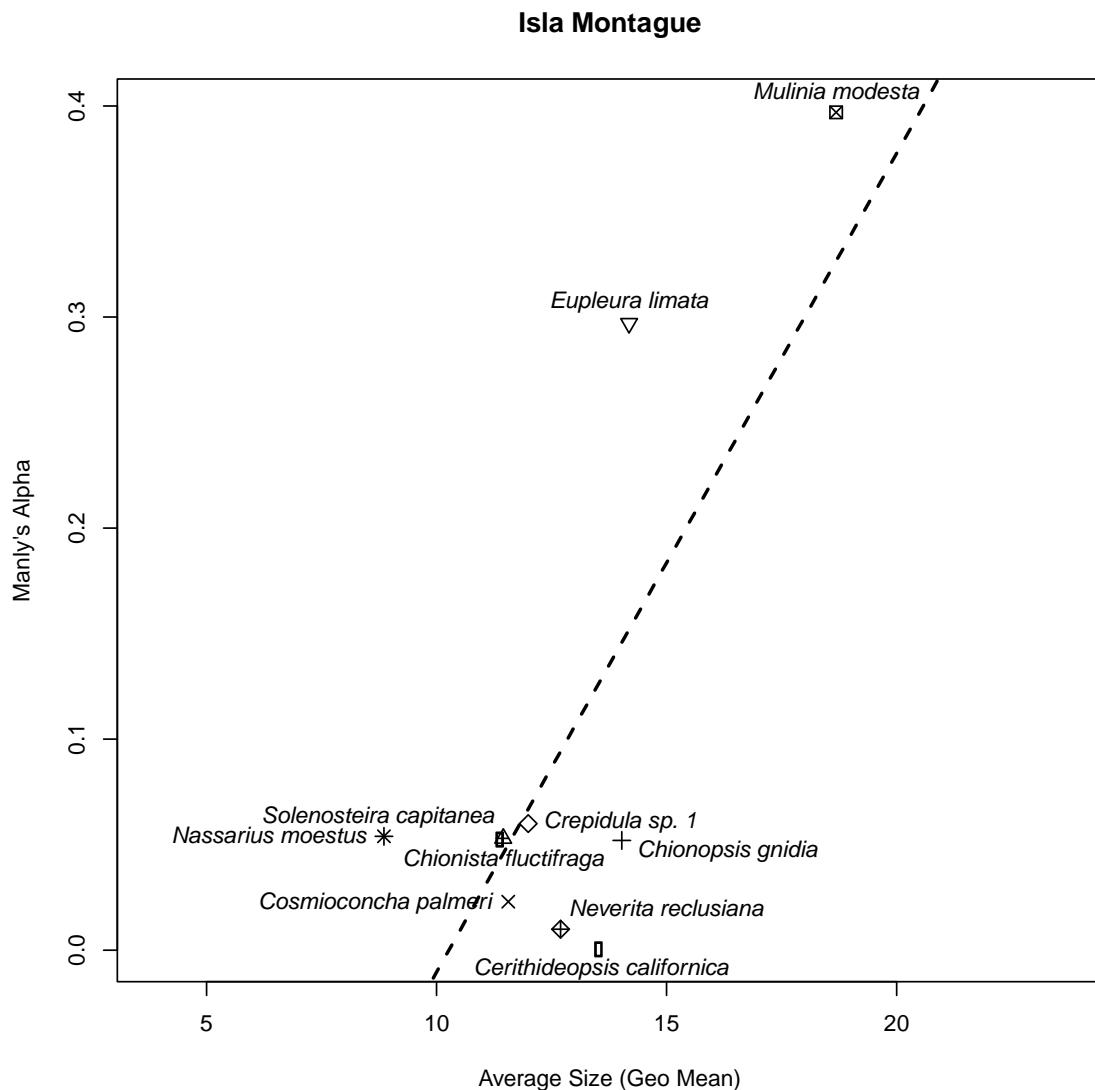
Appendix Table 10 Predator preference at all three localities when only species that occurred at all three localities are included in analysis.

Locality	TAXON	Neutral	Manly's alpha	95% Credibility Interval	Probability alpha > neutral	Probability alpha < neutral	Probability <i>Mulinia</i> alpha is greater	# drilled valves	# Individuals
Isla Montague	<i>Mulinia modesta</i>	0.1	0.314	0.162 - 0.482	0.999	0.001	-	36	194
	<i>Eupleura limata</i>	0.1	0.235	0.107 - 0.392	0.984	0.016	0.861	17	121
	<i>Solenosteira capitanea</i>	0.1	0.088	0 - 0.346	0.356	0.644	0.926	0	1
	<i>Crepidula</i> sp. 1	0.1	0.082	0.001 - 0.361	0.29	0.71	0.932	0	1
	<i>Chionopsis gnidia</i>	0.1	0.075	0 - 0.372	0.279	0.721	0.895	0	1
	<i>Cosmioconcha palmeri</i>	0.1	0.068	0 - 0.266	0.248	0.752	0.972	0	6
	<i>Chionista fluctifraga</i>	0.1	0.06	0.007 - 0.162	0.161	0.839	0.999	1	41
	<i>Neverita reclusiana</i>	0.1	0.031	0 - 0.149	0.072	0.928	0.999	0	17
	<i>Nassarius moestus</i>	0.1	0.045	0.015 - 0.093	0.017	0.983	1	7	281
	<i>Cerithideopsis californica</i>	0.1	0.003	0 - 0.014	0	1	1	0	297
Las Isletas	<i>Chionopsis gnidia</i>	0.1	0.337	0.271 - 0.409	1	0	0	66	103
	<i>Eupleura limata</i>	0.1	0.151	0.108 - 0.202	0.991	0.009	0.168	33	118
	<i>Mulinia modesta</i>	0.1	0.12	0.088 - 0.157	0.867	0.133	-	55	245
	<i>Cosmioconcha palmeri</i>	0.1	0.128	0.069 - 0.202	0.762	0.238	0.47	9	37
	<i>Chionista fluctifraga</i>	0.1	0.091	0.049 - 0.148	0.315	0.685	0.846	14	85
	<i>Cerithideopsis californica</i>	0.1	0.037	0.002 - 0.136	0.053	0.947	0.96	0	11
	<i>Neverita reclusiana</i>	0.1	0.053	0.027 - 0.089	0.005	0.995	0.998	12	129
	<i>Solenosteira capitanea</i>	0.1	0.016	0.001 - 0.058	0.003	0.997	0.998	0	26
	<i>Crepidula</i> sp. 1	0.1	0.024	0.004 - 0.062	0.002	0.998	1	1	36
	<i>Nassarius moestus</i>	0.1	0.042	0.027 - 0.061	0	1	1	24	311
Campo don Abel	<i>Chionopsis gnidia</i>	0.1	0.21	0.135 - 0.298	1	0	0	27	49
	<i>Nassarius moestus</i>	0.1	0.12	0.077 - 0.174	0.808	0.192	0.003	73	241
	<i>Chionista fluctifraga</i>	0.1	0.114	0.038 - 0.212	0.583	0.417	0.179	4	14
	<i>Cosmioconcha palmeri</i>	0.1	0.115	0.039 - 0.262	0.514	0.486	0.32	2	6
	<i>Eupleura limata</i>	0.1	0.103	0.01 - 0.269	0.469	0.531	0.349	1	4
	<i>Solenosteira capitanea</i>	0.1	0.088	0.007 - 0.254	0.35	0.65	0.512	0	1
	<i>Neverita reclusiana</i>	0.1	0.072	0.014 - 0.151	0.227	0.773	0.55	2	12
	<i>Crepidula</i> sp. 1	0.1	0.067	0.007 - 0.178	0.199	0.801	0.626	0	2
	<i>Cerithideopsis californica</i>	0.1	0.037	0 - 0.145	0.084	0.916	0.828	0	9
	<i>Mulinia modesta</i>	0.1	0.074	0.047 - 0.11	0.062	0.938	-	47	251

A7.2 Testing for the effect of prey size on *Neverita reclusiana* preference

Naticid predator-prey interactions are often size-dependent, which, if not controlled for, may bias the interpretation of preference hierarchies (Kelley, 1988; Dietl and Kosloski, 2013; Smith and Dietl, 2016). In the present study, however, prey size was not a good predictor of predator preference. All specimens were measured and the average sizes of the prey species were plotted against Manly's alpha (independently for each locality). Gastropod height was measured from the tip of the apex to the base of the aperture/siphonal canal and width was measured perpendicular to height, across the aperture. Bivalve height was measured from the umbo to the edge of the shell—perpendicular to growth lines—and width was measured across the widest intersecting line. Geometric means—the square root of the sum of the squared length and width measurements—were used for analysis to account for variability in shape between species. After plotting, the effect of prey size on predator preference was evaluated with a linear regression for those species that were drilled at least once. At Isla Montague, there was initially a significant fit (Adjusted $R^2=0.506$, F-statistic=10.21, p-value=0.0127; Appendix Figure 1); however, closer inspection of the data using Cook's Distance—a diagnostic tool to assess the influence of data on a linear fit—showed *M. modesta* was a leverage point in the analysis (Appendix Table 11). When *M. modesta* is removed from the analysis, the linear regression no longer provides a significant fit (Adjusted $R^2= -0.0477$, F-statistic=0.636, p-value=0.451). The linear regression for Las Isletas showed no effect of size (Adjusted $R^2=0.506$, F-statistic=10.21, p-value=0.0127; Appendix Figure 2). Likewise, there was no effect for

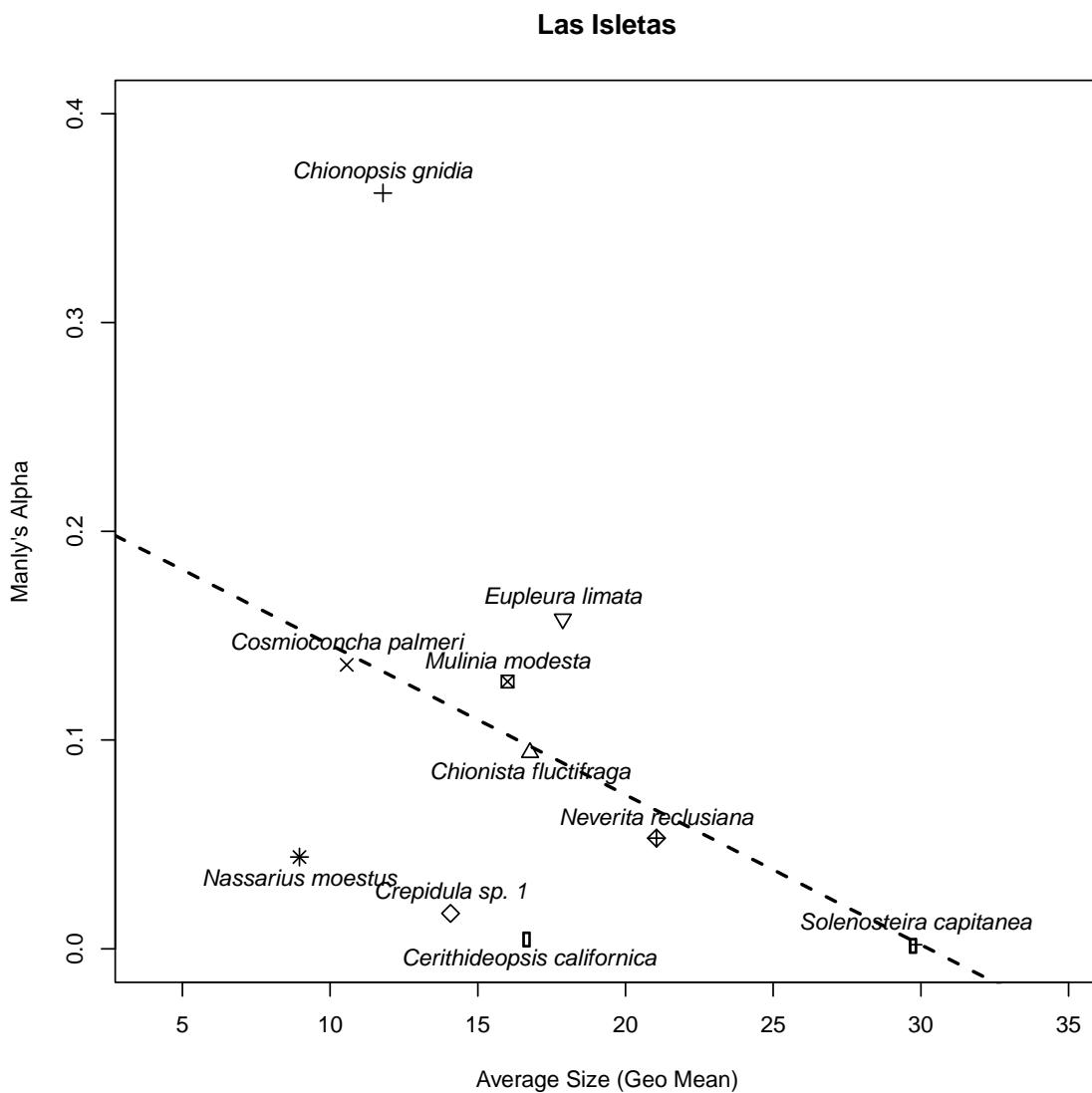
Campo don Abel (Adjusted R²= -0.11, F-statistic=1.11, p-value=0.749; Appendix Figure 3).



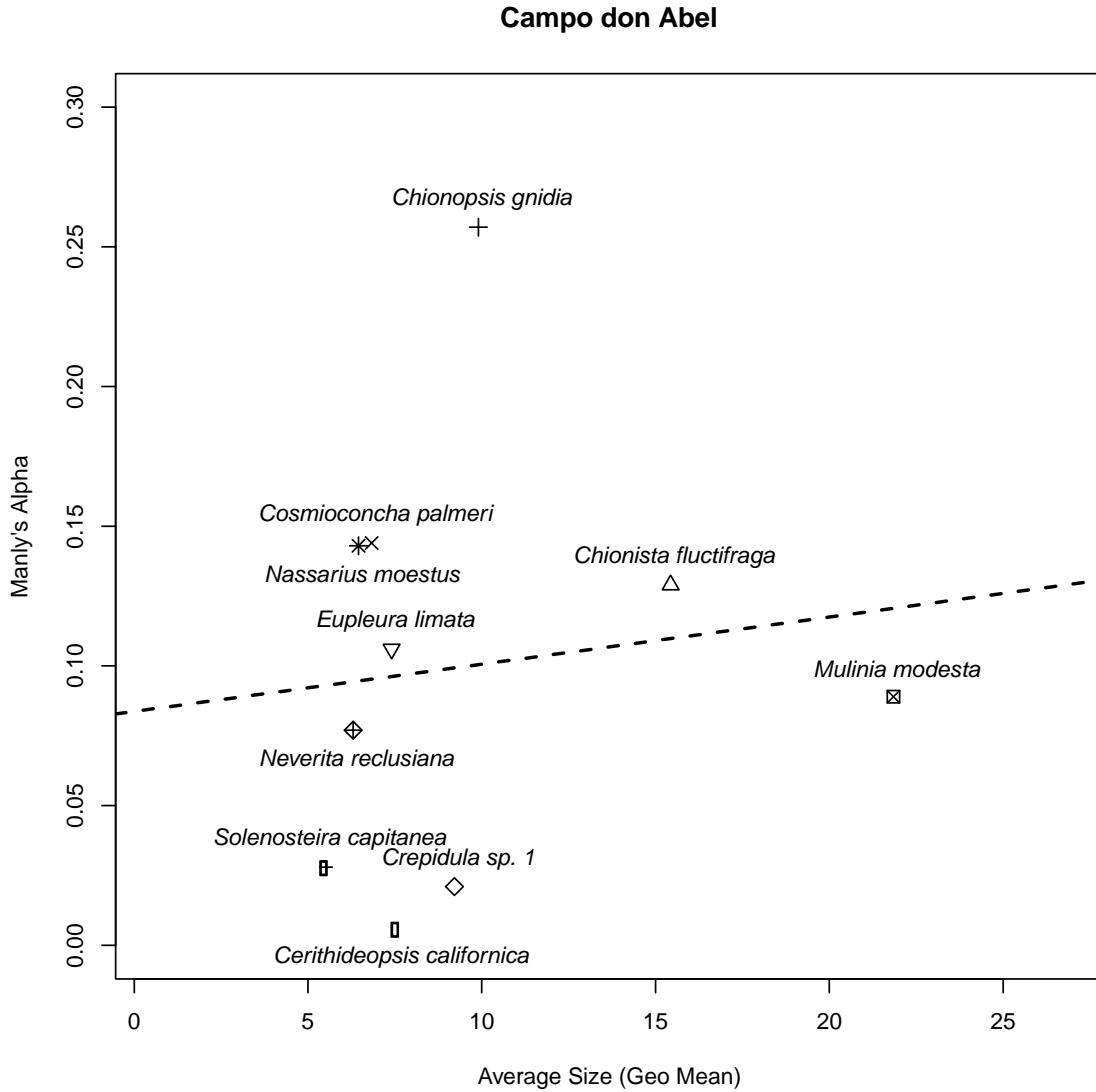
Appendix Figure 1 Manly's alpha as a function of average prey size at Isla Montague. Geo Mean = Geometric mean (millimeters).

Appendix Table 11 Cook's Distances for each species from Isla Montague. Values greater than 1 indicate significant influence and are bolded.

Species	Cook's Distance
<i>Cerithideopsis californica</i>	0.1256
<i>Chionista fluctifraga</i>	0.0005
<i>Chionopsis gnidia</i>	0.0797
<i>Cosmioconcha palmeri</i>	0.0069
<i>Crepidula</i> sp. 1	0.0004
<i>Eupleura limata</i>	0.2037
<i>Mulinia modesta</i>	1.6917
<i>Nassarius moestus</i>	0.6039
<i>Neverita reclusiana</i>	0.0496
<i>Solenosteira capitanea</i>	0.0006



Appendix Figure 2 Manly's alpha as a function of average prey size at Las Isletas.
Geo Mean = Geometric mean (millimeters).



Appendix Figure 3 Manly's alpha as a function of average prey size at Campo don Abel. Geo Mean = Geometric mean (millimeters).

R Code for Body Size Analyses:

```
# relate Manly's alpha values and body size measurements for taxa common to all
# three sites
# sizes must be per site

RawData = read.csv(file = "Raw.csv", header = T, stringsAsFactors = FALSE)
# Filter by sample:
# Isla Montague samples: (1) IM_2_B1; (2) IM_3_B2; (3) IM_4_B1
```

```

# Las Isletas samples: (1) LI_A1_SB1; (2) LI_A1_SB3; (3) LI_A1_SB5
# Campo don Abel samples: (1) CDA_1_B1; (2) CDA_1_B2; (3) CDA_1_B3;
# (4)CDA_1_B4; (5)CDA_1_B5

pos = ((RawData$Locality == "Campo don Abel" and RawData$Sample.Number %in% c("B1","B2","B3","B4","B5")))
|
(RawData$Locality == "Las Isletas" and RawData$Sample.Number %in% c("SB1","SB3","SB5"))
|
(RawData$Locality == "Isla Montague" and RawData$Sample.Number %in% c("B1","B2")))

sum(pos)
# 5162

RawData = RawData[pos,]
dim(RawData)

CDA_Common_Counts
LI_Common_Counts
IM_Common_Counts

Las_Isletas_Common.bayes =
ManlyBayes(LI_Common_Counts,"LI_Common",comparison_taxon = "Mulinia modesta")
Campo_don_Abel_Common.bayes =
ManlyBayes(CDA_Common_Counts,"CDA_Common",comparison_taxon = "Mulinia modesta")
Isla_Montague_Common.bayes =
ManlyBayes(IM_Common_Counts,"IM_Common",comparison_taxon = "Mulinia modesta")

Genus =
c("Cerithideopsis","Chionista","Chionopsis","Cosmioconcha","Crepidula","Eupleura",
"Mulinia","Nassarius","Neverita","Solenosteira")
Species =
c("californica","fluctifraga","gnidia","palmeri","flat","limata","modesta","moestus","reclusiana","capitanea")

# for each of these, need to extract the individuals of each taxon and get size statistics
Las_Isletas_Common_Sizes = RawData[(RawData$Species %in%
c(as.character(LI_Common_Counts$Taxon)))and(RawData$Locality == "Las Isletas"),c("Geo.Mean","Species")]
plot(Geo.Mean~factor(Species),Las_Isletas_Common_Sizes)

```

```

LI.fit = lm(Geo.Mean~factor(Species)+(-1),Las_Isletas_Common_Sizes)
yoffset = c(-0.01,0.01,0.01,0.01,0.01,0.01,-0.01,-0.01,0.01)
png("LI.png", width = 800, height = 800)
Taxa = as.character(Las_Isletas_Common.bayes$Taxon)
Taxa[5] = "Crepidula sp. 1"
plot(coef(LI.fit),Las_Isletas_Common.bayes$Bayes, xlab = "Average Size (Geo
Mean)", ylab = "Manly's Alpha", main = "Las Isletas", xlim = c(min(coef(LI.fit))-5),
max(coef(LI.fit))+5), ylim = c(0,0.4),pch = 1:10, cex = 1.2)
text(coef(LI.fit),Las_Isletas_Common.bayes$Bayes+yoffset, Taxa, cex = 1, font = 3)
#summary(lm(Las_Isletas_Common.bayes$Bayes ~ coef(LI.fit) ))
abline(lm(Las_Isletas_Common.bayes$Bayes ~ coef(LI.fit) ), lwd = 2, lty = 2)
dev.off()

Campo_don_Abel_Common_Sizes = RawData[(RawData$Species %in%
c(as.character(CDA_Common_Counts$Taxon)))and(RawData$Locality == "Campo
don Abel"),c("Geo.Mean", "Species")]
plot(Geo.Mean~factor(Species),Campo_don_Abel_Common_Sizes)
CDA.fit = lm(Geo.Mean~factor(Species)+(-1),Campo_don_Abel_Common_Sizes)
png("CDA.png", width = 800, height = 800)
Taxa = as.charcter(Campo_don_Abel_Common.bayes$Taxon)
Taxa[5] = "Crepidula sp. 1"
plot(coef(CDA.fit),Campo_don_Abel_Common.bayes$Bayes, xlab = "Average Size
(Geo Mean)", ylab = "Manly's Alpha", main = "Campo don Abel", xlim =
c(min(coef(CDA.fit))-5), max(coef(CDA.fit))+5), ylim = c(0, 0.3), pch = 1:10, cex =
1.2, col = "black")
yoffset = c(-0.01,0.01,0.01,0.01,0.01,0.01,-0.01,-0.01,0.01)
text(coef(CDA.fit)+0.1,Campo_don_Abel_Common.bayes$Bayes + yoffset, Taxa, cex
= 1, font = 3) #, srt = 30, adj = -0.1) #,srt=30)
#summary(lm(Campo_don_Abel_Common.bayes$Bayes ~ coef(CDA.fit) ))
abline(lm(Campo_don_Abel_Common.bayes$Bayes ~ coef(CDA.fit) ), lwd = 2, lty =
2)
dev.off()

Isla_Montague_Common_Sizes = RawData[(RawData$Species %in%
c(as.character(IM_Common_Counts$Taxon)))and(RawData$Locality == "Isla
Montague"),c("Geo.Mean", "Species")]
plot(Geo.Mean~factor(Species),Isla_Montague_Common_Sizes)
IM.fit = lm(Geo.Mean~factor(Species)+(-1),Isla_Montague_Common_Sizes)
png("IM.png", width = 800, height = 800)
Taxa = as.charcter(Isla_Montague_Common.bayes$Taxon)
Taxa[5] = "Crepidula sp. 1"
plot(coef(IM.fit),Isla_Montague_Common.bayes$Bayes, xlab = "Average Size (Geo
Mean)", ylab = "Manly's Alpha", main = "Isla Montague", xlim = c(min(coef(IM.fit))-5),
max(coef(IM.fit))+5), pch = 1:10, cex = 1.2, col = 1)

```

```

yoffset = c(-0.01,-0.01,0.01,0.01,0.01,0.01,0.01,-0.01,0.01,0.01)
xoffset = c(0,0.9,1,0,0,0,0,0,1,-1.7)
text(coef(IM.fit)+xoffset,Isla_Montague_Common.bayes$Bayes + yoffset,
Isla_Montague_Common.bayes$Taxon, cex = 1, srt = 0,col = 1, font = 3)
#legend("topleft", legend = Isla_Montague_Common.bayes$Taxon, bty = "n", pch =
1:10, cex =0.8)
#summary(lm(Isla_Montague_Common.bayes$Bayes ~ coef(IM.fit) ))
abline(lm(Isla_Montague_Common.bayes$Bayes ~ coef(IM.fit) ), lwd = 2, lty = 2)
dev.off()
cooks.distance(lm(Isla_Montague_Common.bayes$Bayes ~ coef(IM.fit) ))
data.frame(Isla_Montague_Common.bayes$Taxon,cooks.distance(lm(Isla_Montague_
Common.bayes$Bayes ~ coef(IM.fit) )))
summary(lm(Campo_don_Abel_Common.bayes$Bayes[-7] ~ coef(CDA.fit)[-7] ))

```

A7.3 Assessment of shell fragmentation to evaluate potential bias from durophagous predation

Between-species differences along the north-south gradient in the intensity of shell-crushing (i.e., durophagous) predation by crabs could influence the interpretation of our naticid predation data. Shell-crushing predation removes an undrilled individual from the set of individuals used to estimate drilling frequency. Thus, a high incidence of crushing predation can artificially inflate observed drilling frequencies. If the behavior of shell-crushing predators changed from north to south, such that certain species were consumed more or less at a given site, the results of our study may be subject to misinterpretation. To address this potential bias, we assessed the proportion of broken versus complete individuals in commonly occurring bivalve species (after Scarponi et al., 2017). Shell fragmentation can occur post-mortem (Kowalewski et al., 1994), meaning our analysis likely overestimates the frequency of shell-crushing predation.

Appendix Table 12 Results of fragmentation analysis for commonly occurring bivalves in the Colorado River estuary. IM = Isla Montague; LI = Las Isletas; CDA = Campo don Abel; values in parentheses are counts of all individuals (broken + complete); * indicates a significant p-value.

Species	IM	LI	CDA	p-value
<i>Chionista fluctifraga</i>	0.41 (70)	0.44 (153)	0.59 (34)	0.2341
<i>Chionopsis gnidia</i>	0.00 (1)	0.23 (134)	0.22 (63)	0.9999
<i>Mulinia modesta</i>	0.59 (472)	0.63 (664)	0.51 (516)	0.0003*
<i>Tellina hiberna</i>	-	0.02 (48)	0.06 (52)	0.6185
<i>Lamelliconcha concinnus</i>	-	0.00 (9)	0.10 (10)	0.9999

Analysis with the fisher.test function in R found non-significant between-site differences in shell fragmentation for four of five species. Based on these results, it is unlikely that shell-crushing predation had a significant impact on observed drilling predation intensity. The lone significant result was for a reduction in breakage at the southernmost site, Campo don Abel, in *M. modesta*. This result suggests that, holding all other variables constant, drilling frequency on *M. modesta* at the southernmost site was underestimated compared to those from the two more northern sites. For *M. modesta* in the south, 265 of 516 (51%) individuals were broken. Applying a breakage of 61%, which is an average of the northern two sites, the number of complete individuals drops from 251 to 201. Recalculating drilling frequency based on 201 individuals and 45 drill holes yields a frequency of 22%, or an increase of 4% from the observed drilling frequency. Recalling that mean drilling frequency at Campo don Abel was 23%—or 24% if the 50 undrilled *M. modesta* are removed from the calculation—*M. modesta* was still drilled less frequently than predicted under neutral conditions. Thus, despite the significant result for *M. modesta*, the difference in fragmentation cannot explain the north-south trend in predation intensity.

Furthermore, the only evidence required to support the hypothesis that *N. reclusiana* was able to switch prey is that other prey species were also preferred and such evidence holds regardless of the slight difference due to *M. modesta* fragmentation.

R Code:

```
#C.fluctifraga
C.flu <- fisher.test(matrix(c(29, 68, 20, 41, 85, 14), nrow=2, ncol=3, byrow=TRUE))
#C.gnidia
C.gni <- fisher.test(matrix(c(0, 31, 14, 1, 103, 49), nrow=2, ncol=3, byrow=TRUE))
#M.modesta
M.mod <- fisher.test(matrix(c(278, 419, 265, 194, 245, 251), nrow=2, ncol=3,
byrow=TRUE))
#T. hiberna
T.hib <- fisher.test(matrix(c(1, 3, 47, 49), nrow=2, ncol=2, byrow=TRUE))
#L. concinnus
L.con <- fisher.test(matrix(c(0, 1, 9, 9), nrow=2, ncol=2, byrow=TRUE))
```

A7.4 Assessment of potential bias in predator preference due to the presence of multiple predators

In the event that multiple drilling predators were responsible for the drill holes observed in this study, the data may reflect an average of predator preferences rather than the sole preference of *N. reclusiana*. As discussed in the introduction and methods of the main text, our samples were taken from the active cheniers in the CRE. These cheniers are composed of shells that, for the most part (>75%), originated during the pre-dam era (Kowalewski et al., 1998). During the pre-dam era, only one naticid was present in the CRE; however, the range of a second naticid species, *Notocochlis chemnitzii*, has extended into the CRE in the post-dam era (Smith and Dietl, 2016). Therefore, the fraction of shells in the active cheniers that originated in the post-dam era may have been subject to predation by two naticid species. Although naticids might be expected to have similar prey preferences, small differences may

alter overall preferences. For example, *N. chemnitzii* are more capable predators of thick-shelled bivalve prey due to their utilization of edge drilling, wherein the prey shell is drilled through the thin margin of the shell rather than the thicker umbonal region. In this study, however, no prey individuals with drill holes were excluded on the basis of edge drilling, which suggests that the contribution of *N. chemnitzii* to the sum total of naticid drilling predation was likely small.

As reported by Smith and Dietl (2016), *N. chemnitzii* are also relatively uncommon in the active cheniers. No *N. chemnitzii* were found at Isla Montague, compared to 947 *N. reclusiana*. In the active chenier at Las Isletas, 80 *N. chemnitzii* were found. By comparison, 1,581 *N. reclusiana* were collected in the same sampling effort, suggesting a recent arrival of *N. chemnitzii* and no more than a minor contribution to predator-prey dynamics at Las Isletas (Smith and Dietl, 2016). Similarly, no *N. chemnitzii* have been collected from Campo don Abel, whereas 20 *N. reclusiana* were collected in the samples used in this study. These collections from Isla Montague and Las Isletas are a combination of bulk and target sampling, which accounts for the differences in sample sizes. In target sampling, the entire outcrop is scanned for species of interest and all are collected regardless of preservational quality (Ottens et al., 2012). Bulk sampling is restricted to a defined volume from a few locations on the outcrop (Kowalewski, 2002). Considering only bulk samples from Isla Montague (n=15), 97 *N. reclusiana* were found and for Las Isletas (n=6) there were 241 *N. reclusiana* and seven *N. chemnitzii*, or a ratio of 35:1. Any contribution from *N. chemnitzii*—which is rare compared to *N. reclusiana* and would have been restricted to <25% of the prey individuals—to the sum total of naticid drilling

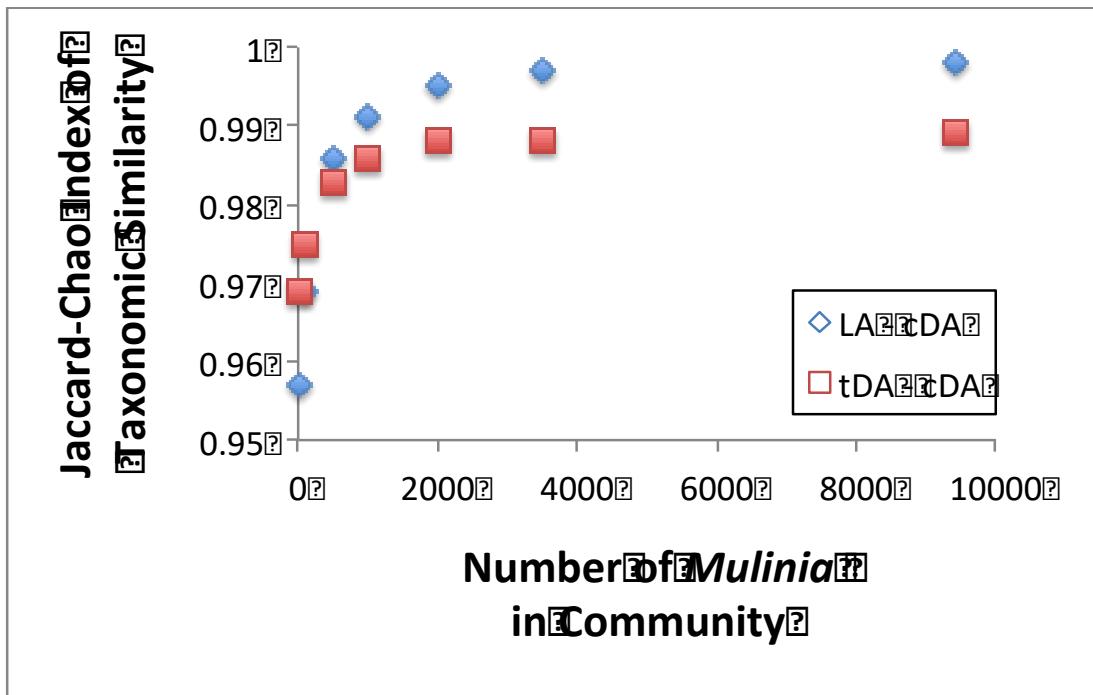
predation would have been small and cannot explain the north-south trend in prey preference.

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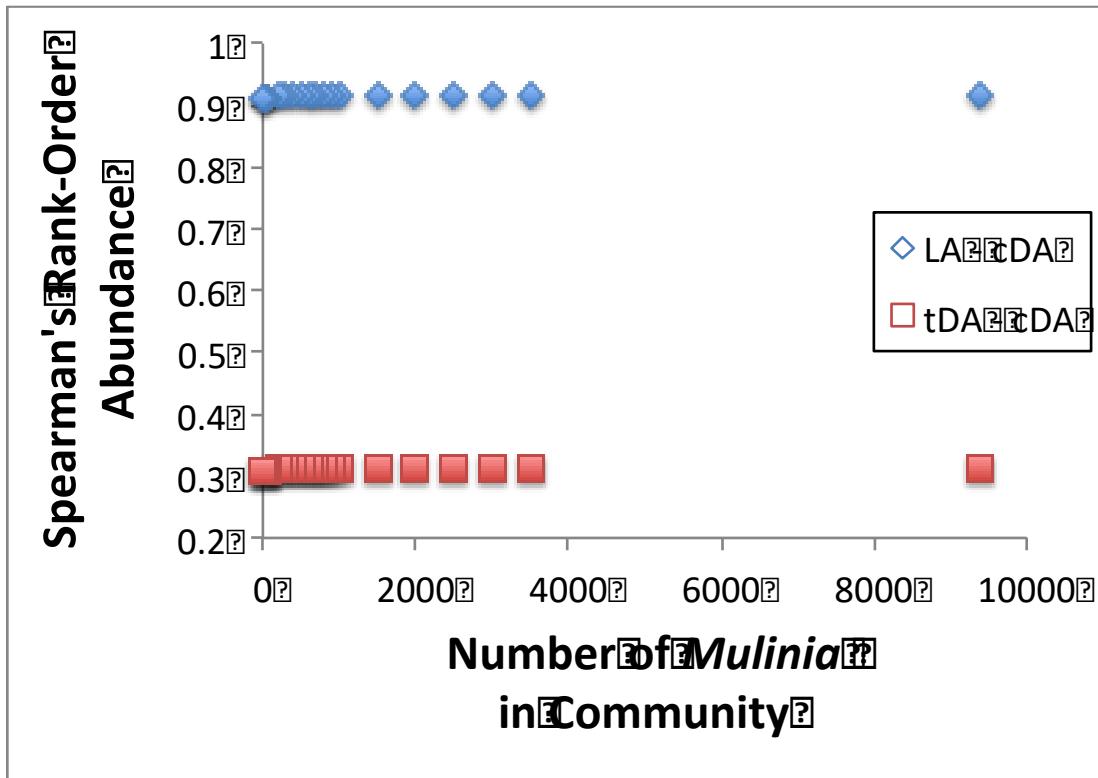
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Appendix 8: Influence of *Mulinia modesta* on community metrics



Appendix Figure 4 Effect of *Mulinia modesta* abundance on Jaccard-Chao index of taxonomic similarity for comparisons between the live assemblage (LA) and the chenier death assemblage (cDA) and between the tidal flat death assemblage (tDA) and the cDA. The number of *M. modesta* in the cDA was varied from 9410 (number of *M. modesta* in cDA) to 10 and the corresponding change to the index was plotted. Abundance of all other species was held constant. Despite decreasing *M. modesta* abundance in the cDA by three orders of magnitude, the Jaccard-Chao index changed only by a few hundredths.



Appendix Figure 5 Effect of *Mulinia modesta* abundance on Spearman's rank-order abundance (Rho) for comparisons between the live assemblage (LA) and the chenier death assemblage (cDA) and between the tidal flat death assemblage (tDA) and the cDA. The number of *M. modesta* in the cDA was varied from 9410 (number of *M. modesta* in cDA) to 10 and the corresponding change to the index was plotted. Abundance of all other species was held constant. Despite decreasing *M. modesta* abundance in the cDA by three orders of magnitude, Rho changed only by a few thousandths.

Appendix 9: Alternative explanations for pattern in community metrics

The evidence for ecological change in the bivalve community is strong. When there are differences between LAs and DAs, however, Kidwell (Kidwell, 2013) proposed four alternative explanations: under-sampling, collection bias, time-averaging, and taphonomic bias. Each of these alternatives merits consideration and must be eliminated before accepting ecological change as the definitive explanation for assemblage-level differences (Smith and Dietl, 2016).

A9.1 Under-sampling

Under-sampling can result in differences between assemblages when there is a large discrepancy in sample sizes (Kidwell, 2013). In the present study, there is a considerable difference between the LA ($n=84$), tDA ($n=2,665$), and cDA ($n=9,633$) sample sizes (Table 1). These differences, however, have been accounted for in the calculation of the metrics. For instance, richness was assessed using a rarefaction curve that was standardized to the lowest sample size ($n=84$, LA) and it has been documented that PIE is not sensitive to sample size (Gotelli and Graves, 1996). Hence, because of the metrics that were employed here, under-sampling can be accounted for and eliminated as a potential explanation for the differences between the pre- and post-dam era bivalve communities.

A9.2 Collection Bias

Collection bias occurs when sampling methodology disproportionately favors the collection of certain species over others (Kidwell, 2013). In the present study, the

most likely case for collection bias is the exclusion of deep-burrowing (> 20 cm depth) species relative to shallow burrowers in the LA. Of the 18 bivalve species that were sampled in this study only one, *Tagelus affinis*, is deep burrowing and may have been negatively affected by collection bias. Despite this potential bias, *T. affinis* was sampled in the LA (n=1) and represents 1.2% of the live community. Comparatively, *T. affinis* represented 7.1% of the tDA (n=188) and 0.09% of the cDA (n=88), suggesting that the sampling method used in this study was adequate (i.e., 20 cm was deep enough to sample *T. affinis*). Furthermore, Kowalewski et al. (2000) noted that *T. affinis* is rare on the CRE tidal flat and seldom exceeds 1 individual/meter². Thus, we can rule out collection bias as an explanation for the differences between the LA, tDA, and cDA.

A9.3 Time-Averaging

Time-averaging is most commonly an explanation for differences between assemblages when a species occurs in the DA but not in the LA (Kidwell, 2013). As discussed above, if time-averaging were a biasing factor in this study, the cDA would have the highest richness due to the accumulation of rare species over the centuries that it is averaged. Instead, the LA and tDA both have greater richness when sample size is standardized. Even in a comparison with raw data, the tDA, which is likely averaged over a few decades, has greater richness than the cDA despite having thousands of fewer specimens. Therefore, given that the time-averaging trend is opposite of what would be expected under biasing conditions, time-averaging can be dismissed as an explanation for differences between pre- and post-dam era

assemblages. The greater overall richness in the tDA compared to the LA is likely the result of time-averaging. This difference may be a positive attribute rather than a biasing factor because short-term variations are often averaged out in DAs (Kowalewski et al., 1998). Thus, whereas the LA provides only a snapshot of the post-dam era bivalve community, the tDA, which is heavily influenced by input from the post-dam era, represents the community averaged on the scale of decades.

A9.4 Taphonomic Bias

Taphonomic bias is most likely to occur under two scenarios: (1) a species occurs in the LA but not the DA (tidal flat or chenier) due to low preservation potential, or (2) a species does not occur in the LA but is found in the DA (tidal flat or chenier) due to postmortem transport from an adjacent habitat (Kidwell, 2013). The first scenario can be eliminated because all of the LA species also occur in the tDA and cDA, even those species having low preservation potential based on shell durability (Kosnik et al., 2009). Although the presence of these species' fragile shells may not be unexpected (Behrensmeyer et al., 2005), their persistence, especially the high abundance of *M. modesta*, in the DAs is strong evidence that the tDA and cDA record high-fidelity ecological signals.

The second scenario, postmortem transport from an adjacent habitat, is also an unlikely explanation for LA-DA differences in the CRE. Between-habitat shell transport is unlikely to occur in the northern Gulf of California today (Flessa et al., 1993) and it did not occur commonly in geological past (Meldahl, 1993). Shells in the cDA have been transported off of the tidal flat onto the nearby shore but, because

cheniers form by consolidating shell material from the tidal flat (Augustinus, 1989), shells in the cDA are unlikely to have originated in another habitat (Smith and Dietl, 2016). Thus, neither scenario, preservation potential or postmortem transport, can explain differences between the LA and DAs (tidal flat and chenier).

Taphonomy is also an unlikely explanation for differences between the tDA and cDA. Three conditions must be met in order for taphonomy to explain the tDA-cDA differences detected in the metrics here. (1) All of the species found in the cDA but not the tDA ($n=4$) would need to have accumulated due to an extended period of time-averaging in the cDA. (2) All of the species in the tDA that are not present in the cDA ($n=5$) would need to have a preservation potential such that they could survive intra-habitat shell transport and accumulate in the tDA on a decadal scale, but not in the cDA on the centennial scale. (3) For the sake of consistency, all taxa shared by the tDA and cDA, but not found in the LA, must have a high preservation potential and occur in greater abundances in the cDA than tDA due to the extended period of time-averaging.

The first condition is the expected result based on decades of research on time-averaging (e.g., (Kidwell and Bosence, 1991; Olszewski and Kidwell, 2007; Kidwell and Tomasovych, 2013) but it runs counter to the conclusion drawn in the preceding section (9.3 Time-averaging). The second condition is feasible, even if it is unlikely. The third condition loses credibility after a closer examination of the species in the tDA and cDA and need not be true (Behrensmeyer et al., 2005). For example, the tDA has two species of *Tellina*, which can be assumed to have similar preservation potential, while the cDA has only one tellinid species. Additionally, *A. peruviana*,

which has very low preservation potential, is found in the cDA but not in the tDA. Therefore, by rejecting the third condition, the second condition becomes untenable, and the first condition becomes questionable at best. Although taphonomic bias cannot be outright rejected as an alternative explanation to ecological change, it is an extremely doubtful explanation due to the set of circumstances that it would have required.

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Appendix 10: R code for fitting species abundance distributions, goodness of fit diagnostic plots, and R code for analysis of environmental preference and commonness

A10.1 R code for model fitting

Three species abundance distribution (SAD) models were fit to data for the entire Colorado River estuary (CRE) molluscan metacommunity and for the communities at each of the three CRE sites. The three models, Poisson log-normal, log-series, and metacommunity zero-sum multinomial were fit using the ‘sads’ package (Prado and Miranda, 2014) in R. The following code runs the model fit on the data for the metacommunity. The same code was used to fit the models for the sites using the data presented for each site.

```
WC_CRE <- data ##cumulative counts for all species from Table 1 ## of Appendix S2
WC_CRE.ls <- fitsad(WC_CRE, sad = "ls")
```

```

WC_CRE.pln <- fitsad(WC_CRE, sad = "poilog")
WC_CRE.mzsm <- fitsad(WC_CRE, sad = "mzsm")

AICctab(WC_CRE.ls, WC_CRE.pln, WC_CRE.mzsm, nobs=length(WC_CRE),
base=TRUE)

WC_CRE.ls.oc <- octavpred(WC_CRE.ls)
WC_CRE.pln.oc <- octavpred(WC_CRE.pln)
WC_CRE.mzsm.oc <- octavpred(WC_CRE.mzsm)

## Creates plot similar to those in Figure 2 of the main text
plot(octav(WC_CRE), xlab="Species Abundance", ylab="Number of Species",
cex.axis=5)
lines(WC_CRE.ls.oc, pch=16, col = "seagreen3", cex=1.5, lwd=3)
lines(WC_CRE.pln.oc, pch=17, col = "red3", cex=1.5, lwd=3)
lines(WC_CRE.mzsm.oc, pch=15, col = "royalblue1", cex=1.5, lwd=3)
legend("topright", c("LS", "PLN", "MZSM"), lty=1, col=c("seagreen3","red3",
"royalblue1"))

```

A10.2 Goodness of fit diagnostic plots

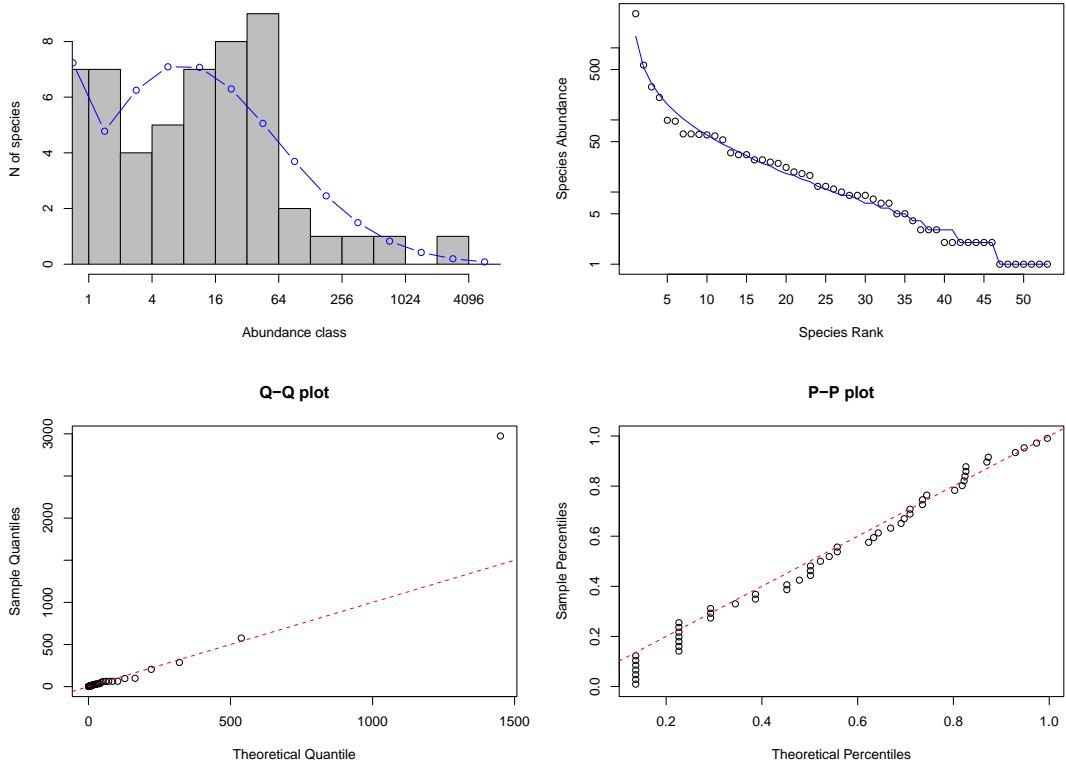
In the following figures, model diagnostic plots—generated using the `plot()` function in R (e.g., `plot(WC_CRE.ls)`)—are presented for the whole community (Appendix Figures 7-9), Isla Montague (northern, estuarine site; Appendix Figures 10-16), Las Isletas (middle, intermediate salinity site; Appendix Figures 13-15), and Campo don Abel (southern, marine site; Figures 16-18). For each of these sets of figures, the order of model fits is: Poisson log-normal, log-series, zero-sum multinomial. In each figure, the top panels show the model fit overlaid on the real data, visualized as a SAD (top left) and a rank abundance distribution (top right). The bottom panels show plots of quartile-quartile (bottom left) and percentile-percentile (bottom right) agreement.

Goodness of fit was assessed for each model fit using these diagnostic plots. In general, the SAD models did not provide particularly good fits to the CRE data (e.g.,

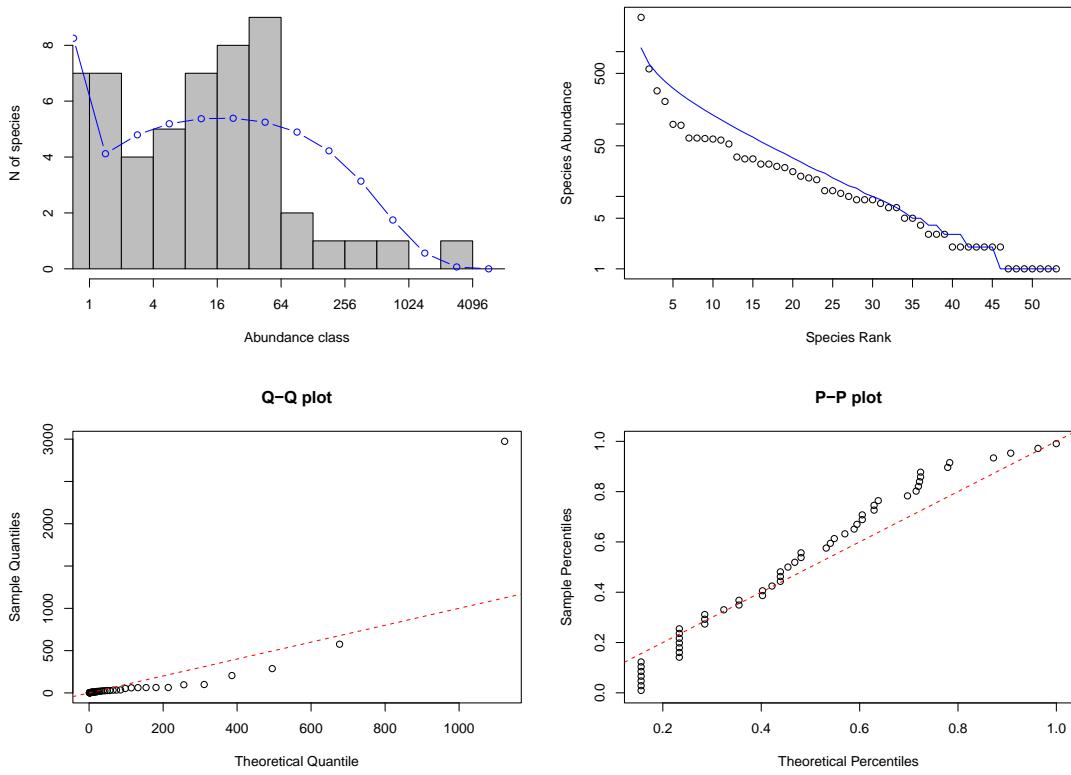
real data points deviated from the 1:1 line for theoretical and sample quartiles in the Q-Q plot). As has been discussed by others (e.g., Ugland and Gray, 1982; Matthews et al., 2014), SAD models are often compromised by the presence of multiple modes in the SAD corresponding to different groups of species (e.g., marine, estuarine). Ugland and Gray (1982) suggested there might commonly be three modes in SADs of benthic marine communities (i.e., rare, common, very common), with the “very common” group represented by very few species. Visual inspection of the SAD in Appendix Figure 7 confirms this pattern, with *Mulinia modesta* representing the lone “very common” species in the community. This multimodality can lead to poor model fits, unless models are expressly designed to accommodate multiple modes (e.g., Matthews et al., 2014).

In the CRE data, *M. modesta* is often an outlier in quartile-quartile plots. Whereas removal of *M. modesta* would likely improve the fit of the models, doing so would depreciate the ecological value of the assessment, as this species is the most common in the community and thus likely plays a large role in community processes (Gaston, 2010; Connolly et al., 2014). As demonstrated in Appendix Figures 16–18, model fits are improved when there is not a highly abundant species (i.e., *M. modesta* composed only 39% of the Campo don Abel community). Regardless, the objective of this analysis was to dismiss neutrality as an explanatory paradigm for community assembly in the CRE molluscan community. Visual inspection of the fits for the neutral zero-sum multinomial model (Appendix Figures 9, 12, 15, 18) suggests poor model fits—there is considerable deviation between the real data and predicted data under a zero-sum multinomial model—particularly as compared to the log-normal and

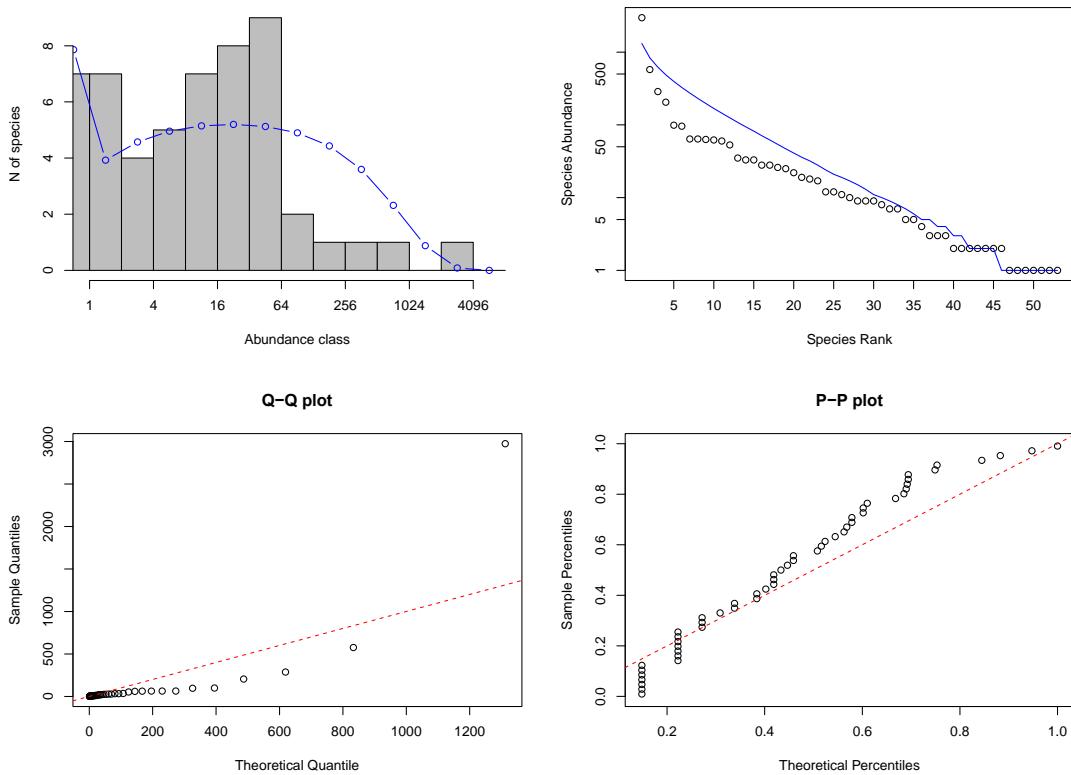
log-series models. Thus, there is no evidence to support neutrality as the explanatory paradigm for community assembly in the CRE molluscan community.



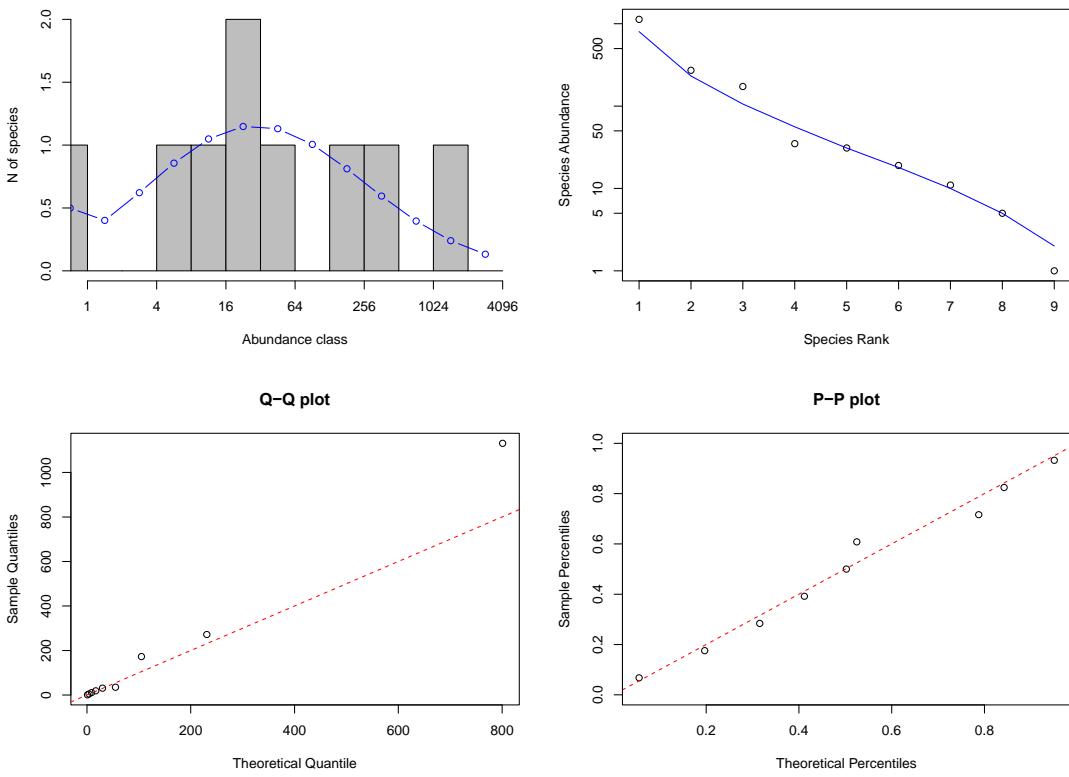
Appendix Figure 7 Diagnostic plots for Poisson log-normal model fitting the whole-community data.



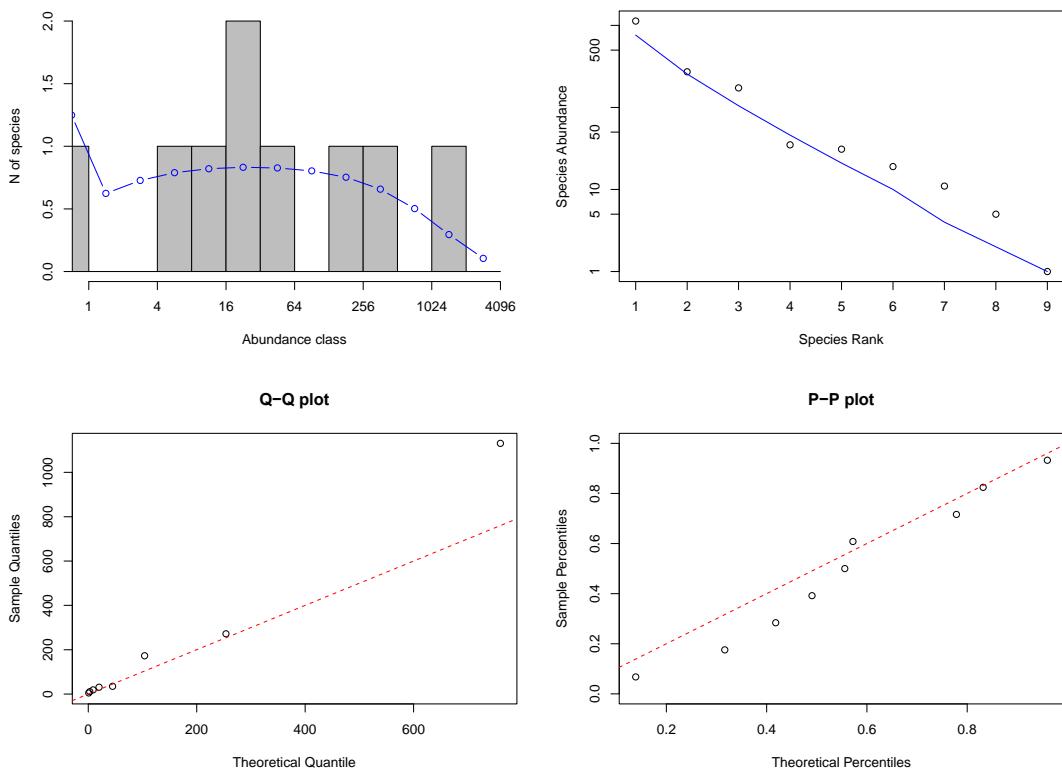
Appendix Figure 8 Diagnostic plots for log-series model fitting the whole-community data.



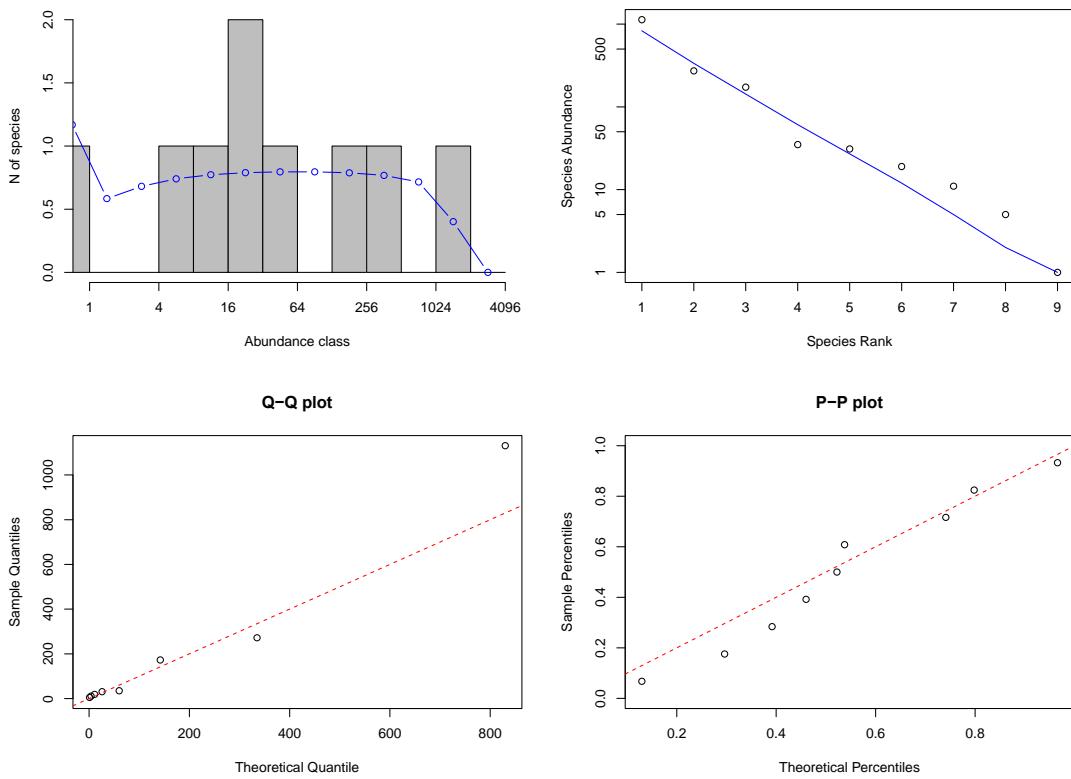
Appendix Figure 9 Diagnostic plots for zero-sum multinomial model fitting the whole-community data.



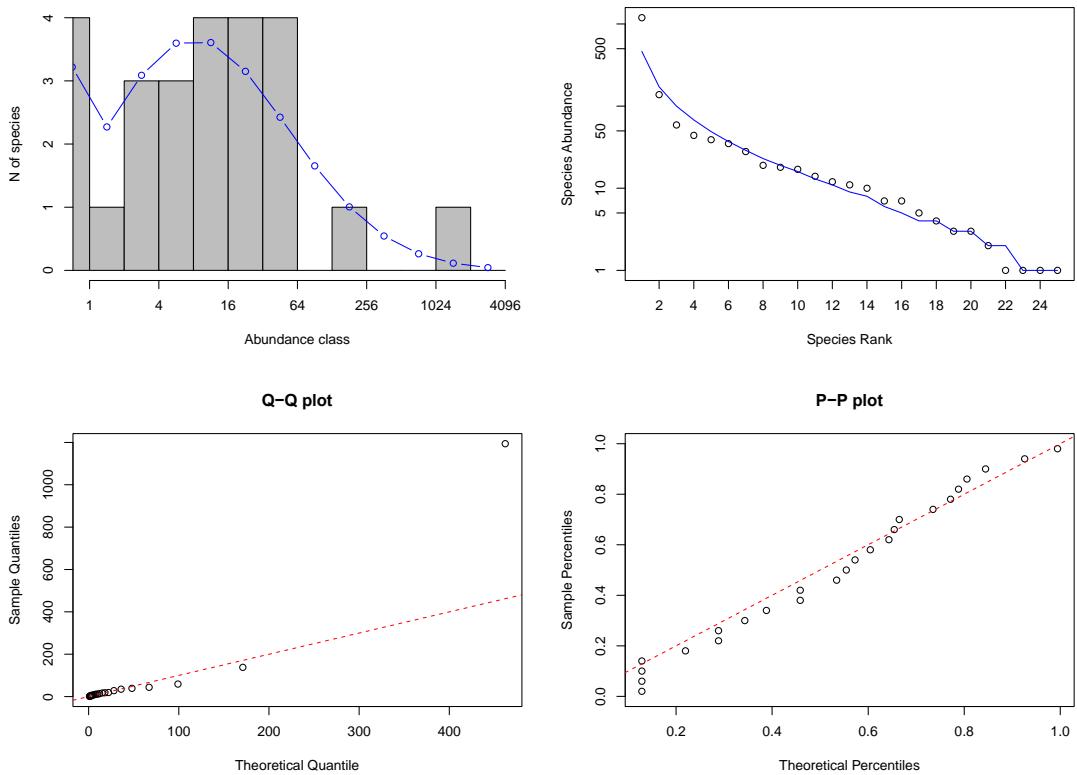
Appendix Figure 10 Diagnostic plots for Poisson log-normal model fitting the Isla Montague data.



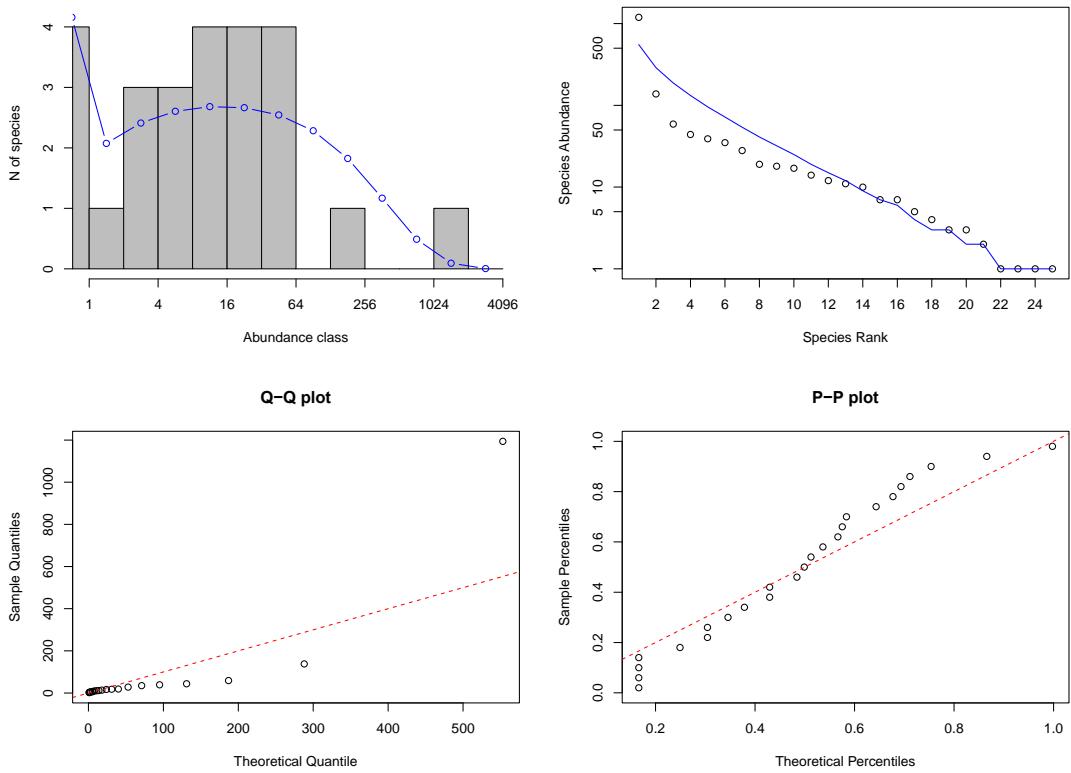
Appendix Figure 11 Diagnostic plots for log-series model fitting the Isla Montague data.



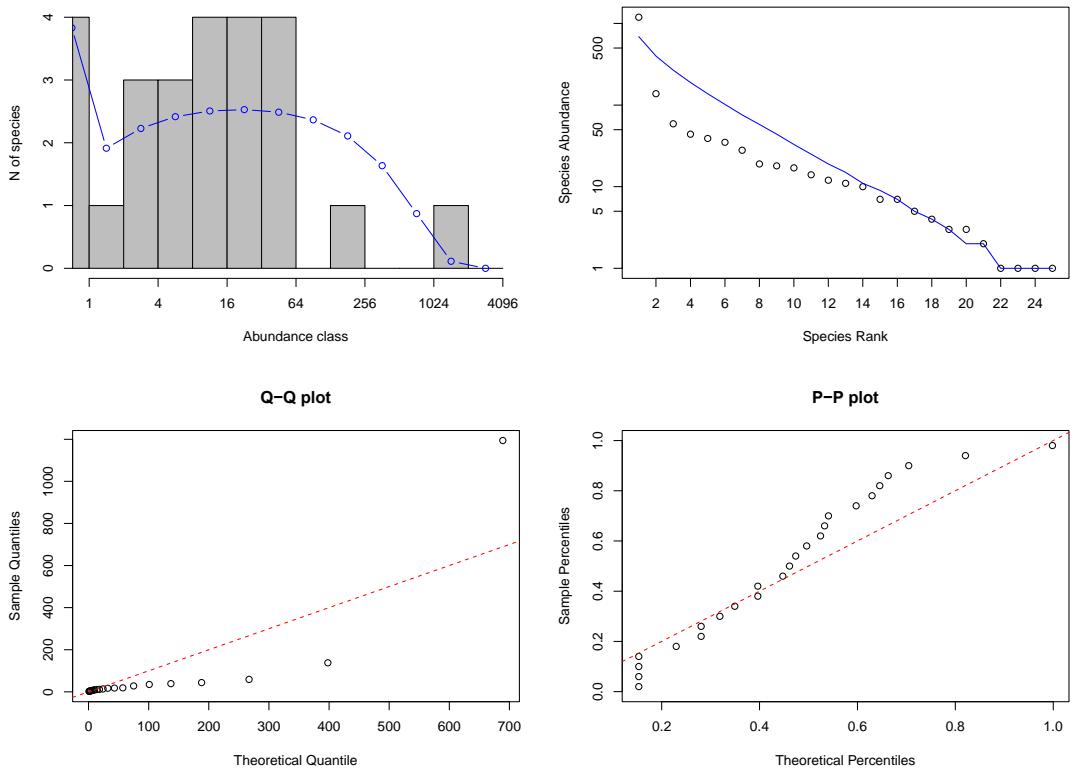
Appendix Figure 12 Diagnostic plots for zero-sum multinomial model fitting the Isla Montague data.



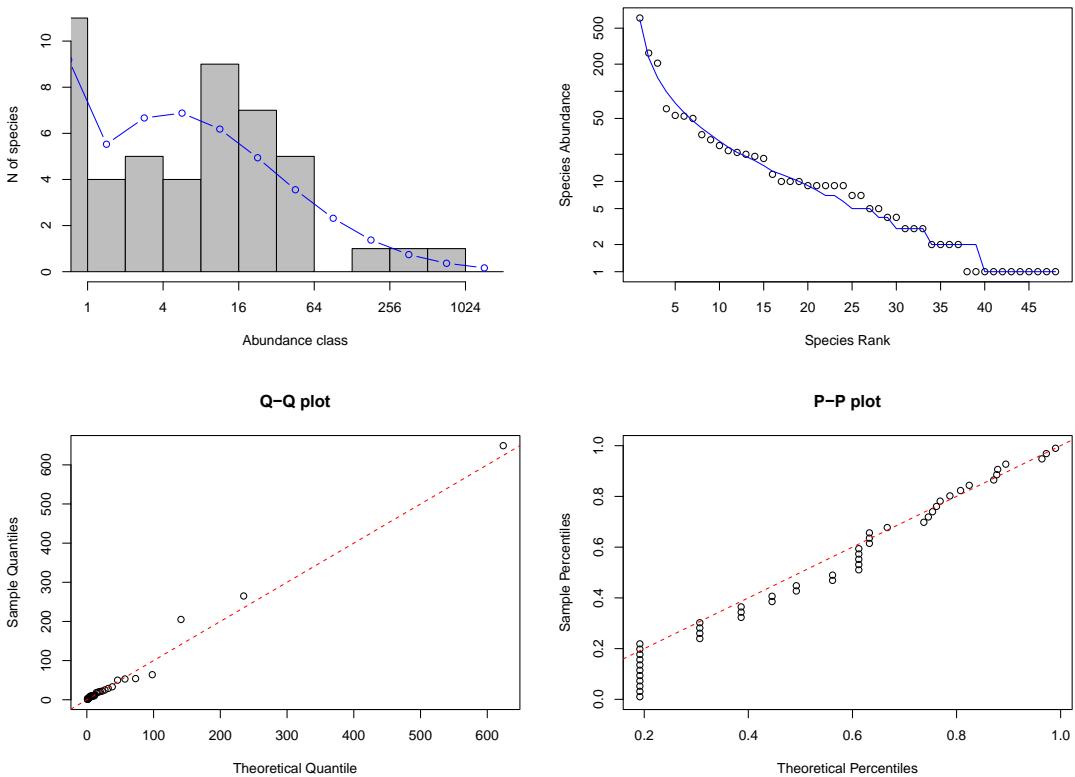
Appendix Figure 13 Diagnostic plots for Poisson log-normal model fitting the Las Isletas data.



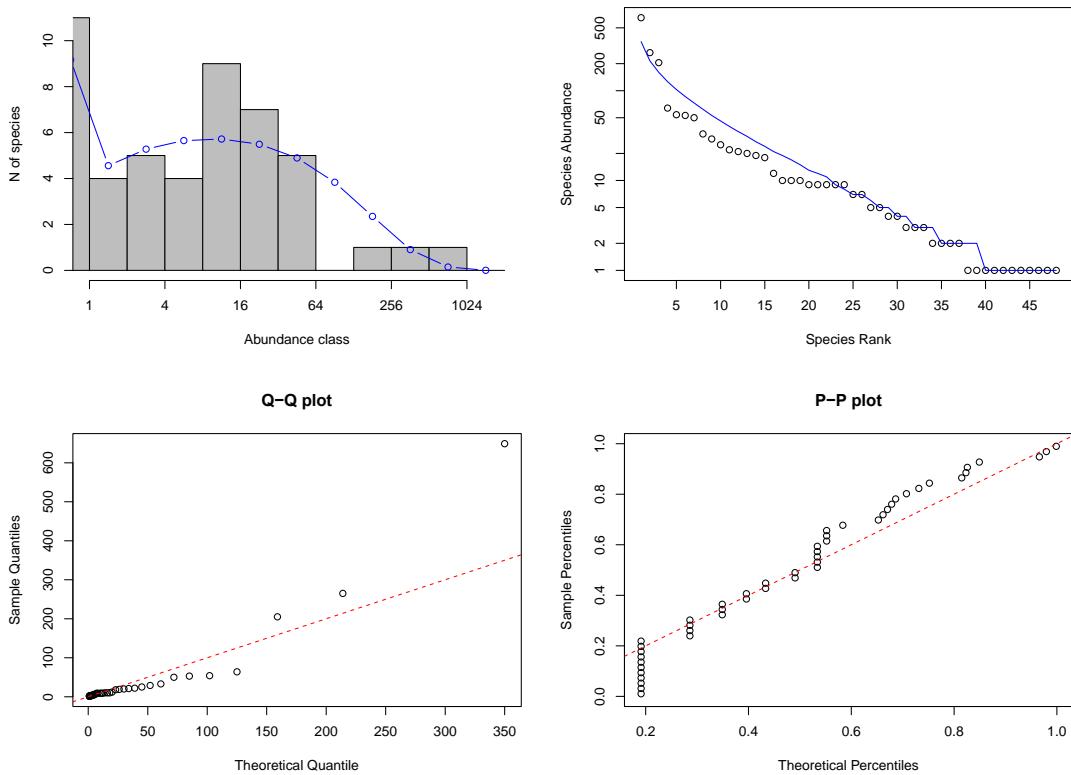
Appendix Figure 14 Diagnostic plots for log-series model fitting the Las Isletas data.



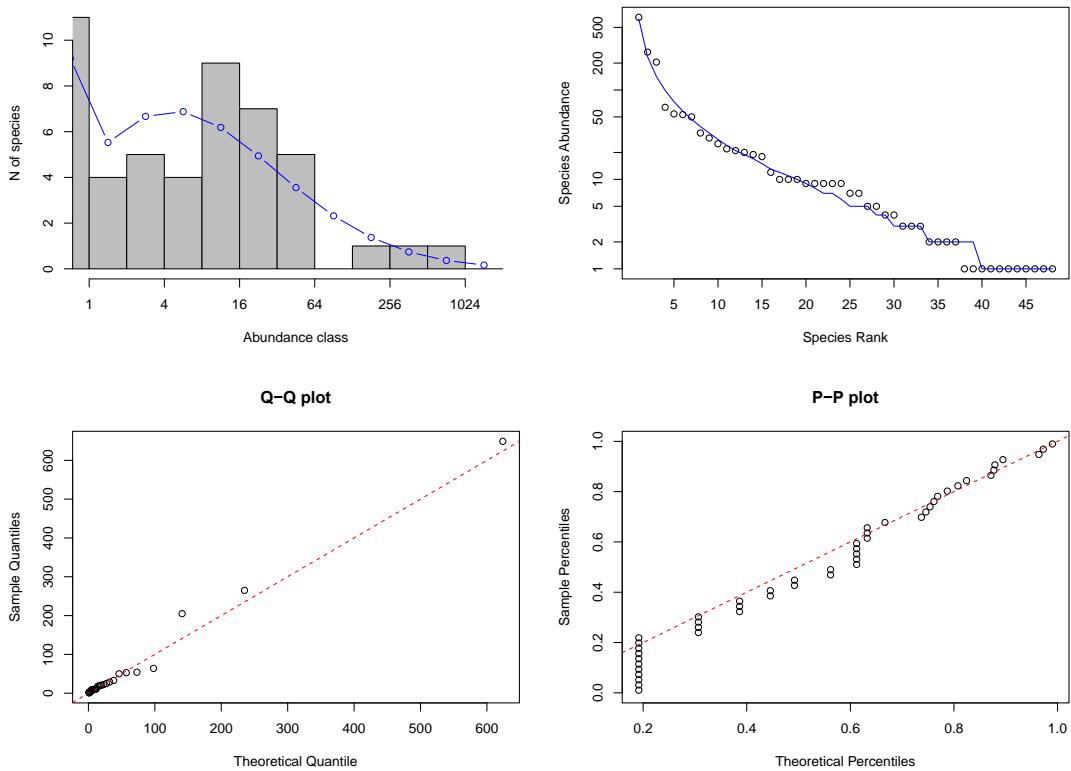
Appendix Figure 15 Diagnostic plots for zero-sum multinomial model fitting the Las Isletas data.



Appendix Figure 16 Diagnostic plots for Poisson log-normal model fitting the Campo don Abel data.



Appendix Figure 17 Diagnostic plots for log-series model fitting the Campo don Abel data.



Appendix Figure 18 Diagnostic plots for zero-sum multinomial model fitting the Campo don Abel data.

A10.3 R code for analysis of environmental preference and commonness

The following code fits a binomial model to the data from the core components at the CRE sites, testing the association between commonness and environmental preference. From the model simulations ($n=2000$), Bayesian probabilities were generated for the likelihood of finding species with respective environmental preferences in the core component at each site relative to each of the other sites.

```
RAM <- read.csv("data.file")
RAMod <- glm(cbind(Estuarine, Marine)~Site, family=binomial, data=RAM)

## Generate probabilities of finding estuarine species in the
## core components of the respective sites
```

```

pCDA <- plogis(coef(RAmod)[1])
pIM <- plogis(coef(RAmod)[1]+coef(RAmod)[2])
pLI <- plogis(coef(RAmod)[1]+coef(RAmod)[3])

## Generate diagnostic plots
plot(RAmod)

## Simulation based on RAmod
nsim<-2000
bsim<-sim(RAmod, n.sim=nsim)

RAnew <- data.frame(Site=factor(c("CDA", "IM", "LI"), levels=c("CDA", "IM",
"LI")))
Xmat<-model.matrix(~Site, RAnew)
fitmat<-matrix(nrow=nrow(RAnew), ncol=nsim)
for(i in 1:nsim) fitmat[,i]<-plogis(Xmat%*%bsim@coef[i,])

RAnew$lwr <- apply(fitmat, 1, quantile, prob=0.025)
RAnew$upr <- apply(fitmat, 1, quantile, prob=0.975)
RAnew$fit <- plogis(Xmat%*%coef(RAmod)) ## model estimates

## Probability the proportion of estuarine species at one site ## is greater than at
another ([1,] = Campo don Abel; [2,] =
## Isla Montague; [3,] = Las Isletas)
sum(fitmat[2,] > fitmat[1,])/nsim
sum(fitmat[2,] > fitmat[3,])/nsim
sum(fitmat[3,] > fitmat[1,])/nsim

```

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Appendix 11: Raw data and sources for species environmental preferences

Appendix Table 13 Raw abundance data for the molluscan species from the three sites in the Colorado River estuary. Species' ecological preferences are given as Marine (salinity \geq 34 psu) or Estuarine (salinity $<$ 34 psu) based on a literature search using exact species names. When species-specific data were not available, preferences were assigned based on those of congeners. A single asterisk (*) indicates preference was assigned based on congeners and a double asterisk (**) indicates preference was assigned based on species-specific information. Commonness designation for each species at each site indicated with S = satellite and C = Core.

Genus	Isla Montague	Las Isletas	Campo don Abel	Preference	Preference Reference
Bivalvia					
<i>Abra palmeri</i>		1 (S)	1 (S)	Marine**	Parker, 1963; Hendrickx et al., 2014; Pires-Vanin et al., 2014
<i>Acorylus rickettsi</i>			10 (S)	Marine*	Parker, 1963; Stump, 1975; Beckvar, 1988; Avila-Serrano et al., 2006; Pires-Vanin et al., 2014
<i>Anomia peruviana</i>		59 (C)	1 (S)	Marine**	Beckvar, 1988; Schröder et al., 2013
<i>Argopecten</i> sp.		19 (C)	9 (S)	Marine*	Parker, 1963
<i>Cavilinga lingualis</i>			9 (S)	Marine*	Parker, 1963; Beckvar, 1988
<i>Chionista flustifraga</i>	19 (C)	44 (C)	33 (C)	Marine**	Schöne et al., 2003
<i>Chionopsis gnidia</i>		35 (C)	64	Marine**	Stump, 1975; Roopnarine et al., 1998; Pires-Vanin et al., 2014; López de Mesa and Cantera, 2015
<i>Chionopsis pulicaria</i>			7 (S)	Marine**	Stump, 1975; Ríos-Jara et al., 2008; Pires-Vanin et al., 2014; López de Mesa and Cantera, 2015
<i>Cumingia pacifica</i>		17 (C)		Estuarine**	Coan and Valentich-Scott, 2012
<i>Cyclinella saccata</i>			2 (S)	Marine**	Ríos-Jara et al., 2007; Pires-Vanin et al., 2014; López de Mesa and Cantera, 2015
<i>Dallocardia senticosum</i>			5 (S)	Marine**	Parker, 1963; Stump, 1975; Ríos-Jara et al., 2008
<i>Diplodonta soror</i>			22 (C)	Marine**	Parker, 1963; Esqueda-González et al., 2014; Hendrickx et al., 2014; Pires-Vanin et al., 2014
<i>Donax californicus</i>			205 (C)	Marine**	Parker, 1963; Peterson, 1975; Avila-Serrano et al., 2006; Esqueda-González et al., 2014
<i>Lamelliconcha</i>		3 (S)	9 (S)	Marine**	Parker, 1963; Ríos-Jara et al.,

<i>concinus</i>					2008; Pires-Vanin et al., 2014
<i>Limaria orbignyi</i>			9 (S)	Marine*	Beckvar, 1988; Esqueda-González et al., 2014; Pires-Vanin et al., 2014
<i>Mulinia modesta</i>	1131 (C)	1194 (C)	649 (C)	Estuarine**	Parker, 1963; Rodriguez et al., 2001; Montagna et al., 2008; Pollack et al., 2009
<i>Nuculana marella</i>			2 (S)	Marine**	Parker, 1963; Cruz, 1983; Hendrickx et al., 2014
<i>Ostrea</i> sp.			19 (C)	Marine*	Parker, 1963; Stump, 1975
<i>Psammotreta aurora</i>		3 (S)		Marine*	Stump, 1975; López de Mesa and Cantera, 2015
<i>Sacella acrita</i>			7 (S)	Marine**	Parker, 1963; Cruz, 1983; Paredes et al., 2012
<i>Semele</i> sp. 1		2 (S)		Marine*	Parker, 1963
<i>Semele</i> sp. 2		1 (S)		Marine*	Parker, 1963
<i>Semelina campbellorum</i>			25 (C)	Marine**	Coan, 2003; Pires-Vanin et al., 2014
<i>Solen gemmelli</i>			1 (S)	Marine**	von Cosel, 1992; Pires-Vanin et al., 2014
<i>Sphenia gulfensis</i>			18 (C)	Marine**	Coan, 1999; Esqueda-González et al., 2014; López de Mesa and Cantera, 2015
<i>Strigilla cicercula</i>			9 (S)	Marine**	Ríos-Jara et al., 2008; Esqueda-González et al., 2014; Pires-Vanin et al., 2014
<i>Tagelus affinis</i>	11 (S)	14 (S)	1 (S)	Estuarine**	Springer and Flessa, 1996; Montagna et al., 2008; Burnaford et al., 2011
<i>Tampaella meropsis</i>		1 (S)	3 (S)	Marine**	Parker, 1963; Stump, 1975; Beckvar, 1988; Avila-Serrano et al., 2006; Pires-Vanin et al., 2014
<i>Tellina hiberna</i>		10 (S)	54 (C)	Marine*	Parker, 1963; Stump, 1975; Beckvar, 1988; Avila-Serrano et al., 2006; Pires-Vanin et al., 2014
<i>Trachycardium procerum</i>			5 (S)	Marine**	Rollins et al., 1987; Ríos-Jara et al., 2008
Veneridae sp.			53 (C)	Marine*	Parker, 1963; Stump, 1975; Fursich and Flessa, 1987; Pires-Vanin et al., 2014
Gastropoda					
<i>Calliostoma palmeri</i>			1 (S)	Marine**	Parker, 1963; Hendrickx et al., 2014; Pires-Vanin et al., 2014; López de Mesa and Cantera, 2015
<i>Calyptaea mamillaris</i>		12 (S)	50 (C)	Marine**	Parker, 1963; Beckvar, 1988; Ríos-Jara et al., 2007; Pires-Vanin et al., 2014

<i>Cerithideopsis californica</i>	272 (C)	5 (S)	10 (S)	Estuarine**	Parker, 1963; Stump, 1975; Race, 1981; Springer and Flessa, 1996
<i>Cosmioconcha palmeri</i>	1 (S)	11 (S)	21 (C)	Marine**	Keen, 1971; Fortunato, 2007; Vargas-Zamora and Sibaja-Cordero, 2011
<i>Crepidula perforans</i>		18 (C)	10 (S)	Marine*	Parker, 1963; Beckvar, 1988; Pires-Vanin et al., 2014
<i>Crepidula onyx</i>		7 (S)	4 (S)	Marine*	Parker, 1963; Beckvar, 1988; Pires-Vanin et al., 2014
<i>Crucibulum spinosum</i>		4 (S)	29 (C)	Marine**	Parker, 1963; Ulbrick, 1969; Beckvar, 1988
<i>Eupleura limata</i>	31 (C)	31 (C)	4 (S)	Estuarine**	Herbert, 2005
<i>Kylix</i> sp.			3 (S)	Marine*	López de Mesa and Cantera, 2015
<i>Marginella</i> sp.			1 (S)	Marine*	Parker, 1963
<i>Melampus olivaceus</i>	35 (C)			Estuarine**	Parker, 1963
<i>Nassarius guaymasensis</i>			2 (S)	Marine**	Keen, 1971; Hendrickx et al., 2014
<i>Nassarius moestus</i>	173 (C)	138 (C)	265 (C)	Estuarine ^Ψ	Long and Langer, 1995; Avila-Serrano et al., 2006
<i>Neverita reclusiana</i>	5 (S)	39 (C)	20 (C)	Marine**	Smith et al., submitted
<i>Olivella</i> sp.			12 (S)	Marine*	Parker, 1963; Pires-Vanin et al., 2014
<i>Solenosteira capitanea</i>		7 (S)	1 (S)	Marine*	Avila-Serrano et al., 2006; Kamel et al., 2014
<i>Terebra</i> sp.			1 (S)	Marine*	Parker, 1963; Stump, 1975
Turridae sp. 1		1 (S)	1 (S)	Marine*	Shimek, 1986
Turridae sp. 2			1 (S)	Marine*	Shimek, 1986
Turridae sp. 3			2 (S)	Marine*	Shimek, 1986
<i>Turritella leucostoma</i>			3 (S)	Marine**	Waite and Allmon, 2013; López de Mesa and Cantera, 2015
Unidentified Gastropod sp.			1 (S)		

^Ψ More than any other species considered here, *Nassarius moestus* thrives in a wide range of environmental conditions. This small, omnivorous snail species is often found foraging on the tidal flat at low tide, where salinities can exceed 50 psu (per. obs.) due to evaporation from direct overhead sun exposure (Long and Langer, 1995). As such, the salinity range considered here (28-34 psu) represents a small portion of the range of salinities experienced by this snail at every tidal cycle. Whether *N. moestus* is classified as Estuarine or Marine, or excluded entirely, the results of this study do not change. When *N. moestus* is classified as marine, probabilities of estuarine species being found at Isla Montague remain high compared to Las Isletas ($P=0.9945$) and Campo don Abel ($P=0.9995$). When *N. moestus* is excluded probabilities remain similar, at 0.9995 and 0.9975, respectively.

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Appendix 12: Determining molluscan larval mode

The larval mode of molluscan species can be determined from the morphology of the larval shell, called a prodissoconch for bivalves and a protoconch for gastropods (Thorson, 1950; Ockelmann, 1965; Shuto, 1974; Scheltema, 1978; Lutz et al., 1980; Jablonski and Lutz, 1983). Several sets of terminology have been proposed to categorize molluscan larvae, all of which consider three larval types: (1) free-swimming, feeding larvae; (2) free-swimming, non-feeding larvae; and, (3) non-swimming, benthic juveniles (Jablonski and Lutz, 1983). We follow Jablonski and Lutz (1983) in using a binary categorization where the latter two larval types are combined as “Nonplanktotrophic” and the first type is “Planktotrophic.” We apply this categorization when considering dispersal capacity because free-swimming, non-feeding larvae (often referred to as lecithotrophic larvae) only remain in the water

column for a short time (hours or days) compared to planktotrophic larvae (days to weeks), which diminishes their dispersal capacities.

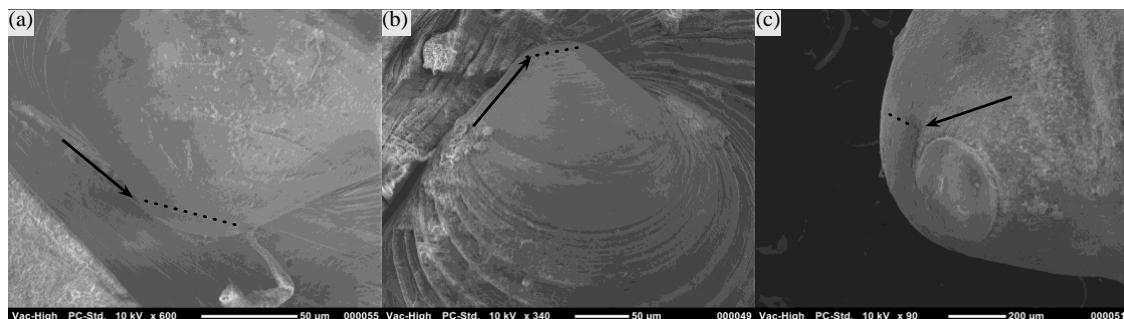
In order to differentiate between nonplanktotrophic and planktotrophic larvae for gastropods, the maximum diameter (D ; in mm) of the protoconch is measured and divided by the number of volutions (Vol)—a 360° spiral of the gastropod shell—observed in the protoconch (Shuto, 1974). The protoconch can be distinguished from the adult shell by a lack of shell sculpture and differences in appearance resulting from differences in microstructure. For gastropod larvae, if D/Vol is in the range of $0.3 - 1.0$ and there are fewer than 2.25 volutions then the larvae is classified as nonplanktotrophic. If D/Vol is less than 0.3 and more than 3 volutions are present then the larvae is classified as planktotrophic. A larvae with a high D/Vol value ($0.3 - 1.0$) and fewer than 3 volutions may be either larval type (Shuto, 1974; Jablonski and Lutz, 1983). For bivalves, only the maximum diameter of the prodissoconch is measured and its absolute size is the determining factor for larval type. The prodissoconch is differentiable from the adult shell by its lack of concentric growth rings, having instead a pitted surface. A small prodissoconch (< 0.150 mm) indicates planktotrophic larvae and a large prodissoconch ($0.2 - 0.6$ mm) indicates nonplanktotrophic larvae (Ockelmann, 1965; Lutz et al., 1980).

For this study, exemplar specimens from species of interest—species with core designations at sites where the salinity did not match their environmental preferences—were imaged using a bench-top Scanning Electron Microscope (JEOL NeoScope JCM-5000). Both of the bivalve species considered here, *Mulinia modesta* (Appendix Figure 19a) and *Chionista fluctifraga* (Appendix Figure 19b), have small

prodissococonchs, indicating planktotrophic larvae (Appendix Table 13). In contrast, the large size and few volutions in the protoconch from *Crepidula onyx* (Appendix Figure 19c) suggests nonplanktotrophic larvae (Appendix Table 13).

Appendix Table 13 Determination of larval mode for three molluscan species from the Colorado River estuary. PT = planktotrophic; NPT = Non-planktotrophic.

Species	Diameter (mm)	Volutions	D/Vol	Larval Type
<i>Mulinia modesta</i>	0.05	-	-	PT
<i>Chionista fluctifraga</i>	0.075	-	-	PT
<i>Crepidula onyx</i>	0.5	1.5	0.333	NPT



Appendix Figure 19 Prodissococonchs for *Mulinia modesta* (a) and *Chionista fluctifraga* (b) and protoconch *Crepidula onyx* (c). Arrows and dashed lines indicate distal edge of the prodissococonch/protoconch.

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