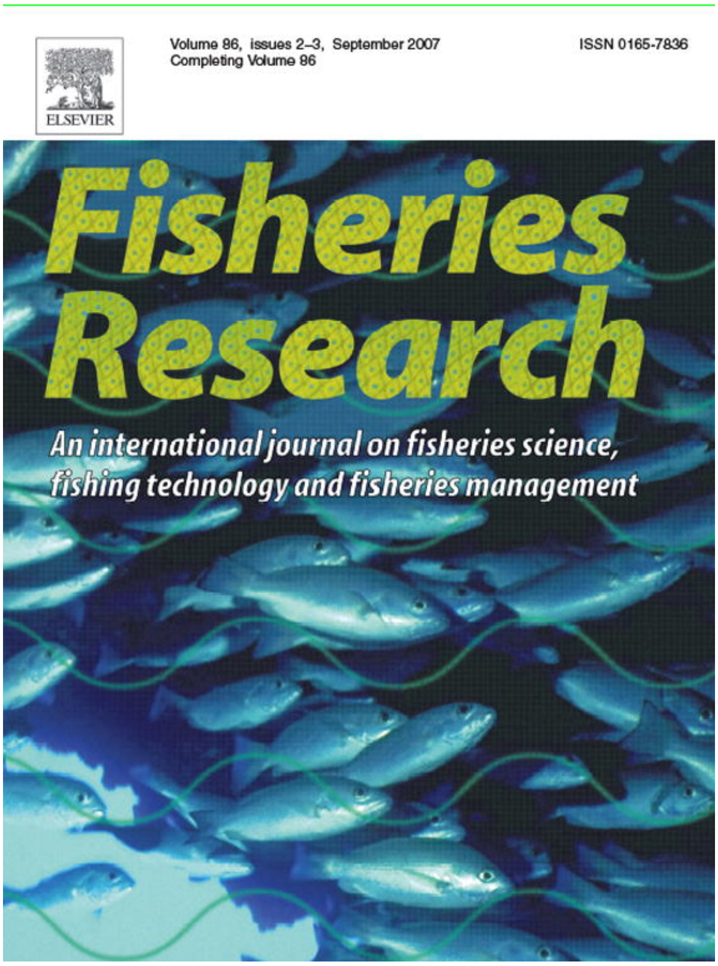
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Possible causes related to historic stock depletion of the totoaba, *Totoaba macdonaldi* (Perciformes: Sciaenidae), endemic to the Gulf of California

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Abstract

Totoaba macdonaldi is the largest sciaenid fish. It is endemic to the Gulf of California within a protected area and listed as threatened by the IUCN red list. The history of the totoaba fishery begun around 1920 and formally finished in 1975, when an official ban was established as a result of the collapse of the fishery. Several previous studies had mentioned the decrease in Colorado River flow and overfishing as possible reasons of the catch and stock reduction. This paper extends the exploration of the causes of the collapse analyzing the co-variation of the trends in catch, biomass, abundance, and fishing mortality with the Colorado River flow, diverse climatic indexes as well as the reconstructed fishing effort. Our results confirm the important role of the Colorado River flow cessation on the decrement of the catch, and the simultaneous increase of the fishing effort during 1940–1954. A new and stronger correlation was unveiled between catch, abundance and stock biomass with the Pacific Decadal Oscillation Index (PDOI). This fact points out the influence of large temporal and spatial scale processes and stresses the importance of the interaction of anthropogenic and natural factors when exploring the historical causes of a population decline and in planning stock recovery actions. The relative role of each of the factors analyzed as well as the possible mechanisms involved is briefly discussed.

Keywords: *Totoaba macdonaldi*; Gulf of California; PDOI; Colorado River

1. Introduction

The totoaba (*Totoaba macdonaldi*: Gilbert, 1891) is the largest amongst sciaenid fish, measuring up to 2 m long reaching a weight of 135 kg (Berdegué, 1956; Cannon, 1966; Román-Rodríguez and Hamman, 1997; Froese and Pauly, 2004). It is endemic to the Gulf of California, where it shows an ontogenetic migration pattern (Cisneros-Mata et al., 1997) using the estuary of the Colorado River as nursery ground. Juveniles feed on benthic invertebrates and adults mainly on small pelagic fishes (Román-Rodríguez, 1990; Cisneros-Mata et al., 1995). This particular species was heavily exploited through several decades of the 20th century, until the Mexican Government closed the fishery (Barrera-Guevara, 1990). The fishery begun around the 1920s, increasing fishing intensity until 1942, when about 2300 metric tonnes were caught. Catch followed a systematic decrease until 1958 when catch was only 280 tonnes. However, minimum catch was only 59 tonnes in 1975. In 1974 the fishery was closed.

The Mexican Government applied several management regulations to manage the fishery and to protect the stock; between 1950 and 1955, a closed season was applied trying to protect spawning; then the mouth of the Colorado River was declared as protected area, where fishing of totoaba and other stocks was prohibited. This protected area was declared as National Reserve in 1974, when it was closed to any fishing activity. The totoaba was declared protected species in Mexico and the United States and 1 year later it was declared as endangered by IUCN (Baillie and Groombridge, 1996; IUCN, 2004). The establishment of the Upper Gulf of California and Colorado River Delta Biosphere Reserve, in 1993, was the most important institutional effort to enhance the conservation of *T. macdonaldi* as well as the vaquita marina (*Phocoena sinus*).

Possible causes of stock depletion have been examined by Flanagan and Hendrickson (1976), from where three hypotheses were proposed: overfishing, loss of spawning habitat, and loss of

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nursery habitat caused by cessation of the Colorado River flow induced by the construction of the Hoover and Glenn Canyon dams in 1935 and 1963, respectively. The conclusion of these studies suggests that the most likely cause of the totoaba collapse until 1958 was the overfishing of recruits. In addition to this, a relation between the Colorado River discharge and recruitment failure was suggested due to a loss of spawning areas and secondarily a loss of nursery grounds. In addition to the possible causes described above, nowadays Cisneros-Mata et al. (1995) and Pedrín-Osuna et al. (2001), suggest that adult poaching and juvenile by-catch by the shrimp fishery may contribute to the still low abundances of the totoaba stock.

Despite previous attempts to elucidate the possible causes of the collapse, an effort to establish the relation between oceanographic processes and the behavior of the totoaba fishery has not been made. For instance, patterns of oceanic variability at different scales and its relationship to many fisheries has been documented through the last years (Mantua, 2001). Particularly, fluctuations of the sardine fishery in the Gulf of California have been related to intra decadal events like El Niño, La Niña (Lluch-Belda et al., 1986). Furthermore, interdecadal variation of air and ocean temperatures are highly coherent with indices of abundance of the California sardine (Lluch-Belda et al., 1992).

In this context, the present paper deals with an analysis of the history of the totoaba *T. macdonaldi* fishery, looking for some correlations between catch, stock biomass and abundance, with indicators of climatic regimes in oceanic variability, trying to find further evidence helping to thoroughly explain the main causes for its stock depletion.

2. Material and methods

The analysis was based on the search of statistical correlations and patterns of co-variation between biological variables of the totoaba and its fishery with environmental data as ecological factors likely responsible for changes of the stock biomass. We explored for relationships between catch, biomass, abundance and recruitment with the Colorado River runoff, the Pacific Decadal Oscillation Index (PDOI), the Southern Oscillation Index (SOI), and the Atlantic Oscillation Index (AOI).

Historic catch records ranging from 1929 to 1970 were obtained from Arvizu and Chávez (1972). Parameter values of the von Bertalanffy growth equation ($K = 0.154$; $L = 169.9$ cm; to $= -0.61$; $t_c = 1.5$ years) where taken from Cisneros-Mata et al. (1995) who compiled previous studies and constructed an age-length key. Natural mortality ($M = 0.23$) was estimated by the methods described by Sparre and Venema (1995), Chávez (2005) and by applying the Beverton invariants (Jensen, 1996, 1997). Length–weight exponential relationship values ($a = 0.000035$ and $b = 2.59$), where obtained from Almeida-Paz et al. (1992).

Additionally, we used historical catch data (Flanagan and Hendrickson, 1976) to apply the FISMO simulation model (Chávez, 2005), which reconstructs the age structure and population size of a fishery to assess the stock and some important reference points useful for decision-making and management using the last 15 years of catch data only; the model uses this number of years only to minimize errors in rebuilding age structure. Reconstruction of cohorts is made as numbers and biomass per age group. Here, the model carries out assessments using the totoaba population parameter values (growth rate, length–weight, age at maturity, age at first catch [t_c], catchability, total catch value, costs of fishing operations, number of fishing days per year, fleet size, and catch data are used as input. The model also estimates natural mortality, longevity, asymptotic weight, the benefit/cost ratio, and total profits. The stock-recruitment relationship is determined so that simulated cohorts can be linked over time and, using the yield equation, the model estimates fishing mortality (F) for each year. Yield and profits are simulated too by assuming that t_c and fishing gear selectivity patterns have remained unchanged over time. This method of analysis was applied to the years when catch data were available (1929–1974); the analysis departs from the same two equations as the analysis carried on for stock assessment (Gulland, 1983; Sparre and Venema, 1995), age was used here instead of lengths, such that

$$N_{a+1} = N_a \mathrm{e}^{(-Z_t)} \tag{1}$$

where N_{a+1} is the number of individuals of age $a+1$ and N_a is the number of individuals of age a in age classes; z_t is the total mortality coefficient ($M+F$). Time units are years. The age of first catch used in this analysis is 3 years, corresponding to a total length of 75 cm.

The catch in numbers per age group in a given year is estimated using the age-length key, the growth parameters and the length–weight relationship. Thereafter, population abundance at each age class is estimated using the catch Eq. (2):

$$C_{a,y} = N_{a,y} \frac{F_t}{(F_t + M)} (1 - \mathrm{e}^{(-F_t - M)}) \tag{2}$$

where C_a is the biomass of fish caught at age a, N_a the number of fish at age a, F the fishing mortality coefficient, and M is the natural mortality coefficient. This method was applied to each year of catch data.

Biological and fishery variables obtained by the simulation model were explored in order to assess the importance of the fishing pressure on the stock depletion of *T. macdonaldi*. To evaluate the relative impact of non-biological forces, comparison of the biological variables of the totoaba stock with the Colorado River runoff as well as some climatic indices as the Pacific Decadal Oscillation Index (PDOI) as described by Mantua et al. (1997), the Southern Oscillation Index (SOI) and the Atlantic Oscillation Index were made.

Reconstructed fishing effort (number of boats) data from 1940 to 1975 were taken from unpublished data from individual boats, skiff records, logbooks, and files of the upper Gulf of California. Vessels involved in the early totoaba/shrimp fishery were distinguished by their characteristics (tonnage, length, construction material, etc.). Fishing effort was assumed to increase linearly from 1929 to 1939 when no effort data were available.

Linear regression analysis was used to explore significant correlations between each of the biological variables and the environmental forcing factors. With the aim to determine the association between catch and the several independent variables (i.e. effort, F, PDOI, Colorado River flow, and SOI), a multiple regression analysis was performed. Using the partial correlation analysis, we described the relationship between two of the variables while taking away the effects of others. In this way, the relative role of the several variables as predictors of the totoaba catch was explored.

3. Results

Fig. 1 shows the tendency of the totoaba catch and the fishing effort (number of boats) increase. Three phases can be recognized, first, a sharp linear increase of the catch between 1929 and 1942, when the historical maximum was reached (ca. 2300 tonnes). The second one is an exponential decreasing period between 1942 and 1958, concurrent with a dramatic increase in the fishing effort from 15 to almost 200 boats. The third phase shows a new increase in the catch followed by a continuous increase of fishing effort until the maximum of 280 boats was attained; after this the catch and the effort decreased simultaneously. Because these three phases are so different, fitting a simple linear or non-linear regression between effort and catch was not advised.

After the application of the simulation model using catch data and the population parameter values, the main trends in stock biomass, and number of 1-year old recruits is shown in Fig. 2A, showing a dramatic decrease in the stock biomass and the number of recruits during the last 15 years of the fishery. In Fig. 2B catch data are shown in bars, as well as *E* (Exploitation rate) for each year as well as *E* at the maximum yield level, identified as the *F* values at the apex of the yield curve, and corresponds to the threshold of overexploitation; in this case the effect of fishing intensity on the stock is evident. An overall decrease in the stock biomass during all time series is evident. However, fishing mortality showed a different pattern. The catch series, abruptly declines from 1942 to 1955, and then showed a secondary increase from 1957 to 1965. By contrast, fishing mortality showed oscillating high values during this decadal period.

The increase in effort from 1929 to 1942, corresponds well with the increase in catch in the same period, concurrently with high PDOI values (Fig. 3A) and high Colorado River flow

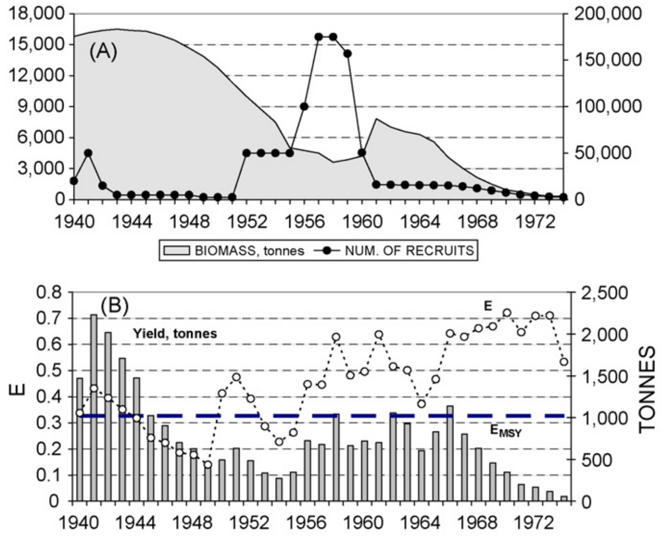

Fig. 2. (A) Temporal trends in stock biomass (tonnes, left *y*-axis), and recruit numbers estimated (right *y*-axis) by the model for the years 1940–1974. (B) Recorded catch (bars, right scale), exploitation rate (*E*, dotted line, left axis), and exploitation rate at the maximum yield level (horizontal broken line). Data are based in a reconstruction of age structure by the FISMO simulation model. The line showing exploitation rate evaluated for each year indicates that the stock was overexploited throughout all the last 19 years of the fishery.

(Fig. 3B). The exponential increase in effort after 1942 was in opposition to the catch, flow and PDOI decreasing trends until 1954, when a secondary increasing period was recorded in catch as well as in the river flow and the PDOI; there is a remarkable coincidence between the peak in recruitment that followed the increase in the river flow of the years 1950–1952. The secondary maximum catch closely corresponds with the historical maximum effort recorded between 1960 and 1962 and with a new increase in the PDOI values (Fig. 3A) as well as in the river flow discharge (Fig. 3B). From 1963 to 1975, the effort and catch decreased in conjunction with the Colorado River flow. By the last years of the analysis the stock was fully depleted.

Linear models showing significant relationships (Table 1), explained better the relation among Colorado River runoff, catch, biomass and abundance (Fig. 4). Additionally, significant linear correlation was found between the PDOI and catch (Fig. 5). No significant correlation was found between PDOI and Colorado River flow when considering the full time series.

Multiple regression analysis showed that totoaba catch was significantly influenced by 2 of the 6 independent variables con-

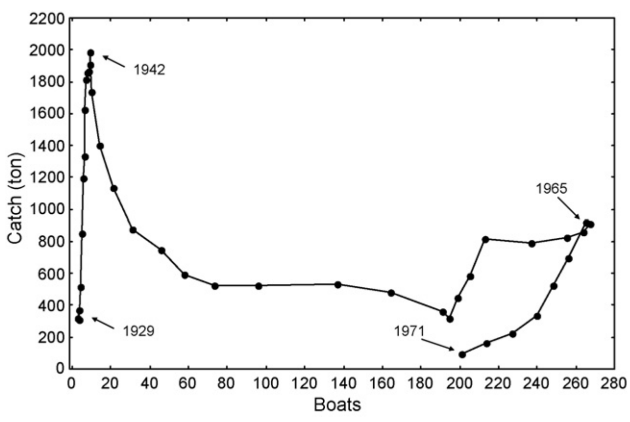

Fig. 1. Evolution of *Totoaba macdonaldi* catch in relation to fishing effort (number of boats) on the upper Gulf of California.

Table 1
Multiple regression between totoaba catch, and PDOI (RM: running mean), Colorado River flow and *F*/*Z*, showing the regression coefficients (S.E.), the partial correlation coefficients and the significant levels for each predictor environmental variable

	Beta (S.E.)	*B* (S.E.)	Partial	*p*-Level
Intercept		861.9 (105.6)		**0.000**
PDOI (RM)	0.707 (0.11)	470.8 (71.1)	0.790	**0.000**
Colorado (lag-2)	0.282 (0.11)	0.04 (0.02)	0.452	**0.013**

Bold: p-level < 0.05. $R = 0.86$, $R^2 = 0.74$, Adj $R^2 = 0.72$, $F(2, 27) = 38.56$, $p <$ **0.00000**.

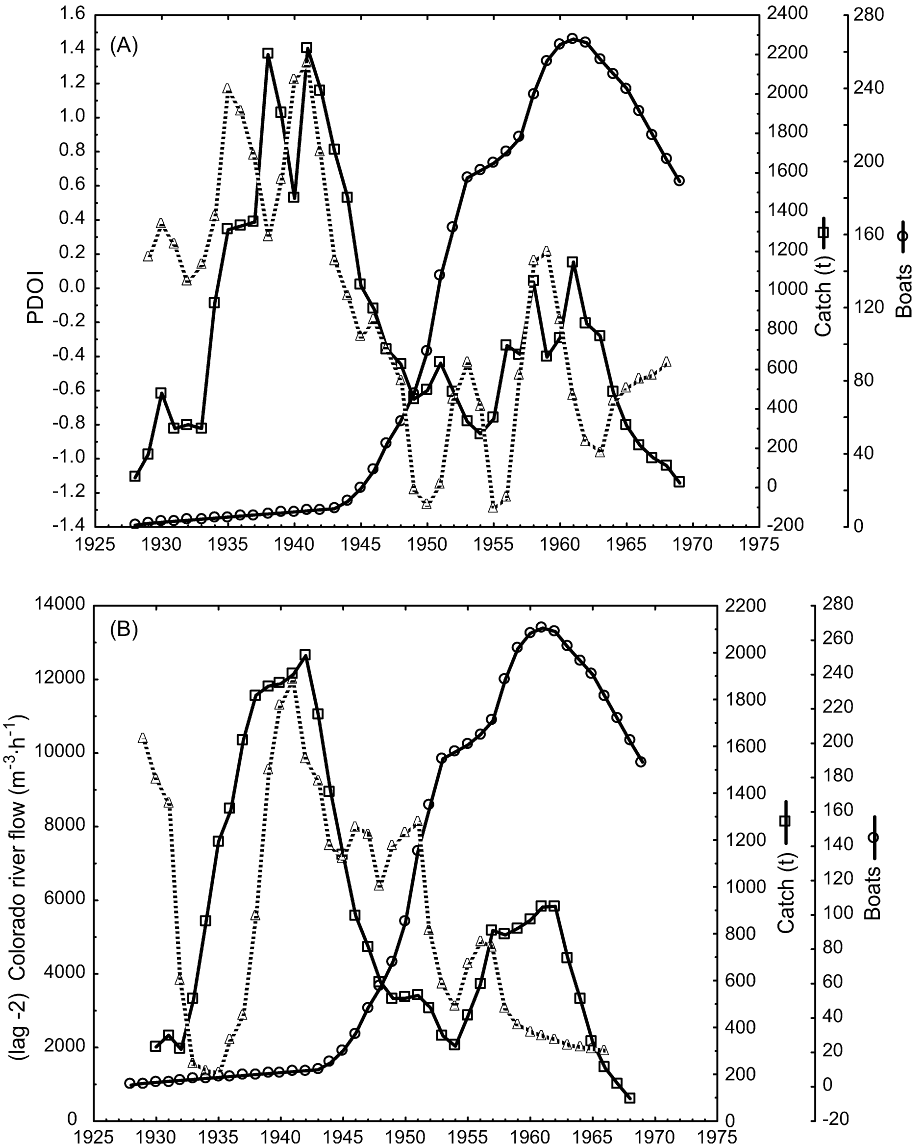

Fig. 3. Time series of: (A) totoaba catch (3 years running mean), PDOI and fishing effort; (B) totoaba catch, Colorado River flow and fishing effort.

sidered, explaining up to 70% of the variability (Table 1) from 1940 to 1971. The most important variable affecting the catch was the PDOI (significant partial correlation coefficient = 0.79) followed by the Colorado River flow (significant partial correlation coefficient = 0.45). No significant correlation was found between catch, SOI, AOI, effort nor fishing mortality. Multiple regression assumptions (linearity, co-linearity and normality) were checked and satisfied.

4. Discussion

Our results show that the decreasing history of the *T. macdonaldi* commercial fishery between 1929 and 1975 was significantly correlated with the PDOI and the Colorado River flow. Particularly, totoaba catch and biomass, showed positive correlation with the PDOI and the Colorado River runoff. These findings reveal that the drastic reduction in the catch and stock of *T. macdonaldi* was a result of the interaction of several co-occurring factors. The reduction of the Colorado River flow and the consequent alteration in spawning and nursery habitats has been recurrently proposed as the main acting factor in the collapse of the totoaba stock biomass (Flanagan and Hendrickson, 1976; Cisneros-Mata et al., 1995).

The significance of freshwater discharge reduction on the environment of the upper Gulf of California was assessed in previous studies (Lavin, 1999; Rodríguez et al., 2001), showing a drastic change in the salinity patterns. Moreover, the increase in salinity produced changes in the circulation of the upper Gulf of California, shaping a negative estuary nowadays (Lavin et al., 1998). These strong environmental perturbations could produce cascade effects on the physiological and behavioral mechanisms involved in the spawning, recruitment, feeding, growth rate, and mortality of *T. macdonaldi* (Flanagan and Hendrickson, 1976). In addition, the significant correlations found between PDOI, and catch, disclose the role of this sea temperature anomaly index as an environmental factor interacting with the fishery com-

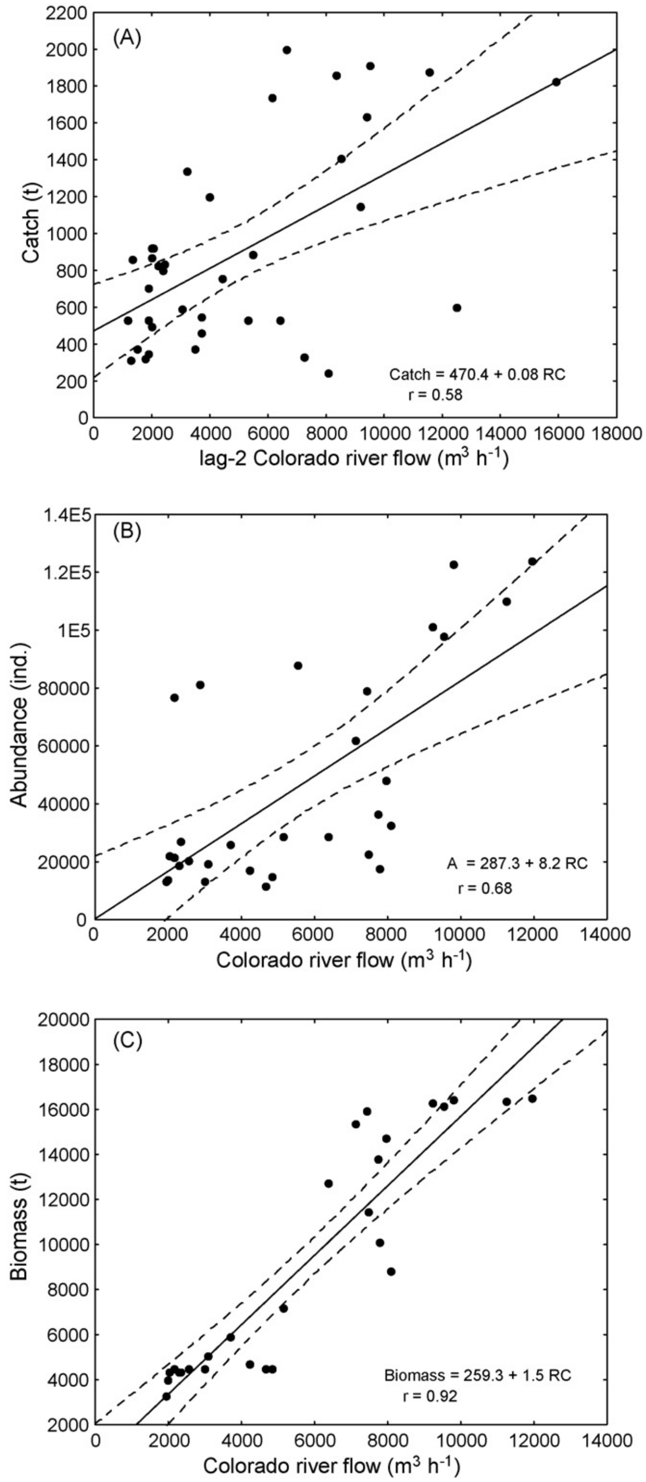

Fig. 4. Linear regression between: (A) Colorado River flow (lag-2) and catch; (B) Colorado River flow and abundance; (C) Colorado River flow and biomass. Dashed lines: 95% confidence level.

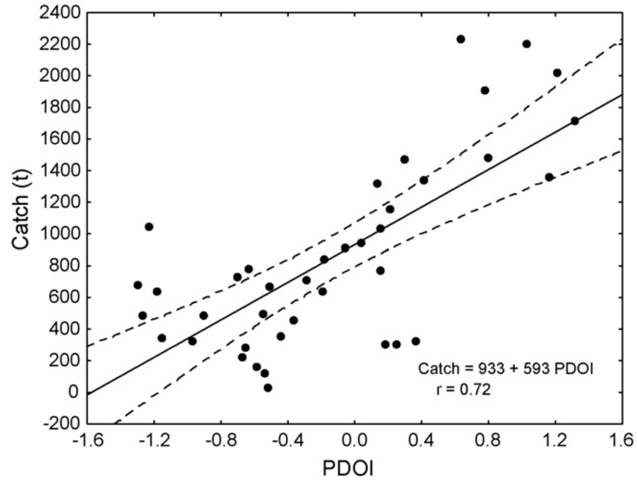

Fig. 5. Linear regression between: PDOI and catch. Dashed line: 95% confidence level.

ponents during the main decaying phase (1940–1970). In this sense, numerous studies documented interdecadal climatic fluctuations in the Pacific Ocean basins, which in turn were related to ecological responses in marine and terrestrial environments. For example, changes in production levels of important commercial fish stocks in Alaska were related to interdecadal climatic variability at the northeast Pacific (Beamish and Bouillon, 1993; Hollowed and Wooster, 1992).

Additionally, similar relationships were observed between salmon production and climatic variability in Washington, Oregon and California (Francis and Sibley, 1991; Anderson, 2000). Even though, Mantua et al. (1997), found a recurrent pattern of climatic variability (PDOI) widely distributed and detectable on diverse Pacific basins, as well as on various ecological systems. Likewise, the PDOI is positively correlated with precipitation over northern Mexico (Mantua et al., 1997; Brito-Castillo et al., 2003). In addition, Brito-Castillo et al. (2003) conclude that regional stream flows into the Gulf of California watershed are climate-driven and associated with the PDOI. It was suggested that the ecological response of marine systems to mid-term environmental changes such as the described by the PDOI, begin in the primary producers and primary consumers, propagating upward through the food web to the top predators in a bottom-up control (Mantua et al., 1997; Francis et al., 1998). The cause-effect mechanisms subtle in the association between PDOI and the totoaba abundance indexes are far from being explained. However, the trophic connection between adult totoaba and sardine in the Gulf of California could be an important factor in this relationship considering the bottom-up control mentioned (Cisneros-Mata et al., 1995; Román-Rodríguez, 1990). In this sense Lluch-Belda et al. (1992) show a strong coherence between the California sardine and the global and local decadal regimes of temperature. Also, there is a demonstrated significant correlation between sardine abundance (i.e. catch; CPUE) and seawater temperature (Lluch-Belda et al., 1986). It was suggested that the older age groups of the *T. macdonaldi* stock are more sensitive to environmental variability than the younger stages (Cisneros-Mata et al., 1997).

Analyzing the simultaneous growth of the catch and fishing effort, is possible to observe that the first peak in catch (1942: maximum historical) was attained with very low effort. As the effort upraises exponentially (after 1942), the catch, in conjunction with the Colorado flow and the PDOI, decline linearly until the middle 1950s. The second production peak near 1960 seems to be produced by a slight increase of the Colorado River flow, together with a raise in PDOI, and notably by the maximum number of boats. The stabilization of the Colorado River flow in the lowest historical levels and the still high fishing effort (up to 200 boats) in the beginning of the 1970s, contributed to the total depletion of the totoaba fishery.

The simulation model shows a decrease in biomass and F, followed by a decline in catch, indicating a suitable representation of the fishery dynamics. Therefore, it is assumed that intrinsic variability of the stock dynamics would be within the range of stock biomass implicit in data analyzed.

Tendency of E evidences that the stock was over exploited during 26 years of the fishery, showing that during the last 19 years the exploitation rates were above 60%, which are extremely high values.

Results obtained with the multiple regression analysis suggest that the variations in catch caused by the fishing effort are less evident than those produced by the environmental factors mentioned above. In this sense, the PDOI performed better as a predictor variable than the Colorado River flow, suggesting a stronger influence of this temperature index on the totoaba catch. However, we can consider a cause-effect sequence, where the PDOI controls the Colorado River flow through precipitation, and the consequent increase in flow benefiting the *T. macdonaldi* stock. The weak non-linear relation found between both variables prevents this conclusion. However, intensive water diversion and retention along the Colorado River must play a significant role precluding a clear association between the PDOI and the Colorado flow.

In summary, our study suggests a multi-causal hypothesis to explain the decline of the totoaba stock and fishery. In addition to the Colorado River flow and the increasing fishing effort, a new factor, the Pacific decadal temperature oscillation was found to be associated with the catch history. The particular extent on which these variables are responsible of the fishery collapse cannot be deduced in this article with the available historical information. Moreover, with the final multiple regression model not including a strong effect of fishing and with the simulation model's estimate of fishing mortality not matching the trend in number of boats, our results are not conclusive. However, the particular effects of these factors could have displayed a synergic interaction to contribute to the end of the fishery.

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