

# Upstream dams and downstream clams: growth rates of bivalve mollusks unveil impact of river management on estuarine ecosystems (Colorado River Delta, Mexico)

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## Abstract

We studied how the extensive diversion of Colorado River water, induced by dams and agricultural activities of the last 70 years, affected the growth rates of two abundant bivalve mollusk species (*Chione cortezi* and *Chione fluctifraga*) in the northern Gulf of California. Shells alive on the delta today ('Post-dam' shells) grow 5.8–27.9% faster than shells alive prior to the construction of dams ('Pre-dam' shells). This increase in annual shell production is linked to the currently sharply reduced freshwater influx to the Colorado River estuary. Before the upstream river management, lower salinity retarded growth rates in these bivalves. Intra-annual growth rates were 50% lower during spring and early summer, when river flow was at its maximum. Growth rates in *Chione* today are largely controlled by temperature and nutrients; prior to the construction of dams and the diversion of the Colorado River flow, seasonal changes in salinity played an important role in regulating calcification rates.

Our study employs sclerochronological (growth increment analysis) and geochemical techniques to assess the impact of reduced freshwater influx on bivalve growth rates in the Colorado River estuary. A combination of both techniques provides an excellent tool to evaluate the impact of river management in areas where no pre-impact studies were made.

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## 1. Introduction

Diversion and damming of rivers turned many arid and semiarid regions of the world into productive agricultural land. The upstream benefits from "reclamation" of land and irrigation were offset by immense downstream environmental costs. Reduced freshwater flow has seriously degraded wetlands and lead to loss of wildlife (e.g. Reisner, 1986; Kingsford and Thomas, 1995; Garba Boyi and Polet, 1996; Lemly et al., 2000).

However, very little is known how the near-cessation of river flow affected the ecosystem of a river's estuary.

In the present study we examine the effects of upstream river management on the biota in the Colorado River Delta. Prior to the completion of Hoover Dam (southern Nevada, USA) in 1935, the Colorado River delivered approximately 18 million cubic meters of freshwater to its estuary every year (U.S. Bureau of Reclamation). The river also supplied an unknown amount of nutrients. Hoover Dam and other upstream dams have facilitated downstream river management, including the diversion of most of the river's flow for agricultural and domestic use in the United States and in Mexico. Since the 1960s, little to no water reached the Colorado's estuary in the northern Gulf of California (Lavín and Sánchez, 1999).

Although the diversion of river water before it reaches its estuary must have had a profound effect on the marine

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biota, documentation of the effect of reduced freshwater inflow into the Colorado River Delta is made difficult by the lack of ecological surveys prior to the era of river management. Fortunately, the shells of organisms provide data that can be used to compare conditions that occurred before extensive water diversion ('Pre-dam') to 'Post-dam' conditions. Kowalewski et al. (2000) compared estimated densities of 'Pre-dam' populations of shelly invertebrates of the Colorado River Delta to densities today and concluded that the lack of river-borne nutrients today may have resulted in a 96% decrease in population size. Rodriguez et al. (2001a) used stable oxygen isotopes in shells of the once-abundant bivalve mollusk *Mulinia coloradoensis* to show that it lived in lower salinity water than present in the estuary today.

Our study presents a novel approach to "put the dead to work" (Kidwell and Flessa, 1995) at reconstructing environmental baseline conditions prior to extensive human impact. We employ sclerochronological (growth increment analysis) and geochemical techniques to reconstruct annual and seasonal growth rates in 'Post-dam' and individually dated 'Pre-dam' shells. Two common and commercially harvested species of bivalve mollusks, *Chione cortezi* (Carpenter) and *Chione fluctifraga* (Sowerby) are found alive on the delta today and both occur in 'Pre-dam' deposits. *Chione* spp. accretes aragonite layers to its shell in distinct daily, fortnightly, and annual increments. Variation in the thickness of these increments results from both ontogenetic and environmental variation (Schöne et al., 2002a). Because the timing of growth events can be dated with increment-counting, each shell has the potential to provide an ultra-high-resolution archive of past growth conditions.

Our main objectives are to determine if annual growth rates in 'Pre-dam' and 'Post-dam' specimens of *Chione cortezi* and *Chione fluctifraga* differ from each other. Do annual growth rates in specimens from near the mouth of the river differ from those specimens distant from the mouth of the river? How is the intra-annual variation in growth rates affected by the influx of Colorado River water to its estuary? What clues can be drawn from that on the seasonal timing of freshwater flow under 'Pre-' and 'Post-dam' conditions? The results of our study can help to understand the observed changes in estuarine biology (population density and faunal composition) before and after the river management.

## 2. Material and methods

The study area is the Colorado River Delta, located in the northern Gulf of California (Fig. 1). The tidal regime is semidiurnal with a mean range of about 5 m. Daily sea surface temperatures exceed 35 °C in summer and drop below 5 °C during the coldest months (satellite

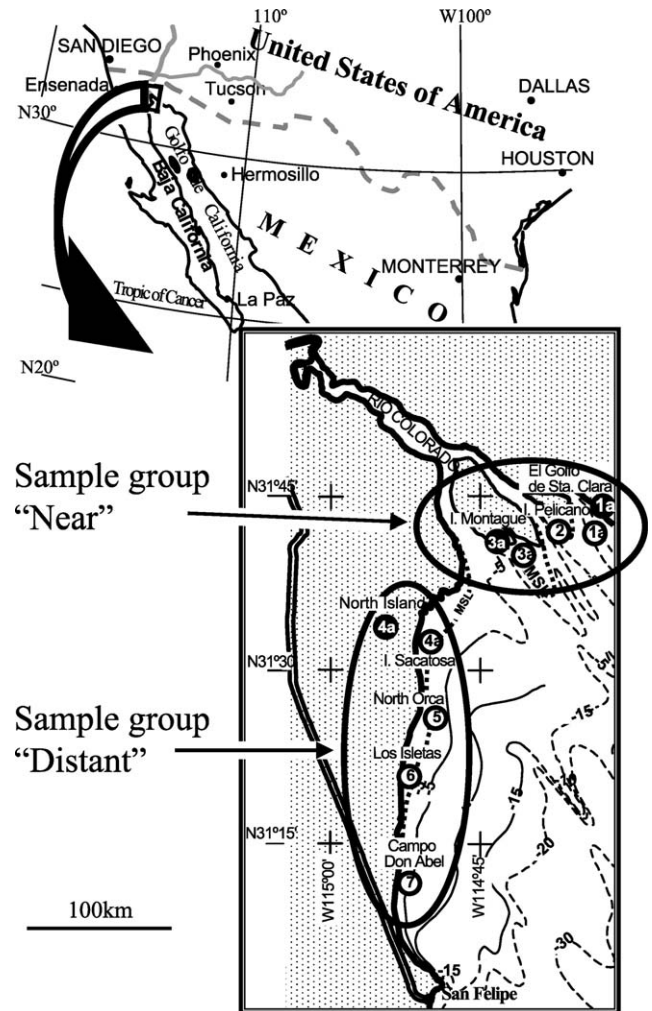


Fig. 1. Sample localities in the northern Gulf of California. Living bivalve mollusks were collected in the intertidal zone at low tide (open circles). 'Pre-dam' specimens were obtained from cheniers (filled circles). Sample group 'Near' includes localities at the Colorado mouth of the river, sample group 'Distant' localities are between 20 and 60 km away from the mouth of the river.

measurements, NCEP-NOAA/GSFC, CIRES; <http://www.cdc.noaa.gov>; see below). Precipitation rates are low (annual mean is about 60 mm, Hastings, 1964) and evaporation rates are high. Sediments range from mud to fine sands. Thompson (1968) provides an excellent description of the region's environmental setting. Salinities (measured using the practical salinity scale) today range from 35 to 45; before water diversion projects, salinities were lower, perhaps in the 32–35 range (see Glenn et al., 2001).

### 2.1. Sample material

A total of 184 *Chione* specimens (112 *Chione cortezi* and 72 *Chione fluctifraga* specimens; see Appendix A) were collected at several localities on the Colorado

Delta during various field trips between 1994 and 2000 (Fig. 1). We collected 87 ‘Post-dam’ (living) specimens at low tide from the intertidal zone and 97 single-valve ‘Pre-dam’ specimens from cheniers (shell-rich deposits, see Thompson, 1968; Kowalewski et al., 1994). The samples were categorized into eight groups by three sets of characters: species (*Chione cortezi*–*Chione fluctifraga*), age (‘Pre-dam’–‘Post-dam’) and distance to the mouth of the river (‘Near’–‘Distant’) (see Table 1). A detailed sample list is given in the Appendix A.

The character sets are defined as follows: specimens that grew near the mouth of the river are here referred to as sample group ‘Near’, specimens collected from between 25 and 60 km from the mouth of the river are placed in sample group called ‘Distant’ (Table 1). Specimens marked as ‘Post-dam’ were collected alive during no-flow conditions (as indicated by data of the U.S. Bureau of Reclamation), whereas ‘Pre-dam’ specimens must have lived within the last 1000 years: viz. prior to the construction of upstream dams. These individuals lived when freshwater flowed into the river’s estuary. The ages of 57 ‘Pre-dam’ specimens were confirmed by means of amino acid racemization dating (Kowalewski et al., 1998) and ranged from AD 950 to 1900. The remaining 30 ‘Pre-dam’ shells were excavated from the same beds. This supports our assumption that they lived before the diversion of the Colorado River as well.

## 2.2. Sample preparation

Internal growth structures, such as growth increments, are best visible in cross-sections (Fig. 2). After cleaning and coating with Devcon® High Strength Plastic Welder™, one valve of each specimen was cut along the axis of maximum growth using a low speed (Buehler® Isomet®) saw. One half of each specimen valve was ground on glass plates (600 and 1000 grit powder) and polished on laps (9, 6 and 0.3 µm) to render fine internal growth structures visible.

Table 1  
Number of specimens collected in the northern Gulf of California

Sample group	Species	Pre-dam	Post-dam	Sum
Near	<i>Chione cortezi</i>	35	51	86
	<i>Chione fluctifraga</i>	12	–	12
Distant	<i>Chione cortezi</i>	17	9	26
	<i>Chione fluctifraga</i>	33	27	60
Sum		97	87	184

‘Pre-dam’ specimens were alive before the construction of upstream dams in the 1930s. ‘Post-dam’ specimens lived during the last 10 years. Specimens of the sample group ‘Near’ grew at the mouth of the river, specimens of sample group ‘Distant’ lived from 25 to 60 km further south.

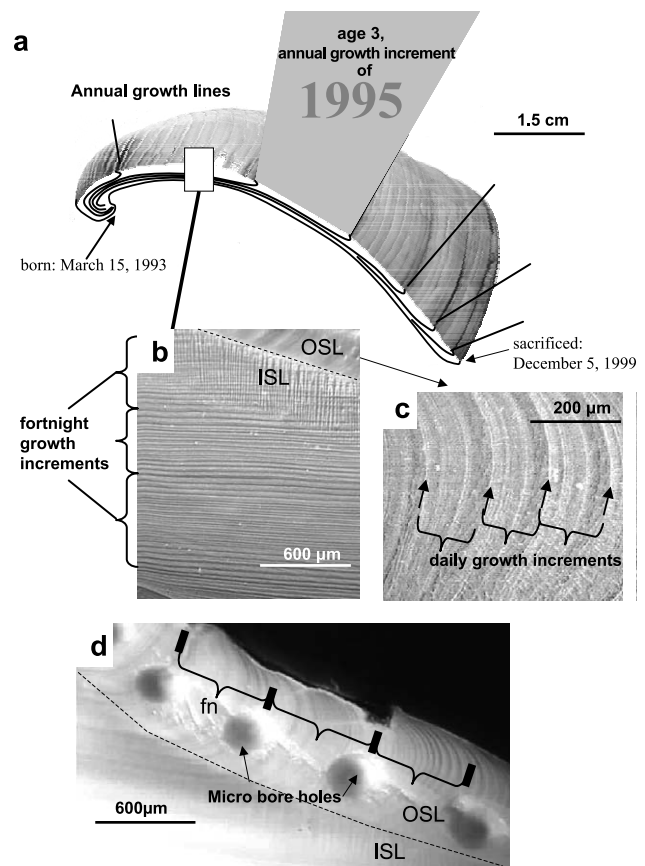


Fig. 2. Growth structures of *Chione* sp. shells. (a) Distinct growth lines on the outer shell surface reflect annual (winter) growth lines. The portion between two winter lines is referred to as annual growth increment. (b,c) At higher magnification more detailed growth structures become apparent within etched cross-sections of the shells. A clear line separates the outer shell layer (OSL) from the inner shell layer (ISL). (b) The ISL shows clear fortnight growth increments. On average, every 14 days the growth rate is at maximum. Each of the fine horizontal striations corresponds to a daily growth line. (c) Daily growth increments are best viewed on the OSL. The arrows indicate daily growth lines. (d) Microbore holes (about 300 µm diameter) were drilled in the OSL of the shells to obtain about 40–60 µg of shell powder per sample for stable isotope analyses. Fn, fortnight growth increments.

## 2.3. Growth increments and measurements

Periodic, distinct growth patterns, i.e., seasonal growth halts or growth lines, form the basis for sclerochronological (skeletal growth rate) analyses. During winter the shell growth rates of *Chione* sp. slows down or ceases and a growth line forms (annual growth break: Fig. 2). These growth lines separate the growth into time intervals of approximately equal duration and can be used for many purposes, including determining the age of an individual bivalve mollusk. The portion between two winter lines is referred to as annual growth increment and is best visible in the outer shell layer (Fig. 2a). Favorable environmental conditions (for instance, prevailing optimal growth temperatures of 25 °C or



higher supply of food) can increase the length of the growing season as well as the shell growth rates and hence the width of growth increments. At higher magnification, microincrements become visible which were demonstrated to form regularly as well, i.e. daily (Fig. 2c) and fortnight growth increments (Fig. 2b). For further information on growth rates in *Chione* spp. refer to the work by Schöne et al. (2002b).

In this study we measured the widths of the second annual growth increments (first winter band to second winter band) of 180 shells under a reflected light microscope using an eyepiece scale to the nearest 50  $\mu\text{m}$ . We measured the second annual growth increments, because some specimens used in the present study were only three years old and died before the completion of the third annual growth increment. In addition, we determined fortnight increment widths in the third year of growth in 10 *Chione cortezi* specimens and in the second year in one *C. cortezi* specimen. Measurements were to the nearest 5  $\mu\text{m}$ . We measured fortnightly growth increments in five 'Pre-dam' specimens (IM4-D44, IM4-D40, IM4-D2, SC2-D3, and NI1-D6) and six 'Post-dam' specimens (IM11-A1, IM11-A2, IM9-A4, IP1-A1, EG1-A2, and ST8-A2). Specimen ST8-A2 was alive in 1998 and specimen IM9-A4 in 1993—these represent years during which controlled freshwater releases occurred early in the year.

#### 2.4. Data analysis

We compared 'Pre-dam' with 'Post-dam' groups and 'Near' with 'Distant' groups of both *Chione cortezi* and *Chione fluctifraga*. The Wilcoxon Mann–Whitney test is used to test whether the group means are significantly different from each other. We used this non-parametric test, because it does not require the assumption that the population is normally distributed. The null hypothesis (=no difference between the medians) is rejected for  $p$ -values smaller than 0.05.

#### 2.5. Oxygen isotope analysis

We examined oxygen isotope variation in four shells in order to evaluate the effect of water temperature and freshwater influx on growth rates. In shells grown in the absence of river water, isotopic variation is largely a function of the ambient temperature (Goodwin et al., 2001), where a one permil shift in the  $\delta^{18}\text{O}$  of the molluscan aragonite results from a temperature change of 4.34  $^{\circ}\text{C}$  (Grossman and Ku, 1986). The addition of river water lowers the  $\delta^{18}\text{O}$  of the water in the estuary's mixing zone, because river water is typically more negative ( $-3$  to  $-20\text{‰}$ ) than sea water ( $0\text{‰}$ ) (Rozanski et al., 1993). Changes in the  $\delta^{18}\text{O}$  of the water are directly recorded in the shell during growth. If the local water changes by  $1\text{‰}$ , due to freshwater inflow, for

example, shell material growing in that water will also change by  $1\text{‰}$ . Thus, isotopic variation below the temperature-driven variation indicates the addition of river water to the estuary (see Dodd and Stanton, 1975; Ingram et al., 1996; Rodriguez et al., 2001a for other applications of stable isotope studies in environmental reconstruction).

For oxygen isotope analysis, the valves of the two 'Pre-dam' (IM4-D44, NI1-D6) and two 'Post-dam' *Chione cortezi* specimens (IP1-A1, ST8-A2) were bathed several times ultrasonically with deionized water prior to sampling. The outer shell layer (prismatic layer) was sampled using a 300  $\mu\text{m}$  drill under a binocular microscope (Fig. 2d). The number of daily increments sampled varied from 3 to 40. Eight to 22 microsamples were taken from each shell. Each of the 58 drill holes yielded 50–200  $\mu\text{g}$  of carbonate for isotopic analysis. An automated carbonate extraction system is used to process the samples (KIEL III<sup>TM</sup> by Finnigan Mat<sup>®</sup>).  $\delta^{18}\text{O}$  is reported relative to V-PDB on a NBS-19 value of  $-2.20\text{‰}$ . Precision is better than  $0.1\text{‰}$ .

#### 2.6. Environmental data

We obtained daily sea surface temperature data for the 1990s from satellite measurements (<http://www.cdc.noaa.gov/>; last accessed on April 18, 2002) from the National Centers for Environmental Prediction (NCEP), a division of the National Oceanic and Atmospheric Administration/Goddard Space Flight Center (NOAA/GSFC) and The Cooperative Institute for Research in Environmental Sciences (CIRES). The data were smoothed with a fifth order polynomial. This effectively removes high-frequency variation from the time-series. Phytoplankton pigment concentration data acquired by the SeaWiFS project (Sea-viewing Wide Field-of-view Sensor data) were obtained from NASA/GSFC homepage (<http://seawifs.gsfc.nasa.gov/seawifs.html>; last accessed on April 18, 2002). Monthly Colorado River flow was recorded by the Yuma Area Office of the Bureau of Reclamation, US Department of Interior.

### 3. Results

#### 3.1. 'Pre-dam' and 'Post-dam' shell growth rates

At the same locality, *Chione cortezi* grows significantly faster today than prior to the construction of upstream dams (Fig. 3). Mean annual increment widths of two-year-old 'Post-dam' shells (no-flow condition) near the mouth of the river exceed annual growth rates of 'Pre-dam' shells by 0.6 cm (=27.9%;  $p < 0.0001$ ; Fig. 3).

Growth rate differences between 'Post-' and 'Pre-dam' shells that grew 20–60 km away from the mouth of the

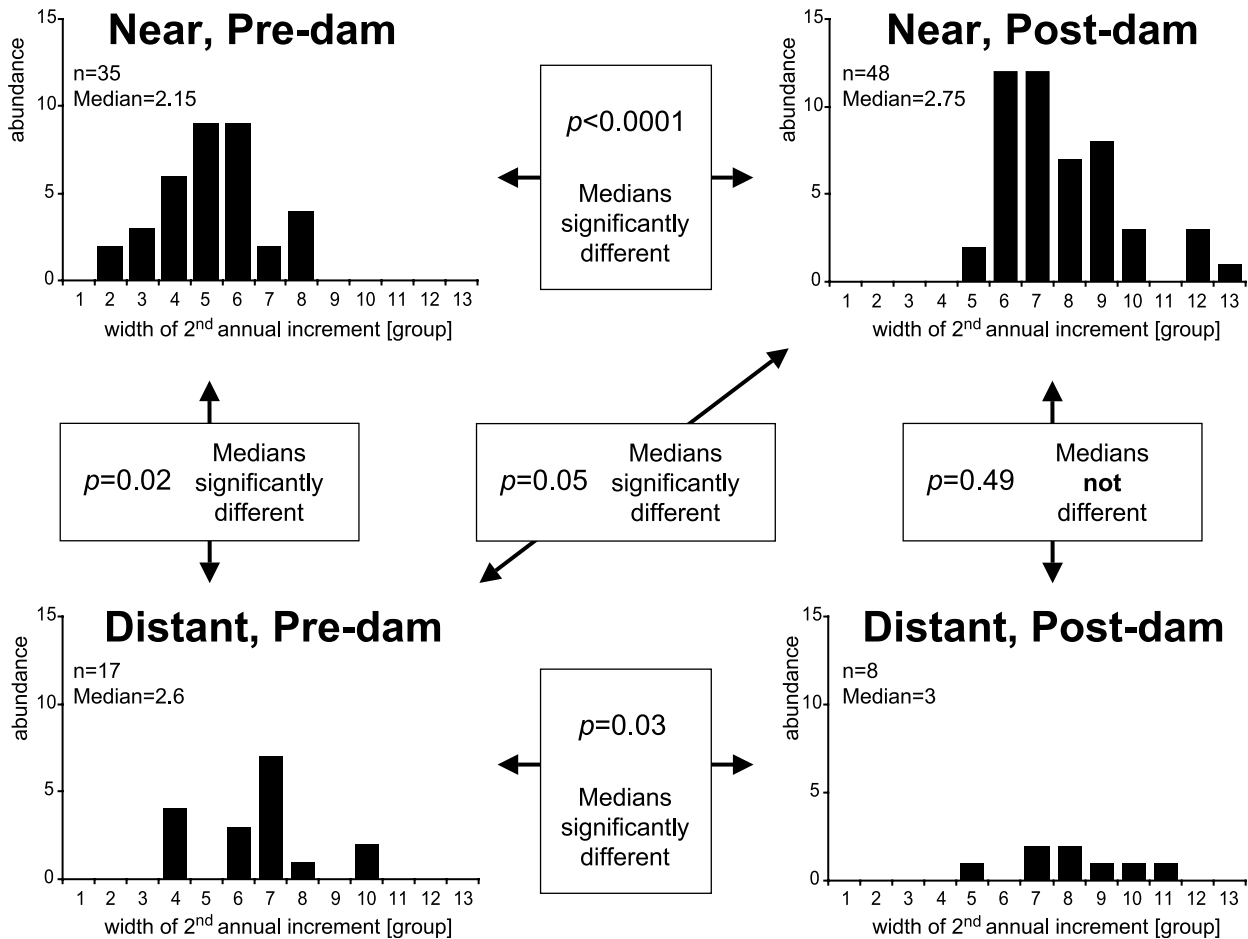


Fig. 3. Annual growth rates in *Chione cortezi*. Groups 1–13 of second annual increment widths are as follows: <1.25, 1.26–1.50, . . . 3.76–4.0, >4.01 cm. Growth rates of *C. cortezi* specimens living at the mouth of the river are today higher than prior to the construction of upstream dams ( $p < 0.0001$ ). This is also true for localities farther away from the mouth of the river ( $p = 0.03$ ). Today no significant difference exists in growth rates in ‘Near’ and ‘Distant’ specimens ( $p = 0.49$ ). Before the Colorado River was dammed and diverted, ‘Distant’ *C. cortezi* specimens grew at higher rates than specimens at the mouth of the river ( $p = 0.02$ ). Specimens at the mouth of the river today grow significantly faster than southern ‘Pre-dam’ specimens ( $p = 0.05$ ).

river are less dramatic, but still significant (Fig. 3;  $p = 0.03$ ). ‘Post-dam’ specimens in the ‘Distant’ samples indicate an average increase of 0.4 cm per year (=15.4%) compared to ‘Pre-dam’ specimens at this geographic position.

Today’s ‘Near’ and ‘Distant’ *Chione cortezi* shells do not grow at significantly ( $p = 0.49$ ) different rates (Fig. 3). Prior to the construction of dams, however, ‘Distant’ specimens grew on average 20.9% (=0.45 cm) faster during the second year than their ‘Near’ relatives (Fig. 3;  $p = 0.02$ ).

Today, the largest *Chione cortezi* specimens near the mouth of the river attain slightly higher growth rates (average increase per year: 0.15 cm = 5.8%) than the fastest growing ‘Pre-dam’ shells that lived 20–60 km distant from the mouth of the river (Fig. 3;  $p = 0.05$ ).

Because we found no living *Chione fluctifraga* specimens at the mouth of the river, we cannot compare ‘Pre-’ and ‘Post-dam’ growth rates in this species. *Chione fluctifraga* is abundant 20–60 km south to the mouth of

the river today and grows 13.5% faster (=0.25 cm) than ‘Pre-dam’ specimens at this location (Fig. 4;  $p = 0.01$ ). Under ‘Pre-dam’ conditions, ‘Near’ and ‘Distant’ *C. fluctifraga* specimens grew at statistically indistinguishable rates during their second year (Fig. 4;  $p = 0.52$ ).

### 3.2. Intra-annual growth patterns and oxygen isotope variation

The typical intra-annual growth pattern in a three-year-old *Chione cortezi* specimen (IP1-A1) under ‘Post-dam’ (1991), no-flow condition, is shown in Fig. 5a (see also Schöne et al., 2002b; Goodwin et al., 2001). Growth starts in March and reaches its maximum rate of almost 3 mm per fortnight when daily water temperatures reach 25 °C. As water temperatures continue to rise, the growth rate decreases sharply and reaches a minimum in the hottest month (August). Growth rates slightly increase when water temperatures cool down to daily averages of about 25 °C again during fall. As temperatures drop

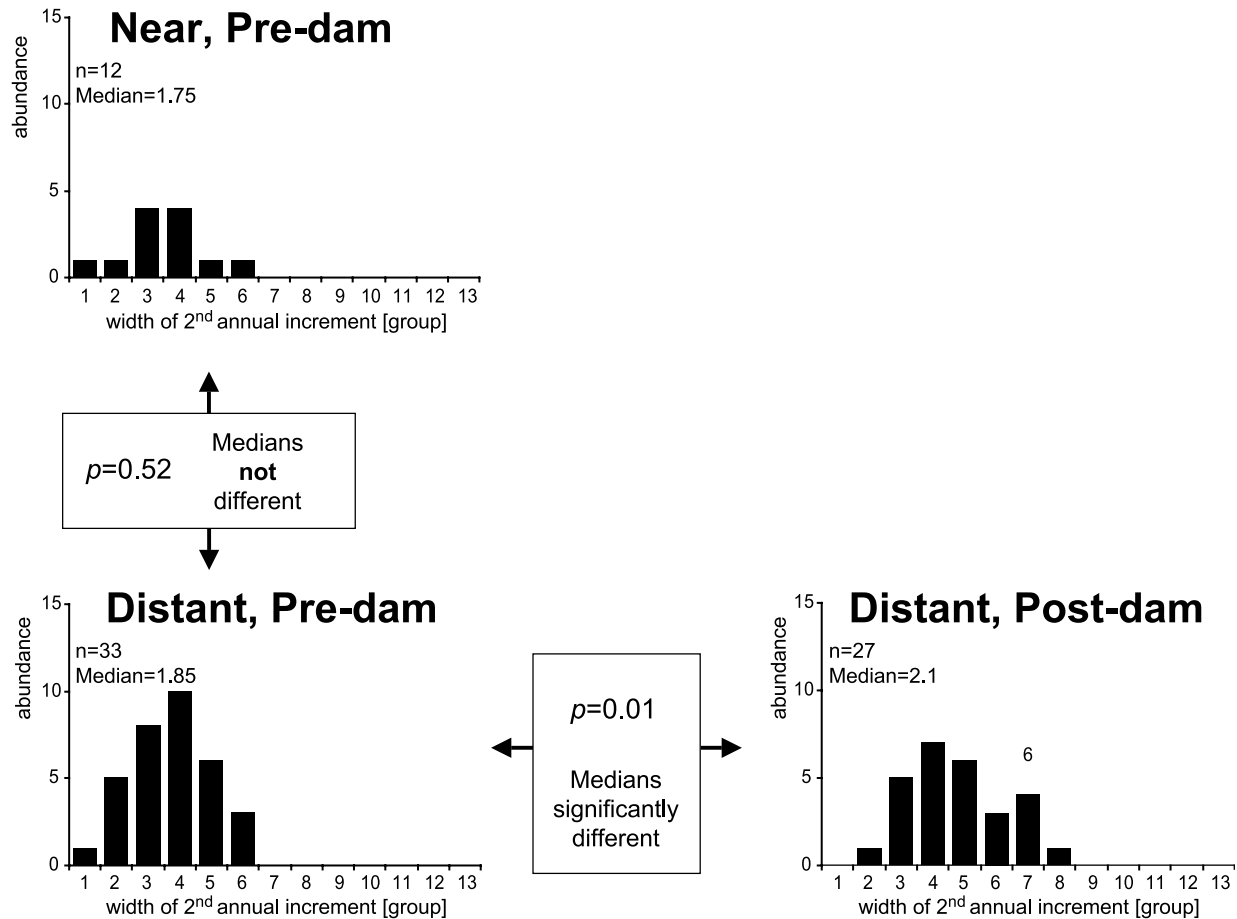


Fig. 4. Annual growth rates in *Chione fluctifraga*. Groups 1–13 of second annual increment widths are as follows: <1.25, 1.26–1.50, . . . 3.76–4.0, >4.01 cm. Growth rates of southern *C. fluctifraga* specimens today are higher than ‘Pre-dam’ specimens ( $p = 0.01$ ). Annual growth rates in ‘Pre-dam’ *C. fluctifraga* specimens living near the mouth of the river were not significantly lower than in specimens at distant sites ( $p = 0.52$ ).

below about 16 °C, the growth may stop for several months during winter, especially in older specimens. The growth increment time-series was arranged so that (1) the maximum growth rates occur in April/May when water temperatures reach about 25 °C and (2) the most negative  $\delta^{18}\text{O}$  values overlap occur at highest measured water temperatures during the hot summer.

The intra-annual oxygen isotope profile of the shell (Fig. 5a) is similar to other live-collected *Chione* spp. specimens in the northern Gulf of California (e.g., Goodwin et al., 2001) with  $\delta^{18}\text{O}$  values ranging from  $-2.47$  to  $0.91\text{‰}$ , corresponding to a water temperature range of 30.45–15.78 °C.

In early 1998, a significant amount of freshwater was released to the Colorado River Delta (Fig. 5b). The peak flow at the end of February 1998 exceeded 735,000,000  $\text{m}^3$  (= 600,000 acre-feet) of river water and is recorded in a  $-1.72\text{‰}$  anomaly in the  $\delta^{18}\text{O}$  profile of a live-collected shell (ST8-A2) belonging to the ‘Distant’ group (Fig. 5a). During the maximum river discharge, fortnightly growth rates reached a minimum. Growth resumed quickly thereafter and reached an all-time growth maximum of slightly more than 2 mm per fortnight,

then slowed during May and early June, increased at the end of July and decreased sharply when daily temperatures rose above 30 °C in the summer. A smaller growth increase occurred in the fall. Intra-annual dating of this specimen is based on daily increment counts from the ventral margin (collected alive on Nov. 12, 1998) towards the umbo.

Similar growth reductions occur in a live-collected *Chione cortezi* shell (IM9-A4) belonging to the ‘Near’ group during a freshwater release in 1993 (Fig. 5c). A  $-3.24\text{‰}$  anomaly in the  $\delta^{18}\text{O}$  profile of this specimen records the maximum flow rate of 1.47 billion cubic meters (=1.2 million acre-feet) of river water in March 1993. During the freshwater influx—large releases carried on for the months of February to May—growth rates were at minimum. As the freshwater discharge decreased in May and June, growth rates suddenly increased. However, maximum growth rates during optimal growth temperatures in May and June barely exceeded 2.3 mm per fortnight. This is about 20% less than the maximum growth rates found in the third year of growth of specimen IP1-A1R during no river flow. Growth rates then decreased as the temperatures went

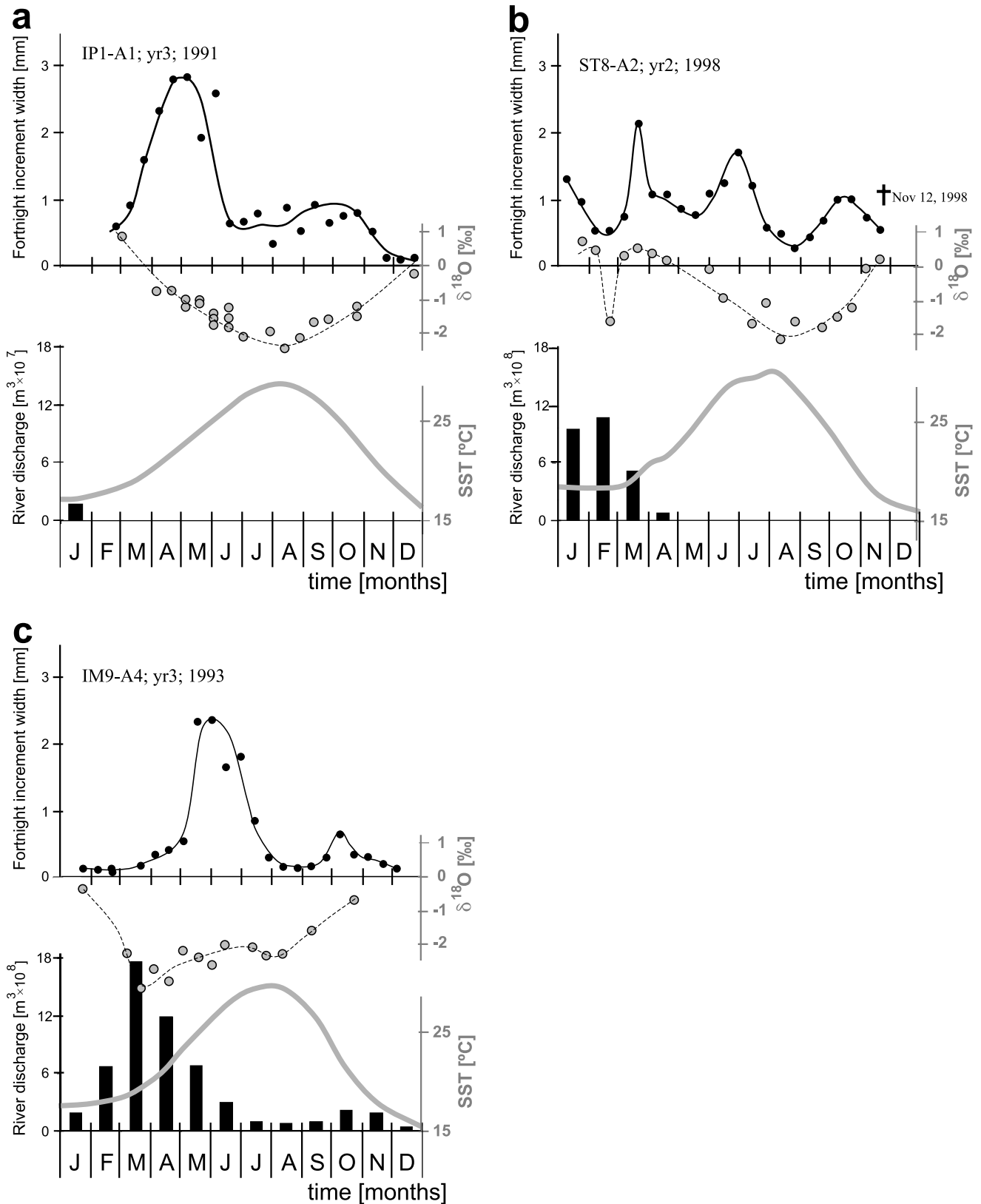


Fig. 5. Intra-annual growth patterns and  $\delta^{18}\text{O}$  profiles of today's *Chione cortezi*, daily sea surface temperatures (smoothed with a fifth order polynomial) and monthly river flow data. (a) Under today's ('Post-dam') no-flow conditions, growth rates are at maximum during spring. During hot summer growth rates are reduced due to high temperatures. At optimum growth temperatures (25 °C) in fall, growth rates are slightly elevated, but not as high as earlier in the year. The  $\delta^{18}\text{O}$  values of the shell reflect a temperature-driven oxygen isotope profile. (b) The controlled river water release in February 1998 is associated with a sharp drop in growth rate and with a negative excursion of the  $\delta^{18}\text{O}$  of the shell of the 'Distant' specimen. Thereafter, growth resumed quickly and exceeded growth rates typical for this time of the year. We have no explanation for the growth rate decline in April and May in these specimens. (c) A freshwater release early in 1993 resulted in low growth rates and a negative excursion of the  $\delta^{18}\text{O}$  of the shell.

up during the hot summer. A small fortnightly growth peak (0.7 mm) was reached during fall. Intra-annual dating of this specimen is based on daily increment counts from the ventral margin towards the umbo.

Intra-annual growth under 'Pre-dam' conditions is documented in two three-year-old *Chione cortezi* specimens. One specimen (IM4-D44) lived at the mouth of the river between 1650 and 1699 AD (Fig. 6a; amino acid racemization dating), the other specimen (NI1-D6) at a distance of about 20 km from the mouth of the river between 1450 and 1499 AD (Fig. 6b). In both shells, the growth rate decreased during maximum river flow in June. Maximum growth rates during spring barely exceeded 1.5 mm per fortnight. After the hot summer slowdown, growth rates reached similar values to those in the previous spring. Based on findings in recent shells, the growth curves of these specimens were arranged so that (1) the growth starts in January and stops in November/December and (2) the most negative  $\delta^{18}\text{O}$  values occur during early summer when river flow was presumably at maximum. The uncertainty of dating is about two to four weeks.

The  $\delta^{18}\text{O}$  values in specimen IM4-D44 (Fig. 6a) that lived near the mouth of the river are more negative than those in specimen NI1-D6 (Fig. 6b).

### 3.3. Evaluation of the clam's intra-annual growth under 'Post-dam' and 'Pre-dam' conditions

Under 'Post-dam' conditions during springtime *Chione cortezi* specimens at the mouth of the river grow faster than under 'Pre-dam' conditions (Fig. 7). 'Pre-dam' shells add, on average, about 1 mm of shell material per fortnight to their valves in spring, whereas 'Post-dam' shells grow almost twice as fast in the same season. At optimal growth temperatures in the fall, 'Post-dam' *Chione cortezi* specimens grow on average at only half the rate achieved in spring, but 'Pre-dam' shells have similar growth rates in fall and spring. No difference, however, exists between 'Pre-dam' and 'Post-dam' shell growth rates during the fall season.

## 4. Discussion

### 4.1. 'Pre-dam' and 'Post-dam' shell growth rates

*Chione cortezi* and *Chione fluctifraga* grow much faster today than under 'Pre-dam' conditions. These results suggest that the increased growth rates in *Chione* spp. are linked to the cessation of freshwater influx. Maybe, *Chione* spp. prefers today's normal to slightly hypersaline conditions in the northern Gulf of California over the brackish conditions in 'Pre-dam' times. Higher amounts of gill-clogging fine-grained sediments

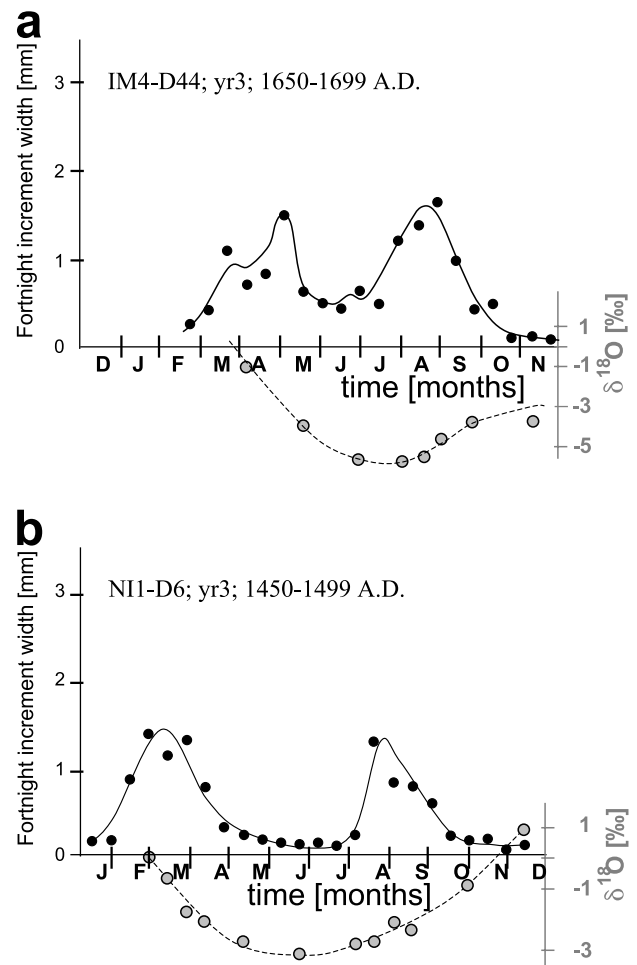


Fig. 6. Intra-annual growth patterns and  $\delta^{18}\text{O}$  profiles of 'Pre-dam' *Chione cortezi*, which grew under the influence of constant freshwater flow. Similar growth rates were reached in spring and fall. (a) Specimen IM4-D44 grew near the mouth of the river. The  $\delta^{18}\text{O}$  values of the shell are much more negative than today (see Fig. 5) and driven by changes in both salinity and temperature. (b) Specimen NI1-D6 was collected about 20 km south of the mouth of the river. The  $\delta^{18}\text{O}$  values of the shell are lower than today (see Fig. 5), but not as negative as in shells that grew near the mouth of the river (Fig. 6a) indicating an enhanced mixing of river water with sea water in some distance to the mouth of the river (see also Rodriguez et al., 2001b).

delivered to the delta during 'Pre-dam' times may have inhibited shell growth.

The growth rate of 'Pre-dam' *Chione cortezi* specimens is greater in sites distant from the mouth of the river. This is likely the result of increasing salinity with increasing distance from the mouth of the river (see also Rodriguez et al., 2001b). In contrast, irrespective of their geographic position, *Chione* specimens today do not grow at significantly different rates. Variation in salinity and/or amounts of fine-grained sediments appears to explain the variation in growth rates between 'Pre-dam' and 'Post-dam' *Chione* spp., and between 'Pre-dam' *Chione cortezi* living near the mouth of the river and those distant from the mouth of the river. It remains unclear why 'Near' and 'Distant' *Chione fluctifraga* shells



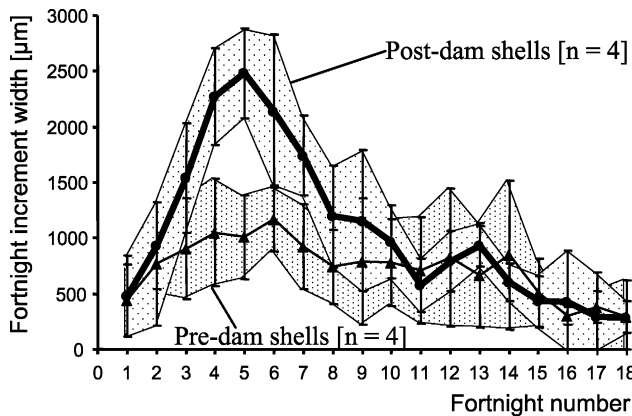


Fig. 7. Comparison of intra-annual growth rates in 'Pre-dam' and 'Post-dam' shells at the mouth of the river. The length of growing season is almost the same in all specimens. We arranged the intra-annual time-series so that the first and last fortnight increments overlap with each other. Today (no-flow conditions), the springtime growth rates of *Chione cortezi* are greater than prior to the construction of dams. Filled circles and triangles represent the means of fortnight increments, the bars indicate their standard deviations.

do not grow at significantly different rates under 'Pre-dam' conditions.

#### 4.2. Growth under controlled freshwater flow

Intra-annual growth patterns and oxygen isotope profiles reveal the direct impact of reduced salinity on growth rates. The 1993 and 1998 controlled freshwater releases resulted in a sudden drop in shell growth and sharply negative  $\delta^{18}\text{O}$  excursions in shell carbonate (Fig. 5). These anomalous  $\delta^{18}\text{O}$  values are about 2‰ (ST8-A2; Fig. 5b) and 3.3‰ (IM9-A4; Fig. 5c) more negative than expected for a solely temperature-driven oxygen isotope ratio (average sea surface temperatures during freshwater release was about 18.4 °C,  $\sim 0.3\text{‰}$  for ST8-A2, Fig. 5b and 19.1 °C,  $\sim 0.15\text{‰}$  for IM9-A4, Fig. 5c). The adverse effects of low salinity waters on marine bivalve mollusks have been reported in previous papers: (1) Marsden and Pilkington (1995) noted reduced growth rates and smaller maximal sizes of *Austrovenus stutchburyi* Finlay in estuarine settings (Avon-Heathcote estuary, New Zealand) compared to marine environments; (2) Navarro (1988) found that extended periods of valve closure and reduced oxygen uptake associated with lower salinities could explain reduced growth rates in *Choromytilus chorus* (Molina) in the estuaries of southern Chile.

Aside from salinity changes, riverine freshwater flow also governs the nutrient availability in the Colorado's estuary. The reduction in growth rate in ST8-A2 associated with river input is followed by a significant increase in the growth rate approximately four weeks after the peak discharge. We suspect that this increase in growth rate is controlled by more than simply the return

to normal marine conditions because *Chione* spp. never grows at rates of 2 mm/fortnight at temperatures below 20 °C (Schöne et al., 2002a,b). The pulse of freshwater may have provided extra nutrients for an enhanced springtime phytoplankton bloom (cf. Smetacek, 1986; Jordan et al., 1991) that, in turn, supported higher shell growth rates. It is known that sudden higher amounts of phytoplankton can increase bivalve mollusks' growth rates significantly (Ansell, 1968; Sato, 1997). Unfortunately, reliable phytoplankton data for the study area are not available to test this idea. Although SeaWiFS data on phytoplankton pigment concentration in the Gulf of California have been recorded since 1997, the spatial and temporal resolution of the data is too poor to detect a temporary and localized phytoplankton bloom. Nor do the few shipboard measurements (Millán-Núñez et al., 1999) provide adequate data to test this idea.

#### 4.3. Intra-annual growth under 'Post-dam' and 'Pre-dam' flow

Seasonal variation in growth rates is very different in 'Pre-dam' and 'Post-dam' shells. Before dams and extensive water diversions, maximum spring and fall growth rates were approximately the same,  $\sim 1$  mm/fortnight. After extensive diversion of the Colorado River water for human use, spring growth rates doubled, while fall growth rates remained the same (Fig. 7). We suspect that the lowered salinity of the estuary during the arrival of the spring snowmelt during the 'Pre-dam' era suppressed growth rates in the two species of *Chione*, but that the lower river discharge in the fall was not sufficient to suppress growth. Since the dams and diversions, normal and even slightly hypersaline conditions have allowed the bivalves to benefit from the springtime peak in productivity.

#### 4.4. Changes in benthic productivity and faunal composition

Before the dams, the Colorado River may have delivered substantial amounts of nutrients to its estuary and the northern Gulf of California. Thus, in the 'Pre-dam' period, productivity may have been much higher than today. Indeed, Kowalewski et al. (2000) attribute the massive (up to 96%) decline in population density of bivalves following extensive water diversion to the loss of river-borne nutrients. More direct evidence supporting the role of the river in supplying nutrients comes from Galindo-Bect et al.'s (2000) study of northern Gulf of California shrimp catches. They noted a positive correlation between controlled river discharges and the size of the following year's shrimp catch. If a drastic drop in nutrient supply is the only result of the diversion of Colorado River water, then its effects are not evident

in increase in growth rates of *Chione cortezi* and *Chione fluctifraga* since the 'Pre-dam' era. Clearly, salinity was a more important limiting factor, directly and indirectly, than nutrient supply in regulating the growth rates of these two species.

Salinity, and perhaps nutrient supply, affected another species of bivalve mollusk on the Colorado River Delta. Rodriguez et al. (2001a) showed that the now rare *Mulinia coloradoensis* Dall thrived during the 'Pre-dam' era, when salinity was lower (and presumably nutrients were much higher).

Although *Chione cortezi* and *Chione fluctifraga* are more abundant today than in accumulations of 'Pre-dam' shells (Kowalewski et al., 1994), their present density is much lower than the density of 'Pre-dam' populations of *Mulinia coloradoensis*. This suggests that the two species of *Chione* have not simply replaced *M. coloradoensis*, but that the abundance of the two species of *Chione* is limited by the lack of nutrients in the 'Post-dam' era while it was limited by low salinity during the 'Pre-dam' era.

## 5. Conclusions

Sharply reduced freshwater discharges to the Colorado River estuary have led to increased growth rates in the bivalves *Chione cortezi* and *Chione fluctifraga*. Before the construction of dams and the diversion of river water, the mixing of river water with seawater reduced salinity and retarded growth rates in these bivalves. In the current 'Post-dam' era, growth rates reach their annual maximum during the spring and early summer, with a much smaller pulse of growth during the fall season. Intra-annual growth rates in 'Pre-dam' shells were significantly lower during the spring and early summer, when river discharge was near its maximum. Although other studies have suggested that influx of Colorado River water to its estuary increased productivity (Galindo-Bect et al., 2000; Kowalewski et al., 2000), the adverse effects of lowered salinity clearly outweighed the benefits of higher nutrient supply for *C. cortezi* and *C. fluctifraga*.

Application of sclerochronological and geochemical techniques permit the assessment of the impact of reduced freshwater influx on bivalve growth rates in the Colorado River estuary. Such techniques can be applied to evaluate the impact of river management in areas where no pre-impact studies were made.

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## Appendix A

### A.1. Annual increment measurements ( $\Sigma = 180$ )

Legend: locality, sample ID, lat/long, date of collection, specimen #

Sample group 'Near' [ $\Sigma = 95$  shells]

*Chione cortezi*, dead collected (Pre-dam) [ $\Sigma = 35$  shells; Fig. 2a, d]

Isla Montague, IM4-bulk: N31 41.2, W114 43.5, Feb. 1997 (4)

El Golfo de Santa Clara, SC1-bulk: N31 44.5, W114 33.9, Feb. 1997 (31)

*Chione cortezi*, live collected (Post-dam) [ $\Sigma = 48$  shells; Fig. 2a, c, e]

Isla Montague, IM2-bulk: N31 40.3, W114 41.4, Feb. 1997 (35)

Isla Montague, IM7-bulk: ~N31 40, ~W114 41, Feb. 1998 (10)

Isla Montague, IM9-bulk: N31 39.9, W114 41.72, Feb. 1999 (3)

*Chione fluctifraga*, dead collected (Pre-dam) [ $\Sigma = 12$  shells; Fig. 3b]

North Island, NI1-bulk: N31 34.2, W114 53.0, Nov. 1996 (12)

Sample group 'Distant' [ $\Sigma = 85$  shells]

*Chione cortezi*, dead collected (Pre-dam) [ $\Sigma = 17$  shells; Fig. 2b, d, e]

North Island, NI2: N31 34.2, W114 53.0, Nov. 1996 (17)

*Chione cortezi*, live collected (Post-dam) [ $\Sigma = 8$  shells; Fig. 2b, c]

North Orca, NO6-bulk: N31 20, W114 53, Dec. 1994 (2)

Isla Sacatosa, ST2: N31 32.6, W114 52.6, 1997 (2)

Isla Sacatosa, ST11-bulk, N31 30.35, W114 50.47, Dec. 2000 (2)

Los Isletas, LS1: N31 21.7, W114 51.9, Nov. 1998 (1)

Campo Don Abel, DA1: N31 11.7, W114 53.2, Nov. 1997 (1)

*Chione fluctifraga*, dead collected (Pre-dam) [ $\Sigma = 33$  shells; Fig. 3a, b]

North Island, NI1-bulk: N31 34.2, W114 53.0, Nov. 1996 (33)

*Chione fluctifraga*, dead collected (Pre-dam) [ $\Sigma = 27$  shells; Fig. 3a]  
 Isla Sacatosa, ST12-bulk: N31 30.2, W114 50.5, Dec. 2000 (19)  
 Isla Sacatosa, ST1: N31 30.2, W114 51.5, 199? (1)  
 Isla Sacatosa, ST13-A1: N31 30.3, W114 51.6, Nov. 1996 (1)  
 Los Isletas, LS2-bulk: N31 30.2, W114 51.5, Nov. 1999 (3)  
 NO4-bulk: N31 20.75, W114 52.25, 199? (3)

## A.2. Fortnight increment measurements ( $\Sigma = 11$ )

### *Chione cortezi*

North ('Near') [ $\Sigma = 9$  shells]  
 Isla Montague, IM11-A1 and IM11-A2: N31 40.22, W114 41.41, Feb. 2000 [Fig. 6]  
 Isla Montague, IM9-A4: N31 39.997, W114 41.72, Feb. 1999 [Figs. 4c, 6]  
 Isla Montague, IM4-D2: N31 41.2, W114 43.5, 1750–1799 AD [Fig. 6]  
 Isla Montague, IM4-D44: N31 41.2, W114 43.5, 1650–1699 AD [Figs. 5a, 6]  
 Isla Montague, IM4-D40: N31 41.2, W114 43.5, 1850–1899 AD [Fig. 6]  
 Isla Pelicano, IP1-A1: N31 45.7, W114 38.9, spring 1996 [Figs. 4a, 6]  
 El Golfo de Santa Clara, EG1-A2: locality unknown: purchased on market 1997 [Fig. 6]  
 El Golfo de Santa Clara, SC2-D3: N31 44.0, W114 33.6, 1200–1249 AD [Fig. 6]  
 South ('Distant') [ $\Sigma = 2$  shells]  
 Isla Sacatosa, ST8-A2: N31 29.6, W114 50.5, Nov. 1998 [Fig. 4b]  
 North Island, NI1-D6: N31 34.2, W114 53.0, 1450–1449 AD [Fig. 5b]

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