BIOLOGICAL CONSERVATION

Diverting the Colorado River leads to a dramatic life history shift in an endangered marine fish

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ABSTRACT

Diversion of river water has diminished freshwater flow into many estuaries worldwide, yet the effects of these diversions on marine fisheries, many of which depend on estuaries, are largely unexplored. We document the impact of diverting Colorado River flow from the Gulf of California on the life history of a now-endangered marine fish (*Totoaba macdonaldi*, Sciaenidae). Growth increments in prehistoric (1000–5000 ybp) otoliths document that pre-dam juveniles grew twice as fast and matured 1–5 years earlier than post-dam fish. Oxygen isotopes link these changes to elimination of estuarine habitat. This study provides evidence that river diversion can have a dramatic effect on life history of marine fishes by slowing growth during the juvenile stage, thus delaying maturation. These findings also provide valuable insight into the relative influence of habitat alteration versus fishing pressure on marine fishes.

1. Introduction

The demand for fresh water resources has prevented many of the world's rivers from emptying into the ocean (Drinkwater and Frank, 1994; Gleick, 2003). The physical and chemical impacts of upstream dams and diversions on estuaries are well-known (Livingston et al., 1997; Gillanders and Kingsford, 2002; Staunton-Smith et al., 2004), but their ecological effects are poorly understood (Grimes and Kingsford, 1996; Gillanders and Kingsford, 2002). This lack of understanding is alarming, as 60% of US commercial fishes spend part of their lives in estuaries (Owen and Chiras, 1995), and it is widely accepted

that most marine fisheries are already in decline (Worm et al., 2006). Fishery declines have been correlated with reduced river flow into estuaries in several cases (Flanagan and Hendrickson, 1976; Gillanders and Kingsford, 2002; Staunton-Smith et al., 2004), but these declines are often also associated with high commercial fishing rates, making it difficult to assess the importance of the alteration to spawning and/or nursery habitat independent of over-fishing. An accurate evaluation of environmental costs associated with river diversions depends on the ability to assess the effects of river regulation on marine fisheries. This assessment is difficult because many rivers and estuaries were modified long before

modern ecological monitoring began (Kennish, 2002), and thus baseline data on past conditions and species life histories are hard to obtain (Dayton et al., 1998; Jackson et al., 2001).

Here we attempt to resolve the lack of baseline information on habitat use and life history and address the impact of river diversion on the collapse of the first commercial fishery in the Gulf of California, Mexico: Totoaba (*Totoaba macdonaldi*). Totoaba is a large, endemic sciaenid that spawns only in the Colorado River estuary (Flanagan and Hendrickson, 1976). It once supported a massive fishery (~2000 metric tons over a four month period), that began to decline following the completion of Hoover Dam (1935) on the Colorado River (Flanagan and Hendrickson, 1976; Cisneros-Mata et al., 1995). This decline has been cited as an example of reduced river inflow affecting a marine fishery (Gillanders and Kingsford, 2002; Helfman et al., 2002), but totoaba's decline is also coincident with a sharp increase in fishing pressure (mainly extensive gill-netting of adults and sub-adults) and shrimp trawling (by-catch of juveniles), confounding any strong conclusions (Cisneros-Mata et al., 1995; García-Caudillo et al., 2000ab). In 1975, *T. macdonaldi* was listed as an endangered species by both Mexico and the USA, ostensibly prohibiting fishing (Cisneros-Mata et al., 1995). Yet recovery efforts have had limited success, even though its estuarine spawning and nursery grounds were included within a biosphere reserve decreed in 1993.

In this paper, we reconstruct missing baseline information using totoaba saccular otoliths (ear bones) collected from aboriginal shell middens. We hypothesize that upstream diversions of Colorado River water have adversely affected the estuarine habitat, making it less suitable for juvenile growth of *T. macdonaldi*. If true, this would help to explain the lack of recovery of this species during the past 30 years of fishing prohibition. To test this hypothesis, we compare growth increments and oxygen isotope variation between these prehistoric (pre-dam) and modern (post-dam) otoliths. We use these data to reconstruct habitat use and to examine effects of river flow on the life history of this endangered species.

2. Field site

Like many large rivers diverted for human needs, the Colorado River no longer reaches the sea – except in abnormally wet years (Gleick, 2003). Pre-dam annual river discharge into the Gulf of California ranged between 8×10^9 and $30.8 \times 10^9 \, m^3 \, yr^1$ (Harding et al., 1995). This flow maintained an estuary comprising ca. 4000 km^2 of the uppermost Gulf of California (Lavín and Sánchez, 1999) and a mixing zone extending ca. 65 km from the river's mouth (Rodriguez et al., 2001) (Fig. 1). Before the dams, more than 70% of the river's annual flow to the estuary occurred during May through July (Harding et al., 1995). Today, the northernmost portion of the Gulf of California is a negative estuary (Lavín et al., 1998). The combination of arid environment, high evaporation rates and decreased river flow has resulted in salinities between 36–40‰ in the upper Gulf (Hernández-Ayón et al., 1993; Lavín and Sánchez, 1999). The only water that crosses the US border in normal years is the annual flow of $1.8 \times 10^9 \, m^3$ required by the 1944 Mexican Water Treaty. This water is almost entirely consumed by municipal and agricultural users in Mexico, though a fraction probably reaches the Gulf via subsurface flow (Hernández-Ayón et al., 1993; Lavín et al., 1998; Rowell et al., 2005).

3. Methods and materials

We compared oxygen isotope ratios ($\delta^{18}O$) and growth increments in totoaba otoliths retrieved from aboriginal shell middens in the upper Gulf of California to $\delta^{18}O$ values and growth increments from otoliths from live-caught totoaba. Because totoaba are now federally protected and only limited systematic excavations have been done in shell middens within this area, our sample size is limited to five pre-dam and five post-dam otoliths. Prehistoric (pre-dam) otoliths came from serendipitous surface finds at two different shell middens on the upper Gulf of California coast. Four specimens were loaned by Scripps Institution of Oceanography Marine Vertebrate Collection (SIO50-119), and were collected in 1955, near San Felipe, Baja California (Fig. 1), from a midden dated between 805 and 1280 cal yr BP using ^{14}C from a marine shell and three charcoal samples (see reference in Stuiver and Reimer (1993) for marine and terrestrial calibrations). The fifth pre-dam otolith was donated by the Guaymas campus of the Instituto Tecnológico y de Estudios Superiores de Monterrey to the University of Arizona (UAZ) Fish Collection and was a shell-midden, surface find from Bahía San Jorge, Sonora. This specimen was dated directly at 4580 ± 130 ^{14}C yr BP, with a 2σ range of 5584–4880 cal yr BP (see reference in Stuiver and Reimer (1993) for calibration). Live-collected specimens (post-dam) were caught under federal permits in 1987 and 1990 and their otoliths extracted for growth studies (Román-Rodríguez and Hammann, 1997). Like the pre-dam otoliths, the post-dam specimens came from fish spawned during different years (1963–1976).

3.1. Oxygen isotopic analysis

The deposition of $\delta^{18}O$ in otolith aragonite is controlled by the isotopic ratio of the local water and ambient temperature (Thorrold et al., 1997; Rowell et al., 2008). The Colorado River is isotopically distinct from the upper Gulf of California. Today the average water $\delta^{18}O$ from the most downstream portion of the Colorado River is −12‰ and in the past reached as low as –16‰ before upstream reservoirs increased evaporation and homogenized the natural seasonal variation (Dettman et al., 2004). Open upper Gulf of California seawater currently averages 0.6‰ (Rowell et al., 2005). The $\delta^{18}O$ in otolith aragonite is inversely related to the temperature of the water: An increase of 1 °C in ambient water results in a decrease of ~0.22‰. In the upper Gulf of California, the approximately 16 °C annual variation in water temperature provides an excellent isotopic seasonal marker of the seasonal cycle in otolith annuli (Rowell et al., 2005). The maximum temperature-driven $\delta^{18}O$ value for purely marine Gulf of California water is −2.4‰ (Rowell et al., 2005). Values that fall below this
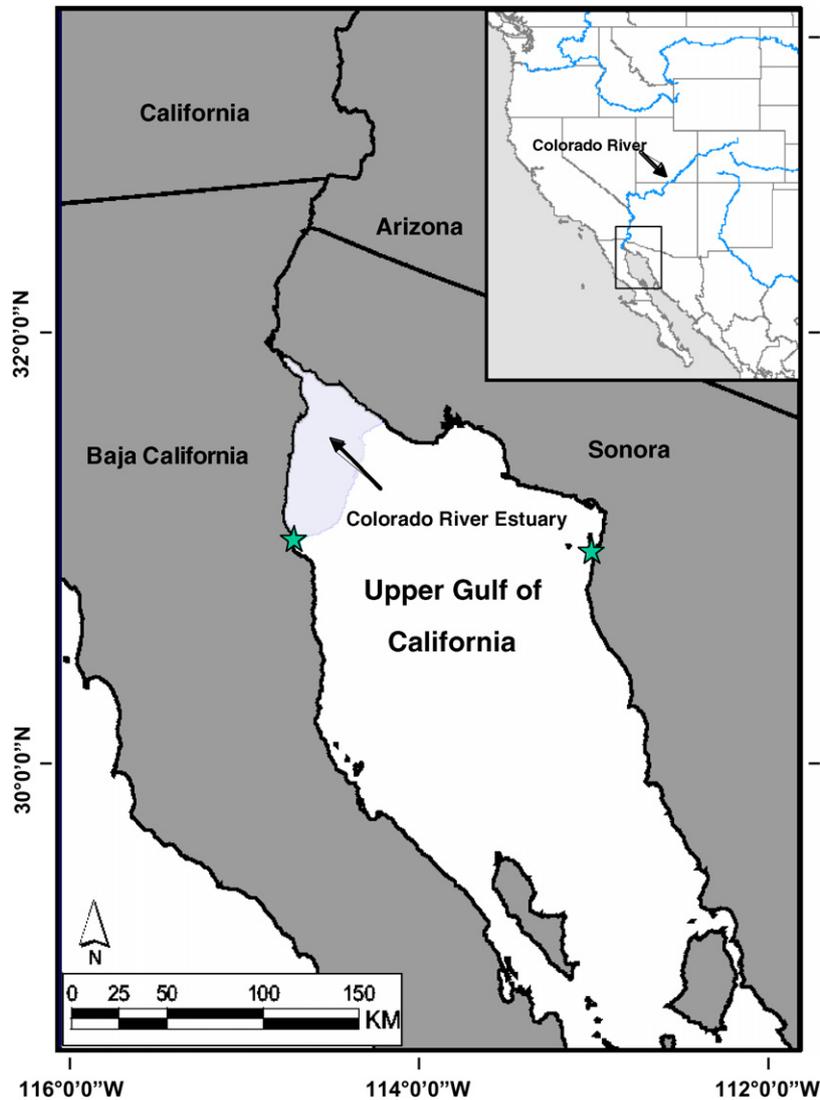
Fig. 1 – Colorado River mouth and upper Gulf of California, light shading indicates estimated extent of pre-dam Colorado River estuary (Lavín and Sánchez,1999; Carbajal et al., 1997). Stars indicate aboriginal shell middens where pre-dam otoliths were collected. Post-dam otoliths came from totoaba caught in the Colorado River estuary area.

are unmistakable records of fish growth in habitats influenced by the isotopically negative Colorado River water.

The juvenile portions of otoliths from the live-caught totoaba represent years 1963–1976 (years of no Colorado inflow), thus we expect post-dam $\delta^{18}O$ values to fall within expected temperature-driven variation for the purely marine setting. Because otolith $\delta^{18}O$ can record the presence of river water when these fish inhabited the estuary (Rowell et al., 2008), and their rate of growth is recorded in the thickness of the annual increments (annuli), we use growth rates of totoaba otoliths in the presence and absence of river influence (determined by the isotopic signature) to help understand how the Colorado River flow may have affected growth.

Material for geochemical analyses was collected along a pie-slice section of each otolith from its perimeter (terminal year) to the core (natal portion) using a micromill drill with a 0.3-mm drill-bit. Samples were taken by milling thin

(between 18 and 200 μm width), sub-annual growth increments from the perimeter and moving toward the core (nucleus) with the drill, resulting in a continuous high-temporal resolution profile (Dettman and Lohmann, 1995) of the otolith throughout the fish's life. If the banding was clearly visible from the area sampled, the type of banding the sample was taken from was noted (e.g., translucent and opaque). Samples weighed between 30 and 60 μg, and were heated to 180 °C in a vacuum oven for one hour to remove volatile materials. Oxygen isotope ratios in carbonates are expressed relative to the Vienna Pee Dee Belemnite (VPDB) standard. Otolith carbonate (aragonite) was analyzed at the Stable Isotope Laboratory of the Department of Geosciences, University of Arizona, using a Finnigan MAT 252 mass spectrometer equipped with a Kiel-III automated carbonate sampling device. Standardization of oxygen and carbon isotope ratios was based on normalization to published ratios of NBS 19 and NBS 18. Analytical error was ±0.1‰.

3.2. Statistical analyses

3.2.1. Oxygen isotopes

To test the hypothesis that *T. macdonaldi* historically used the pre-dam brackish water of the Colorado River estuary as nursery habitat, we compared the maximum (winter) and minimum (summer) $\delta^{18}O$ values of each annual cycle in juvenile years 1–3 between pre- and post-dam otoliths. Annual maxima $\delta^{18}O$ values represent the lowest temperatures of the year and therefore are a seasonal marker for the height of winter, when river run-off is naturally at its annual low. Thus, we don't expect to see much of a difference between pre- and post-dam winter $\delta^{18}O$ values. The annual minimum $\delta^{18}O$ values represent the season of maximum temperature in the post-dam otoliths. If pre-dam fish inhabited the river-influenced estuary, we expect significantly lower $\delta^{18}O$ values than the post-dam otoliths because local (estuarine) waters were influenced by isotopically negative river water. When comparing pre- and post-dam summer $\delta^{18}O$ values, we assumed that temperatures were comparable. It is unlikely that water temperatures were significantly different in pre-dam times; it would take an improbable shift of 4.5 °C to change the $\delta^{18}O$ in the otolith aragonite by 1‰. Using annual maxima (winter) and minima (summer) $\delta^{18}O$ values for each otolith (instead of average annual values) minimizes error due to different growth rates, different sampling densities, averaging of time intervals in the otolith, and seasonal variation in $\delta^{18}O$ values. We predict that river influenced $\delta^{18}O$ values are more likely to be seen in the spring and summer samples, due to historical maximum flows during June (Harding et al., 1995). Because post-dam otoliths represent fish spawned during zero or extreme low-flow conditions, their annual low $\delta^{18}O$ values should be driven by water temperature, not by changes in the contribution of river water. We used a Kruskal–Wallis test to examine differences between the pre-dam and post-dam isotopic signatures for each year of growth.

3.2.2. Growth rates

We compared growth rates for juvenile years 1–3 between pre-dam and post-dam otoliths to test the hypothesis that totoaba grew faster when in the brackish waters of the pre-dam Colorado River estuary. We use the isotopic profile to verify that visual bands are truly annual by noting when a sample was taken from an opaque or translucent band. These notes on band type were compared to the isotopic values for these samples, which will help determine the season (winter or summer) in which these bands formed. Growth was estimated by width of each annual increment, identified by the seasonal isotopic values. There are two reasons we use the isotopic values and growth measurements directly related to the carbonate sample. First, visual measurements of annuli are notoriously subjective due to irregularities within the otolith and differences between individual readers (Campana and Moksness, 1991), compromising the parity between growth axes measured. Variability in visual quality also increases the subjectivity of these measurements (Campana and Moksness, 1991). Second, in our samples, measuring annuli along the sulcus grove, a standardized growth axis, was impossible due to variations in the conspicuousness of the annuli themselves. This was the case for both pre- and

post-dam otoliths, but especially true for the pre-dam otoliths, where the annuli in later years were not conspicuous (probably due to long-term weathering). While using visual markers to measure annuli is the traditional method for measuring otolith growth, we believe that in this system, using a chemical marker through continuous sampling of the oxygen isotope ratio provides a more precise alternative method for determining periodicity. The first year was measured from the natal value to the first winter value (highest $\delta^{18}O$ value). Years two and three were measured from subsequent winter-to-winter $\delta^{18}O$ values. To validate our method of using a chemical marker, we also made measurements of visual annuli for the first three years of growth for both pre- and post-dam otoliths. The average of three visual measurements (using ImageJ software) along the sulcus groove axis for each annuli were compared between treatments. The first year was measured from core to the start of the first check (an opaque growth increment), and years two and three were measured from the start of the check to the next start of the next check. In cases where annuli were not conspicuous along the sulcus grove, measurements were made slightly to the side (50–100 μm). It should be noted that these two measurements of annuli width, the isotopically defined annuli and the visual annuli, were taken in different regions of the otolith and therefore will result in different measurements. Comparisons between pre- and post-dam otoliths were made using the same method, thus are not affected by this difference. A Kruskal–Wallis test was used to compare annual growth between pre- and post-dam otoliths for both chemical and visual annuli.

We converted otolith growth to totoaba body growth using the relationship established by Román-Rodríguez and Hammann (1997), and used the same method mentioned above to measure otolith growth for years one through ten when available (not all fish lived to year 10). Using a Gompertz curve ($y = ab^{q^x}$), Román-Rodríguez and Hammann Román-Rodríguez and Hammann (1997) showed that totoaba otolith radius (axis from otolith nucleus outward along the sulcal groove to perimeter) was a strong predictor of totoaba body size (y = standard length [cm], $a = 30.92$, $b = 1$, $q = 3.86$, $x = [0.99 \times$ radius]; $r^2 = 0.98$, $n = 94$). We used this relationship to convert otolith growth to totoaba somatic growth, allowing a comparison of growth curves for pre- and post-dam fish.

3.2.3. Effects of Colorado River water on life history

If brackish water in the Colorado River estuary is important to totoaba nursery habitat, we expect a negative relationship between $\delta^{18}O$ values and growth; for example, when more fresh water is available in the estuary (i.e., more negative $\delta^{18}O$ values), annual growth should be greater. We used a linear regression to test if a relationship between presence of brackish water habitat and growth exists for years 1 through 3.

3.2.4. Life history influences of river diversion

We estimate age at sexual maturity for pre- and post-dam fish two ways. In our first model, we assume pre- and post-dam fish mature at the same size, and use the previously established size at maturity (1.3 m SL; Cisneros-Mata et al., 1995; Román-Rodríguez and Hammann, 1997. We then use the above relationship between otolith size and somatic growth to calculate

the age of pre- and post-dam fist when they reach 1.3 m in size. We note that previous investigations have found that the age at sexual maturity (ASM) for post-dam totoaba is 5–7 years (Cisneros-Mata et al., 1995; Román-Rodríguez and Hammann, 1997). Because we cannot be sure that pre- and post-dam fish matured at the same body size, we used a second estimation of ASM, growth rate at maturity, in which the growth rate for post-dam otoliths between years 5–7 ($\sim$21 mm/year) served as a marker for when fish shift their energies toward reproduction. We then evaluate at what age do pre-dam totoaba slow growth to a similar rate as the post-dam totoaba. We report results using both methods, providing two estimates of the effects of spawning and nursery habitat alterations on the life-history of this endangered species.

4. Results

The $\delta^{18}O$ values in pre-dam otoliths range from +0.69‰ to -5.49‰ (Fig. 2a–e). In all pre-dam specimens, we found values that are far more negative than expected from summer marine water temperature alone. Even though pre-dam specimens are from a period spanning approximately 4000 years, they share the same trend of increased variability in $\delta^{18}O$ values for the juvenile years. Post-dam otolith $\delta^{18}O$ values from live-collected totoaba range from +0.41‰ to -2.17‰ (Fig. 3a–e), and 99% of sampling points are within the range of $\delta^{18}O$ values expected from seasonal variation in temperature for Gulf of California marine water (Rowell et al., 2005).

Isotopic profiles from the two time periods look remarkably distinct from one another. Although pre- and post-dam have very different $\delta^{18}O$ profiles, they have in common the decrease in annual variation in $\delta^{18}O$ values with older age, which is associated with decreased growth. Also, white (opaque) growth bands, depicted by the arrows in $\delta^{18}O$ profiles, are associated with more positive (winter) $\delta^{18}O$ values and dark (transparent) growth bands are associated with more negative (summer) $\delta^{18}O$ values. When comparing individual annuli, the first year of pre-dam $\delta^{18}O$ summer values are significantly lower than post-dam first year $\delta^{18}O$ summer values ($\chi^2 = 6.82$, $p > 0.009$, (Table 1), Fig. 4). Pre-dam $\delta^{18}O$ summer values also appear somewhat lower in the second and third years, but this difference is not significant. Annual winter values did not differ significantly between pre and post-dam otoliths for any of the first three years (see Table 1).

Growth rates, as measured by width of annual increments, are significantly increased during the first year in pre-dam otoliths compared to those in post-dam otoliths ($\chi^2 = 3.94$, $p > 0.047$, (Fig. 5)). Years two and three showed no significant differences in the rate of growth between pre- and post-dam otoliths (Table 1). Similarly, direct measurements of visual annuli for the first three years also differed significantly between pre- and post-dam for year one ($r^2 = 3.98$, $p > 0.047$) and not for years two and three (Table 1). We found a strong negative correlation between summer $\delta^{18}O$ values and that year's growth for the first three years, but the slope of the relationship is steeper in the first year and becomes less steep with each year (Fig. 6). Because $\delta^{18}O$ values varied between years, each year was tested separately for a relationship between summer $\delta^{18}O$ and growth.

The discrepancy in growth is striking when comparing pre- and post-dam growth curves (Fig. 7). As a result of differences in growth, pre-dam totoaba apparently reached size at sexual maturity (for today's totoaba) between three to five years sooner than did the post-dam fish. Pre-dam totoaba reached size at sexual maturity by the second year (calculated average 1333 mm SL), whereas post-dam fish did not attain this size until sometime between their fifth and seventh year (calculated average 1306–1350 mm SL). Ours estimates of size at ASM for post-dam fish are in line with previously reported ASM (Cisneros-Mata et al., 1995; Román-Rodríguez and Hammann, 1997). Growth rate for today's totoaba when they reach sexual maturity is approximately 21 mm (SL) a year. Pre-dam fish slowed their growth to $\sim$21 mm a year between three and five years of age, at which time these fish were between 1393–1422 mm SL, much larger than today's mature fish (Fig. 7). These two estimates of ASM for pre-dam totoaba indicate that pre-dam totoaba matured between two and five years of age.

5. Discussion

Otolith $\delta^{18}O$ and growth profiles of totoaba that existed before dams are drastically different from those living after the Colorado River had been diverted. Pre-dam otoliths show first summer $\delta^{18}O$ values indicative of a mixed river water and marine environment. These pre-dam fish appear to have grown faster during their first year and, based on two separate estimates, reached sexual maturity earlier than post-dam fish.

Pre-dam and post-dam otolith profiles do share some similarities. Growth checks (opaque bands) were associated with winter $\delta^{18}O$ values and dark (translucent) growth bands were linked to summer (more negative) values. (Figs. 2 and 3) show the association between the winter $\delta^{18}O$ values and the observed annuli for three years. This confirms that visual annuli are being made annually. The majority of the profiles show a trend from to more negative values just following the natal sample. This indicates natal development in spring temperatures, which corresponds with the timing of spawning reported in the literature and with the spring run-off that occurred before dams and diversion on the Colorado. In four cases, the profile becomes more positive after the natal value, suggesting larval development may have occurred in late spring or early summer. It has been suggested by Flannagan and Henderickson (1976) that the totoaba spawning period has shifted towards early summer, however there are no empirical data to support this yet.

Both pre- and post-dam $\delta^{18}O$ profiles also have patterns of reduced seasonal variation in $\delta^{18}O$ with age, especially apparent in adult years. This attenuation in isotopic variation is likely the result of two co-occurring events: slowing of growth and a move to more marine habitat. A similar isotopic pattern was described in association with older age for the Gulf corvina, *Cynoscion othonopterus*, another sciaenid also endemic to the Gulf of California (Rowell et al., 2005); and is well documented in otolith literature (Kalish, 1991; Weidman and Millner, 2000; Campana and Thorrold, 2001). While decreased growth lowers the resolution because of less availability of sample material, during the juvenile and sub-adult period
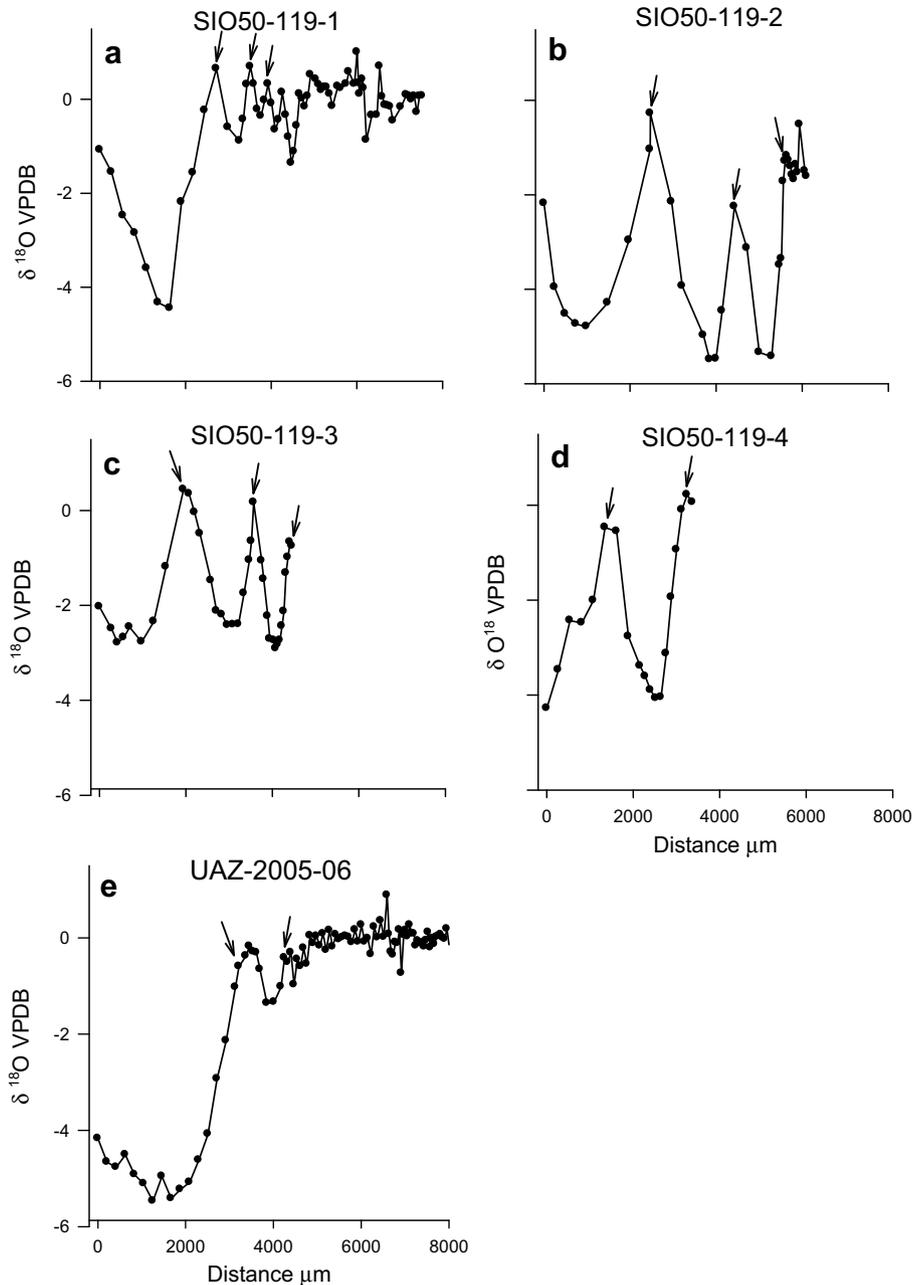
Fig. 2 – (a–e) Otolith δ¹⁸O (VPDB) profiles for pre-dam totoaba. The *x*-axis is distance (μm) from otolith nucleus to its perimeter. Arrows note the beginning of the first three visual annuli (opaque band) associated with carbonate sample. In profile (e), the third annulus was not distinct were therefore could not be distinguished visually in the area sampled. Profiles with specimen prefix "SIO" are from the San Felipe, Baja California site (∼1000 ybp), and UAZ-2005-06 is from the Bahía San Jorge, Sonora site (∼5000 ybp).

these fish (pre and post-dam) are still growing enough to capture the expected temperature-driven isotopic variation in the upper Gulf (see Rowell et al., 2005). Most summer minima in δ¹⁸O are present as adjacent pairs of samples with very similar δ¹⁸O values, implying that sampling resolution is finer than the rate of change in summer environmental conditions. The lack of difference between winter values for pre and post-dam otoliths also gives us confidence that even during the season of slower growth in both pre- and post-dam fish, we are capturing this annual marker equally. Upon reaching

maturity, totoaba make annual spawning migrations along the eastern shore of the northern Gulf of California which culminate at the Colorado River estuary, followed by a southward movement of spent adults and older juveniles mainly along the western coast of the Gulf (Flanagan and Hendrickson, 1976; Cisneros-Mata et al., 1995). This movement to more open marine waters may also explain the attenuation in seasonal variability in oxygen isotopes with age.

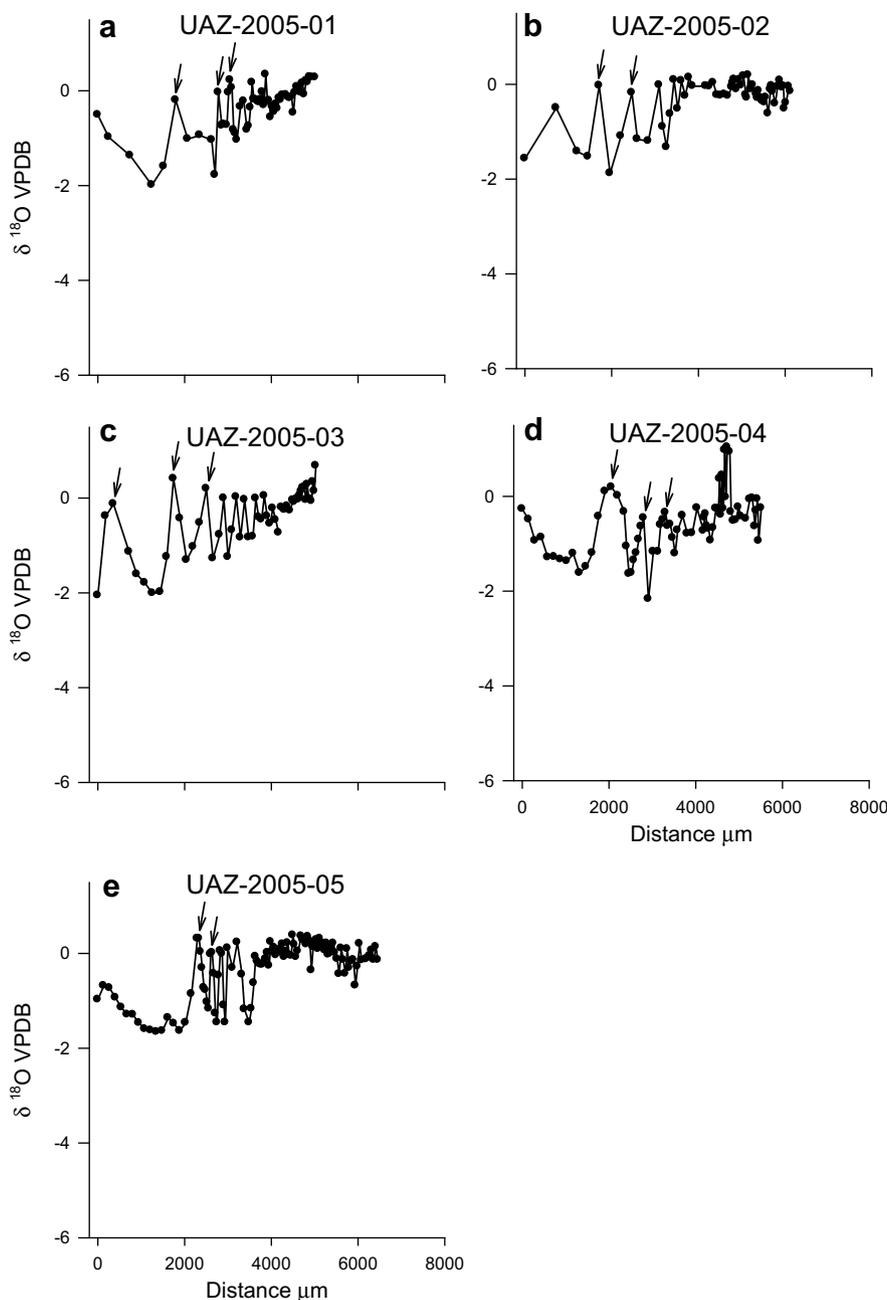Pre-dam otoliths show far greater seasonal variance in early juvenile δ¹⁸O values (within an individual as well as

Fig. 3 – (a–e) Otolith $\delta^{18}O$ (VPDB) profiles for post-dam totoaba. The x-axis is distance (μm) from otolith nucleus to its perimeter. Arrows note the beginning of the first three visual annuli (opaque band) associated with carbonate sample. For profiles (b) and (e) the first annulus was not distinct were therefore could not be distinguished visually in the area sampled.

between individuals), indicating that these individuals inhabited more isotopically heterogeneous waters, such as those typical of contemporary river-influenced estuaries where isotopically distinct continental and marine waters mix (Ingram et al., 1996; Dettman et al., 2004; Rowell et al., 2005). The post-dam $\delta^{18}O$ profiles, however, are remarkably similar among individuals, documenting that even though post-dam fish were spawned in different years, there was little $\delta^{18}O$ variability in their marine-influenced habitats.

$\delta^{18}O$ values of fish otoliths from before river diversions are significantly lower than post-dam values in the first year of development, evidence that pre-dam yearlings lived in habi-

tats strongly influenced by the Colorado River. The magnitude of the difference between pre- and post-dam values is remarkable given the limited sample size and the variance observed in the pre-dam values. In years two and three, values do not differ significantly, although the offset between them suggests that pre-dam totoaba inhabited waters less saline than post-dam individuals. Again, the pre-dam summer values for years 2 and 3 are much more variable than the post-dam values, potentially capturing the variability of their estuarine juvenile habitat before the dams. As pre-dam fish matured, their $\delta^{18}O$ values approach those seen in post-dam otoliths, suggesting that they inhabited more

Table 1 – Results (χ^2 statistic and P-value) of Kruskal–Wallis tests comparing summer pre- and post-dam totoaba otolith δ^{18}O values, winter pre- and post-dam totoaba otolith δ^{18}O values; and pre- and post-dam annual otolith growth determined by the width of chemical (δ^{18}O values) annuli and width of visual annuli for years 1, 2, and 3

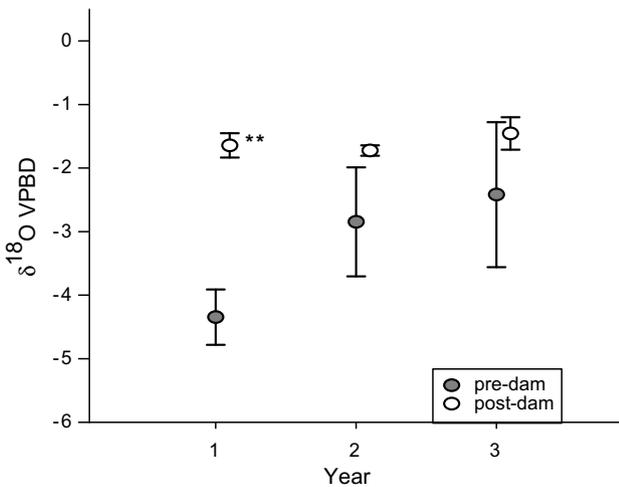| δ^{18}O Values	Summer δ^{18}O χ^2	Summer δ^{18}O P	Winter δ^{18}O χ^2	Winter δ^{18}O P
year 1	6.82	0.009	0.88	0.347
year 2	0.27	0.60	0.01	0.917
year 3	0.06	0.807	0.24	0.624
Annual Growth (μm)	δ^{18}O χ^2	δ^{18}O P	Visual χ^2	Visual P
year 1	3.94	0.047	3.98	0.047
year 2	0.10	0.754	1.32	0.251
year 3	0.33	0.960	0.06	0.807

Fig. 4 – Comparison of pre- and post-dam mean summer extreme δ^{18}O values for *T. macdonaldi* otoliths for first three years of growth. First year minima are significantly lower in pre-dam otoliths (χ^2 = 6.82, *p* > 0.009), indicating that pre-dam yearlings used nursery habitat heavily influenced by Colorado River water.
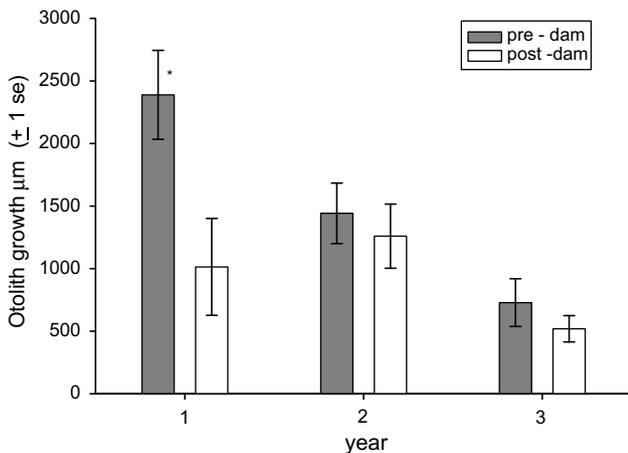

Fig. 5 – Comparison of pre- and post-dam otolith growth determined by width of δ^{18}O annuli for juvenile years 1, 2 and 3.
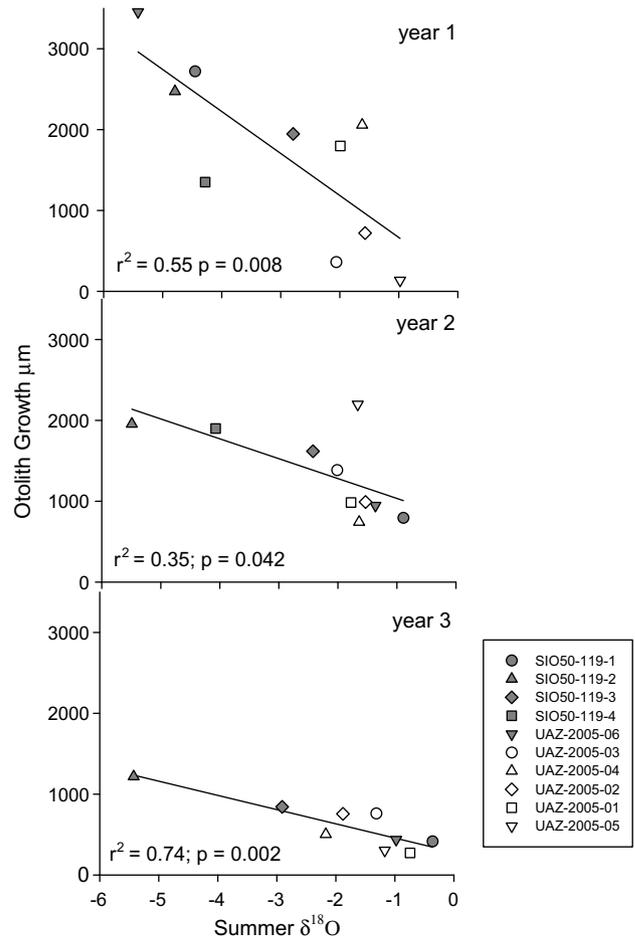

Fig. 6 – Linear regressions for annual minima (summer) δ^{18}O values and otolith growth for pre-dam (filled symbols) and post-dam (open symbols) for first three years of *T. macdonaldi* development.

marine influenced habitats as they aged. Catch records dating back to the 1920s from fishing ports in the Gulf indicate movement away from the mouth of the river with increasing age (Flanagan and Hendrickson, 1976; Barrera-Guevara, 1990; Cisneros-Mata et al., 1995).

Colorado River flow appears to be an important element of optimal habitat for juvenile totoaba: Growth rates in years 1 through 3 were positively correlated with the abundance of
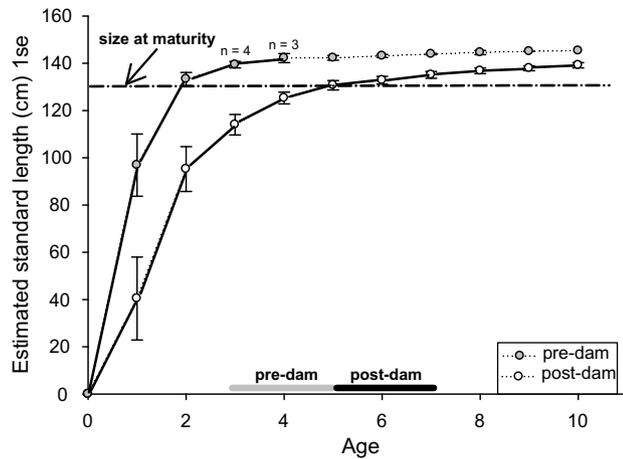
Fig. 7 – Estimated growth curve and body sizes (SL in cm ± SE) of pre- and post-dam _T. macdonaldi_. Dotted line represents _n_ = 2. Bars on _x_-axis indicate the age range where growth rates have slowed to ~21 mm/yr.

isotopically negative river water. The tight relationship between $\delta^{18}O$ and growth rates of pre- and post-dam otoliths is strong evidence that river inflow is linked to growth trajectories. Our results also highlight the importance of early growth. This is particularly obvious in post-dam fish where slowed growth in the first year seems to translate into an extension of the juvenile life-stage. While reconstructing ASM for totoaba 1000–5000 ybp has many assumptions, we found that both of our estimation methods (growth rate and size at maturation) show the same trend: much slower growth rates (roughly half) during the first year of life results in a significantly delayed maturation for totoaba.

The underlying mechanisms for increased growth of pre-dam _T. macdonaldi_ in association with Colorado River water are not yet clear, but increased growth in less saline waters occurs in several other sciaenids (Baltz et al., 1998; Lankford and Targett, 1994). Increased productivity from river-derived nutrients may increase secondary productivity and food quality enough to sustain higher growth rates. Another explanation is that larger nursery grounds created by natural river flow may decrease intra-specific competition. Before the cessation of the Colorado River, a $4000\,km^2$ area of brackishwater habitat existed in the upper Gulf of California (Carbajal et al., 1997; Lavín and Sánchez, 1999; Rodriguez et al., 2001). Today there is little, if any, trace of the Colorado River in the Gulf of California, except in anomalous years. Halpern et al. Halpern et al. (2005) reported that size of juvenile habitat can play a key role in life history dynamics and population viability, especially for long-lived species such as totoaba. Reduced river inflow has caused a drastic reduction in totoaba's estuarine spawning and nursery habitat (Flanagan and Hendrickson, 1976; Cisneros-Mata et al., 1995) and is likely a critical factor limiting recruitment.

Age at first reproduction is a critical life stage for long-lived fishes (Reynolds et al., 2005). Human-caused shifts in sexual maturation have been documented for Atlantic cod (_Gadus morhua_) and Atlantic silverside (_Menidia menidia_) where intense fishing led to selection for maturation at a younger age and a smaller size, thereby lowering fecundity (Conover and Munch,

2002; Olsen et al., 2004). Similarly, average size and age at maturity have declined in response to selective fishing pressure in Chinook salmon (_Oncorhynchus tshawytscha_), vermilion snapper (_Rhomboplites aurorubens_), and gag grouper (_Mycteroperca microlepis_) (Upton, 1992). Floeter et al. Floeter et al. (2006) also showed that increased fishing pressure selects for smaller sized predator reef fish. Here, we document a different type of human-induced shift in the life history of a fish, an apparent delay in sexual maturation caused by habitat degradation. Even if we use the more conservative estimates of ASM (based on growth rates), pre-dam totoaba fish matured on average 2 years earlier and ~80 mm larger, likely increasing their fecundity. The pre-dam estimates for ASM using today's size at maturation fish suggest that pre-dam totoaba matured at least three years earlier. The diversion of Colorado River water appears to have caused delayed maturation, which reduces lifetime fecundity, and possibly impedes the recovery of this endangered species. Today's yearling totoaba are approximately half the size of those existing before diversions of river flow to their nursery grounds. Our conclusion that the cessation of river flow has negatively impacted the totoaba is supported by others investigating the crash of the totoaba fishery (Lercardi and Chávez, 2007). Restoring river flow, perhaps even a relatively small portion of the pre-dam input, would likely aid the recovery of this long-lived fish.

Both reduced river flow and over-fishing have resulted in the endangerment of _T. macdonaldi_, yet recovery efforts to date have focused primarily on reducing _T. macdonaldi_ fishing pressure. Recovery of the totoaba will likely depend on both strict enforcement of its fishing ban and the resumption of some seasonally appropriate river inflow (i.e., higher flows in late spring-early summer) to the Colorado River's estuary. Such restoration flows would benefit other commercial species in the upper Gulf of California, such as shrimp (Galindo-Bect et al., 2000). Because approximately 90% of the river's annual flow is diverted for use in the USA, and the remaining 10% used for urban and agricultural purposes in Mexico, allocation of restoration flows for the estuary will require dedicated bi-national efforts.

The importance of river water to many marine fisheries adds complexity to managing both rivers and such fisheries. Treating rivers and marine ecosystems separately may lead to poor management of estuarine nursery grounds, with results that can cascade through marine ecosystems. Diversity in marine ecosystems has declined in response to alterations in estuaries (Lotze et al., 2006), yet when fisheries begin to decline managers rarely address the integrity of this habitat as a priority. Unfortunately, economic pressures to harness fresh water resources are increasing and further reductions in fresh-water will continue to degrade estuaries and undermine the already-fragile state of marine fisheries (Drinkwater and Frank, 1994). Recognizing and documenting the importance of rivers to the productivity of estuarine nursery habitat is critical for responsible management of the world's large rivers and their adjacent marine habitats.

Acknowledgements

R E F E R E N C E S

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