OBSERVATIONS ON THE COMMERCIAL FISHERY AND REPRODUCTIVE BIOLOGY OF THE TOTOABA, *CYNOSCION MACDONALDI*, IN THE NORTHERN GULF OF CALIFORNIA

CHRISTINE A. FLANAGAN AND JOHN R. HENDRICKSON[1]

ABSTRACT

Information gathered from fishers and records of the failing totoaba, *Cynoscion macdonaldi*, commercial fishery demonstrate the ability of the three principal ports to fully exploit the dwindling population during its annual breeding migration to the mouth of the Colorado River. Gonadal maturation, daily catch, and capture incidence data document the timing and route of the migration, provide evidence for a tendency toward unisexual schooling in its early phase, and point to the possibility that totoaba may form large aggregations before spawning is initiated. A trend toward reduction in the length of the migratory and spawning period, from 5 or 6 mo in 1965 to 1 mo in 1972 is documented with data from the port of Golfo de Santa Clara. In surveys of the hypothesized nursery area, 28 juvenile totoaba (6-12 cm standard length) were collected at 4 of 14 sampling sites. The four collection sites were commonly characterized only by depth (<1 m) and substrate type (soft clay-silt sediments). Three hypothesized causes of the decline of this commercial fishery are examined by statistical analyses of Colorado River flow and annual totoaba catch data: overfishing, loss of spawning grounds, and loss of nursery grounds. Overfishing was found to be the most likely cause of the decline. Recent trends of catch data among the principal commercial fleets, and evidence that regulatory measures may have resulted in temporary recovery of totoaba production, provide further support for the overfishing hypothesis. The journey of the migrant population along a known route and its concentration into a predictable small area, its hypothesized requirement for dense aggregations prior to spawning, and the added mortality of juveniles taken by shrimp trawls in the near-delta waters are important points of vulnerability that render this endemic species particularly susceptible to fishing pressure. The possibility of the extinction of *Cynoscion macdonaldi*, without continuation of the newly decreed prohibition of fishing, is reiterated.

The totoaba,[2] *Cynoscion macdonaldi* Gilbert 1891, is the largest species of the family Sciaenidae, with maximum reported lengths of almost 2 m (Berdegué 1956) and weights exceeding 135 kg (Cannon 1966); the larger females in present-day commercial catches approximate 1.5 m and 35 kg (Arvizu and Chávez 1972). The species is endemic to the Gulf of California, where it used to support a fishing industry and popular sport fishery based on its annual spring breeding migration to the shallow, formerly brackish waters of the Colorado River Delta region at the extreme northern end of the gulf. The major portion of the catch was exported from Mexico to the United States (principally San Diego) and brought a high price per pound under the influence of apparently unlimited demand. Presently an indefinite closed season on the totoaba, declared by the Government of Mexico on 2 August 1975, prohibits all capture of this species by both commercial and sport fisheries (H. Chávez, pers. commun.).

Although the species has been heavily exploited, its life history, population dynamics, and general ecology are poorly known. Species accounts are given in Jordan and Evermann (1898, 1902), Jordan et al. (1930), Gabrielson and Lamonte (1954), and Lanham (1962). The totoaba was included in accounts of commercial sciaenid species by Croker (1932) and Fitch (1949). Aside from these references and others cited here, little has been published on the totoaba; remaining incidental references may be found in Arvizu and Chávez (1972), the most recent summary of all available information on this species. Although notes on the ecology of the totoaba were first published in 1916 by Jordan, most of the presently accepted life history information is based on fisher's lore. These beliefs were first documented by Berdegué in his 1955 study of the fishery in which he also examined scale annuli series and published the only derived

[1]Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721.

[2]The common name is often spelled "totuava" by writers from the United States for no known reason. The spelling used here is that preferred and used by Mexicans; it should become the established spelling.

Manuscript accepted January 1976.

growth estimates for this species. His work concluded with a warning that the totoaba is a declining species, in danger of extinction from a combination of overfishing and the disappearance of brackish water spawning grounds due to diversion of Colorado River waters for agricultural and other purposes. Gause (1969) and Sotomayor (1970) later echoed this view.

In this paper we present a short history of the commercial fishery and report new information on totoaba life history. We summarize what is known about the ecology of the species and speculate on consequences of the present small population size and the intense fishing effort to which the fish have been exposed. We discuss the three most probable causes for the decline in the fishery: degradation of spawning grounds, degradation of nursery grounds, and overfishing. We examine Colorado River flow data and annual catch data in the light of these hypotheses, and discuss our results. In conclusion, we draw together all these elements in an attempt to assess the present and future status of this commercial population.

HISTORY OF THE FISHERY

Until about 1920, commercial exploitation of the totoaba was confined to export of dried air bladders to the Orient as an ingredient of a gourmet soup (Chute 1930). Craig (1926) reported the first export of totoaba flesh to the United States. In these early, developing years, the totoaba fishery was directly responsible for the establishment of three northern gulf fishing villages: Golfo de Santa Clara and Puerto Peñasco in the State of Sonora, Mexico, and San Felipe in the State of Baja California Norte (Berdegué 1955). Analysis of registered catches by all Mexican ports for the 1966-70 period shows that these three ports produced from 94.9 to 97.7% of the total catch (H. Chávez, pers. commun.).

From 1929 (when Mexican Government statistics were first collected) onward, the fishery responded to a growing U.S. market by developing transportation and refrigeration capabilities and by improving fishing gear and boat facilities. Annual yield began to increase rapidly in 1934 and the catch peaked at 2,261 metric tons[3] in 1942

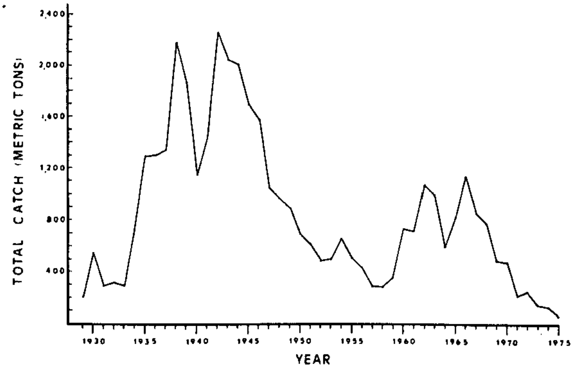

FIGURE 1.—Yield of commercial totoaba fishery, northern Gulf of California for the 1929-75 period. Figure modified from Arvizu and Chávez (1972). Data for 1971-75 were obtained from H. Chávez (pers. commun.).

(Figure 1). After 1942, despite intensified fishing effort and increased gear efficiency, the annual yield exhibited erratic fluctuation to the all-time minimum of approximately 58 metric tons in 1975 (H. Chávez, pers. commun.[4]).

Fishing methods evolved from spearing out of dugout canoes and primitive handlining in the early years, through dynamiting and primitive gill netting, to the use of efficient nylon gill nets. The usual modern net has a stretched mesh size of approximately 25 cm and measures 100-200 × 4-5 m. Gill nets were managed from diesel-powered shrimp trawlers (12-18 m, some temporarily diverted from shrimping during prime season totoaba fishing), and from 4.5- to 7.5-m wooden or fiber glass "pangas" (launches) fitted with outboard motors. The activities of commercial fishers have been largely limited to the prime breeding season (January-March) when the spawning adults are in the shallow waters of the extreme northern gulf. Prior to the 1975 total protection of totoaba, the prime fishing season ended with the advent of an official closed season, 1 April-15 May (Arvizu and Chávez 1972), a protective measure enacted by the Mexican Government in about 1955 (Berdegué 1955).[5] At the same time, a sanctuary was designated at the mouth of the Colorado

[3]We follow the example of Arvizu and Chávez (1972) in giving yields as weights of cleaned fish lacking heads and viscera unless specifically designated otherwise. To convert to whole weights, multiply by 1.1 (H. Chávez, pers. commun.).

[4]The 1975 yield reported here is based on catch from principal ports for the prime season only (through the month of March). The final figures may be as much as 10% higher.

[5]According to Berdegué (1955), before 1955 there was a closed season extending from 20 March to 1 May; the prohibited period was changed to the later dates because active spawning was observed after 1 May. In 1969 and 1970 the beginning of the closed season was delayed 15 days in response to the fishers' petitions when breeding schools had not appeared by the end of March (H. Chávez. pers. commun.).

River. All fishing was prohibited north of an imaginary line extending from Bahía Ometepec on the Baja California coast to the mouth of the Río Santa Clara on the Sonora coast.

In addition to the standard commercial fishery, the Seri Indians of the Bahía Kino and Punta Chueca areas of Sonora were alleged to capture totoaba in coastal waters during the fall and winter, but we have been unable to confirm this by personal observation. Further pressure was exerted on the stocks by an enthusiastic sport fishery, based largely on the Baja California side of the northern gulf, which took unknown numbers of breeding adults during the prime season. In recent years when diminution of the stocks caused the success rate to drop, sport fishing virtually disappeared. At the peak of the sport fishery, large numbers of immature fish resident in the upper gulf waters were also reportedly taken, usually unrecognized as totoaba. For a time, a deepwater handline commercial fishery and accompanying sport fishery continued out of San Felipe during the summer after the adult fish had left the spawning grounds, but this activity also declined in recent years. Craig (1926), Chute (1928), and Berdegué (1955) provided further information on the history of the fishery and contain most of the documented information on the sport fishery.

METHODS AND MATERIALS

The junior author began field studies on the species in 1970 with the primary objective of gathering life history information for conservation purposes. The results reported here derive primarily from data collected by the senior author during three cruises aboard commercial fishing vessels from Puerto Peñasco in March and April 1972. Fishing patterns during these cruises included most of the Gulf of California north of lat. 31°N; with few exceptions, the locations were selected by the fishing captain.

The data were gathered by direct observation of catch and, in a few cases, by reports from fishers on "companion" vessels (as many as five other boats in the cooperating group, in one instance). During 22-24 March 1972 we also collected data from the panga fleet at Golfo de Santa Clara as the catch was landed and cleaned at the port. In both circumstances, our data consisted of information on location, time and size of catch, number of operational net hours, time and state of tide, sexual composition of the catch, and reproductive state of the individual.

All fish examined by us were breeding adults. They were classified according to three mutually exclusive categories of gonadal development: If not running eggs or milt at the time of capture (or within 24 h of capture in the case of several individuals kept alive for a period of hours), they were classified as "unripe"; if milt or hydrated eggs ("applesauce" color and texture) could be expressed with light pressure, they were classified as "ripe"; females with flaccid ovaries and running ripe males taken in the same catch with such females were classified as "spent."

Effort data are reported as the number of operational net hours rather than total time (man-hours or boat-hours) spent fishing because many of the large boats "hunt" for schools suitable for encircling with their nets during the day and then set their gill nets in the usual manner to fish overnight. We believe that recent daytime hunting for schools to encircle was practiced more in memory of times past than as a practical matter of probability. In approximately 50 days aboard such vessels, we have never seen a school located, although one heard of such catches each season. The method persisted because, if successful, it can yield very high tonnage. The larger, diesel-powered trawlers with ice-filled holds frequently stayed at sea for more than a week and commonly traveled considerable distances back to their home ports to land the catch. This is in marked contrast to the methods of the fishers of Golfo de Santa Clara, who fished primarily from pangas and who customarily inspected their nets each day by passing the net over the boat, leaving the weighted ends in place. Such nets "fished" continually, except for occasions when they were taken up to be moved to alternate spots. Lacking storage and refrigeration facilities, the pangas had to return to port each day with their catch from one or two gill nets. Catch in kilograms was recorded by a Mexican government fisheries inspector for each panga, each day. Although we attempted to calculate catch per unit effort, we were unable to resolve its heterogeneous nature. Here we present only our analysis of effort from the panga fishery of Golfo de Santa Clara.

In late May and early June 1972, a number of Sonora and Baja California sites around the perimeter of the extreme northern gulf were surveyed for juvenile totoaba, using both commercial trawl nets and beach seines. Many of these sites were revisited in June 1973. Observations were made of water temperature, salinity, turbidity, and substrate character; associated faunas at each site were sampled. A few juveniles were transported alive back to Tucson, Ariz., and maintained there for about 80 days. Information on distribution and habitat of the juveniles is presented here; notes on behavior of the juveniles in captivity will be reported elsewhere (C. A. Flanagan in prep.).

In our discussion of the hypotheses for the decline of the totoaba fishery, we present statistics of Colorado River flow and annual totoaba yield. The annual yield data are those already presented (Figure 1). For flow, we have attempted to estimate the amount of water delivered to Mexico in the main river channel at the southerly international boundary on the assumption that it will bear some regular relationship to the volume of fresh water entering the Gulf of California. This assumption becomes tenuous with the development of lowland agriculture in Mexico and with significant groundwater pumping in the United States, both in evidence since about 1960. Suitable effort data for the totoaba fishery are unavailable but we have assumed that, following the peak catch in 1942, effort was constant or increasing. This assumption is probably warranted given the demand and high price paid for totoaba flesh. The limitations imposed by our assumptions are that no catch datum before 1942 and no flow datum after 1960 may be considered in these analyses.

RESULTS AND DISCUSSION

Breeding Migration

The fishers believe that the annual migration of totoaba is prompted by the urge to reproduce and is guided by the search for a suitable estuarine spawning environment. According to their beliefs the breeding population, seeking areas of reduced salinity, leaves deep water in the mid-gulf and follows the Sonora coastline northward; eventually the schools reach the mouth of the Colorado River, where they spawn. Following spawning, the totoaba supposedly seek out the clearer, deeper waters to which they are more accustomed and follow the Baja California coastline on their return migration southward. These beliefs are based upon commercial catch experience dating back to the late 1920's.

Localities and dates of capture observed by the senior author in 1972 (Figure 2 and Table 1) appear to document a pattern consonant with the above hypothesis, as do observations by the junior author in earlier years. The regular port statistics also implicitly support the hypothesis, with catches each year reported chronologically first by Puerto Peñasco, then by Golfo de Santa Clara, and last by San Felipe fleets. The data in Figure 2 represent but a small fraction of the total 1972 fishing effort, however, and in the most conservative interpretation demonstrate only that experienced fishers

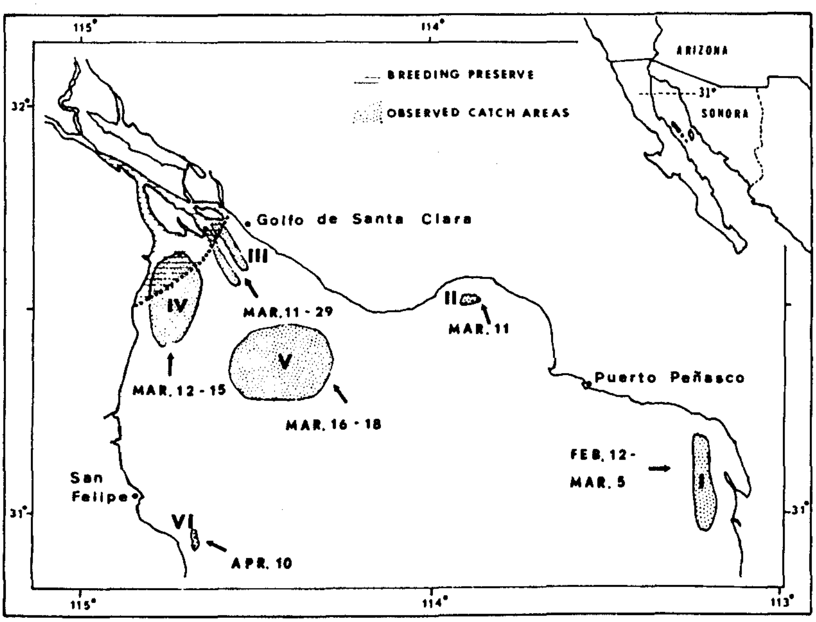

FIGURE 2.—Locations and dates of observed commercial catches of totoaba during the 1972 prime fishing season. Catch information in terms of tonnage by day, boat, and area were also obtained from Fisheries Inspectors. These latter data are reflected in the early capture date of 12 February and the extended capture period of 11-29 March in areas I and III, respectively. Chart shows Gulf of California north of lat. 31°N (see locater in upper right-hand corner).

TABLE 1.—Totoaba captures observed in 1972 (see Figure 2 for areas and timing). The figures shown here are personal observations of the senior author.

Area	No. of observed net sets	No. of successful net sets	Total no. of totoaba caught
I	5	1	1
II	1	1	1
III	(no data)	[1]149	([1])
IV	9	8	42
V	6	5	18
VI	11	1	1

[1]These data are displayed in Figure 5. Although catch data are available for area III only in terms of tonnage, not head count of fish taken, use of the 35-kg average per fish would give a conservative estimate of at least 2,500 individual fish taken in area III during 1972.

know where and when to find fish. Ideally, Figure 2 should reflect the results of an even pattern of standard net sets through the February-June period.

To our knowledge, no one has investigated the salinity preferences or tolerances of spawning adults, but this raises the question of totoaba spawning sites in estuarine areas of other major gulf rivers. Spawning totoaba have never been reported from locations other than the Colorado River mouth. While further investigation is clearly warranted, at present we accept the fisher's hypothesis as an adequate predictor of population migratory patterns.

Spawning Concentration

Because the annual breeding migration results in a high density of fish within a limited area, it has become the single most important aspect of the fishery: total prime season catch is a function of the number of fish arriving in the spawning area before 31 March in an average year. The appearance of migrant schools of totoaba in shallow coastal waters, as signaled by catches from exploratory boats which have ventured out in anticipation of their arrival, usually occurs in mid-February, but may take place as early as December or as late as the end of March.

Three references exist in the literature regarding the spawning period. Nakashima (in Jordan 1916) said that the main spawning period was in early May, while Berdegué (1955) reported the reproductive season as extending from the end of February or early March until early June. Observations by D. A. Thomson (1969) and the junior author over the last four seasons indicate peak spawning as late as April and early May but, more commonly, in mid- to late March. Historical data and existing statistics confirm the fisher's claims that the period of concentrated catch (which apparently coincides with peak spawning) has become progressively abbreviated during the past 20 yr. The monthly catch data for Golfo de Santa Clara for the 1964-72 period show a clear reduction in length of season from 5 or 6 mo to an abbreviated period in March-April at present (Figure 3). We believe (see below) that the catch of the Golfo de Santa Clara fleet is a good reflection of spawning activity and suggest that a pattern of repeated spawnings formerly extending from January-February to May and June has collapsed to a single event which coincides with the old temporal mode. A small remnant population might be expected to react more uniformly to environmental cues than would a large one, a factor leading to progressively shorter migratory and spawning periods. This is consistent with our observation of breeding population residence time of only 18 days on the spawning grounds in 1972 (from 11 March to 29 March, see discussion below).

A limited amount of qualitative data on gonadal maturation, collected during the 1972 prime fishing season (Figure 4), indicates that males ripen before females and retain spawning readiness for longer periods of time—a common occurrence among fishes. It also provides evidence for a

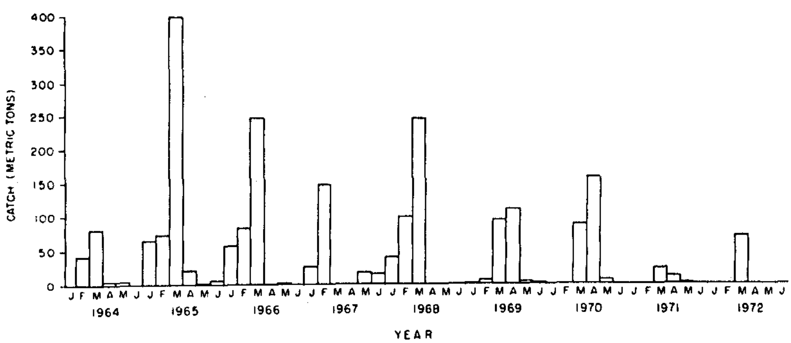

FIGURE 3.—Monthly yield in metric tons of totoaba, port of Golfo de Santa Clara. Data for 1966-70 from Arvizu and Chávez (1972); H. Chávez (pers. commun.) supplied data for 1964-65 and 1971. The 1972 catch data were obtained from F. Aguilera, Fisheries Inspector (15 additional metric tons recorded in 1972 are not shown because month of capture was uncertain).

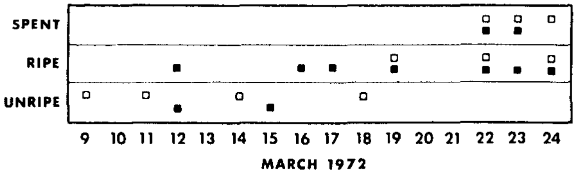

FIGURE 4.–Degree of gonadal maturation observed on specific days during the 1972 prime fishing season. See text for explanation of maturation categories. Each symbol represents one or more individual fish. Open squares represent females; solid squares represent males.

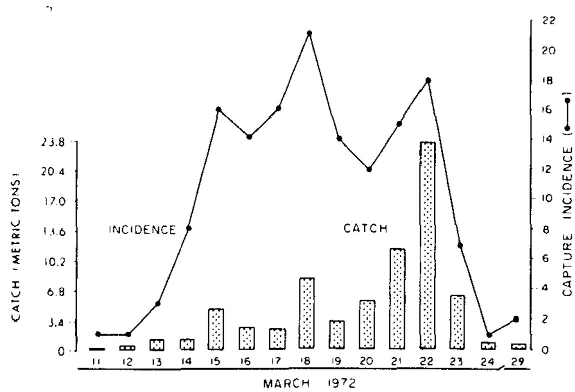

FIGURE 5.–Golfo de Santa Clara catch and capture incidence plotted against days of March for 1972 prime fishing season. See text for explanation of capture incidence unit. Between 15 and 22 March the number of individually successful nets remained comparatively constant, despite the peak catch on 22 March. Official statistics indicate that 15 metric tons in addition to the total of 71 metric tons shown in Figure 3 were recorded for this port in 1972 (H. Chávez, pers. commun.). These additional data cannot be traced to daily catch for inclusion in this figure.

tendency toward sexually segregated schooling, at least in the case of male fish. It will be noted that all the records for the early portion of the period portrayed in Figure 4 show a single sex per catch, while the records for the later portion of the period show both sexes in all but one instance. It must be clearly understood that some of the catch records portrayed in Figure 4 represent single fish, making those data points meaningless in this context, but a majority of the data points represent multiple individuals. This apparent sexual separation of prespawning schools conforms with general observations by Hendrickson in years before 1972 and with the caption for figure 84 in Chute's (1928) paper describing the earlier hook-and-line fishery: "Practically all of the fish in this picture were males . . . ." (the figure, depicting the butchering process, shows about 15 large fish caught by three men in 3 h).

Success of the Golfo de Santa Clara panga fishery is related to the size of the migrant totoaba population, the length of the period in residence on the fishing grounds, and population behavioral patterns. Because the fishing grounds are identical with, near to, or in the path to the spawning grounds, analysis of the panga fishery catch statistics can yield valuable insight into the breeding biology of this species. We have used "capture incidence" as a measure of fishing success, employed here to give a quantitative indicator of the presence of breeding adults on or near the suspected spawning grounds (Figure 5). One capture incident is defined as the catch of at least one totoaba per panga per day; the daily total reflects the number of individually successful net sets. We assume that: 1) fishing effort is constant after a given date within the prime season and 2) fishers individually and collectively fish in the same area each day throughout the period. These assumptions are in keeping with the nature of the Golfo de Santa Clara fishery. This village waited in readiness each year for the arrival of the migrant population and, within a few days of the first catches by exploratory nets, virtually all available gill nets were deployed for fishing of totoaba. Despite daily success or failure, fishing effort continued at this level until the season closed on 1 April. Most of the panga fishers worked a definable area of the delta where "canals" (extensions of Colorado River channels) deep enough to accommodate the large totoaba gill nets are separated by shallow mud bars (see area III in Figure 2).

In 1972 the first catch off Golfo de Santa Clara occurred on 11 March and was followed by a period of increasing catch and capture incidence due to increasing effort until 15 March (Figure 5). During the March 15-22 period, capture incidence was relatively constant and high. During this same period, catch varied somewhat erratically and peaked on 22 March, after which both catch and capture incidence fell off drastically despite no reduction in fishing effort. The 22 March catch amounted to 27% of Golfo de Santa Clara's yield for that year and represented 9% of the total recorded yield from all ports for 1972. The average Golfo de Santa Clara net must have contained over twice as many fish on 22 March as on 21 March and 3-5 times as many as on other "good" days in the prime season.

What factors in totoaba reproductive biology might explain these results? Catch per net may be considered an index of migrant arrivals if we suppose that, as breeding adults reach the northern end of the gulf, they immediately move up into the channels at the mouth of the Colorado River. The arrival of the largest population segment would then be indicated by the peak catch. Alternatively, the peak catch may have signaled a peak of spawning activity by an already-resident breeding population, becoming more vulnerable to the nets by virtue of spatial concentration and/or behavior. While the data do not allow firm conclusions, we favor the second alternative.

A period of behavioral stimulation in schools to induce the spawning act is suggested by the fact that enormous numbers of individuals allegedly used to gather in this relatively small area to spawn (Jordan 1916; Berdegué 1955). Although the population has been drastically reduced, the fish apparently continue this habit. If the release of reproductive behavior patterns depends upon mutual stimulation within large aggregations (consistent with their sound-producing air bladder; see Breder and Rosen 1966), the present small population might be experiencing some breakdown in the behavioral sequence with consequent lowered reproductive success.

Although the significant yields of 21 and 22 March may indicate a peak in spawning activity, this does not preclude the possibility that other fish were later in arrival and that spawning also occurred in April (during the closed season). The Golfo de Santa Clara fleet's near-failure to catch fish during the 25-31 March period, and our failure to find adult fish during the April cruise lend doubt to this possibility, but the existence of more than one breeding population should not be ruled out.

Juvenile Totoaba Distribution, Habitat, and Diet

The microhabitat and residence time of juvenile totoaba on the nursery grounds are largely unknown. Berdegué (1955) reported that juveniles remain in the shallow waters near the Colorado River mouth until they begin a southward migration to join the parent population. The Colorado River Delta is heavily exploited by the shrimp fishery during parts of the year (effort was observed to be especially intense during April, May, and June), and Berdegué first called attention to the increased mortality of juvenile totoaba due to shrimp trawling activity.

In our experience, the juveniles captured in shrimp trawls are individuals ranging in length from about 15 cm to about 45 cm. The holotype in the U.S. National Museum is approximately 25 cm long and was taken in 20 fathoms of water (Gilbert 1891). To our knowledge, the first collection of really small juveniles (6-12 cm size range) which were positively identified as totoaba was made in 1970 near San Felipe, B.C., and described by Chávez (1973). We surveyed probable northern gulf sites for the presence of such small juveniles during May and June 1972 and 1973 (Figure 6).

Substrate and depth appear to be more important than either temperature or salinity in characterizing the habitat of the captured juveniles. For all sites, surface water temperatures ranged from 25° to 29°C and salinities were recorded between 35 and 40‰. Sites where we collected juveniles were shallow as compared to the other sampling locations, and none were collected from depths greater than 1 m. Substrates were composed of fine clay-silt sediments, devoid of sand;

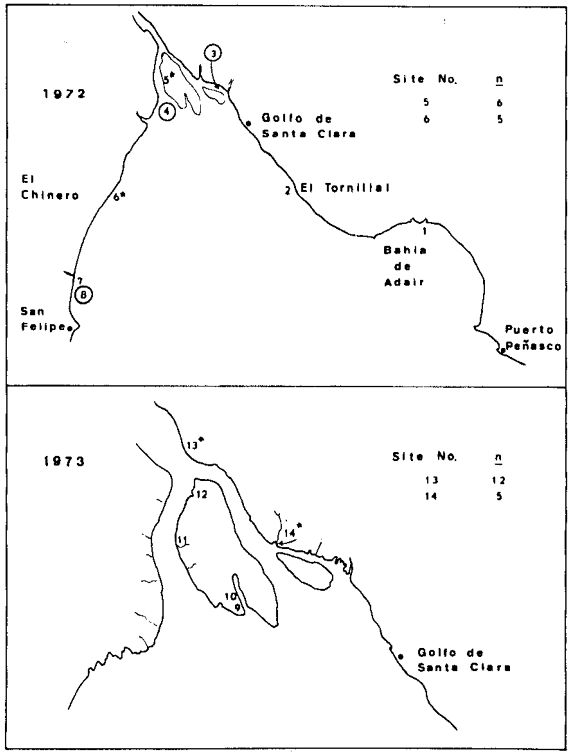

FIGURE 6.—Sites sampled in northern Gulf of California for presence of juvenile totoaba in 1972 and 1973. Circled numbers indicate offshore areas sampled by otter trawl. All other locations are shore stations sampled by seine. Sites where juvenile totoaba were found are indicated by stars. Numbers captured are shown at upper right of each map.

the mud surface layer was very soft. No small juvenile totoaba were collected over firm mud sediments or sandy substrates, as is often the case with the larger individuals taken in shrimp trawls.

Guevara (1974) is presently analyzing the distribution of juvenile totoaba captures in shrimp trawls. Most of his specimens are larger than ours, implying that the fish move into deeper water as their growth continues. Tidal currents in the area are extreme and these may also play a significant role in juvenile distribution.

Juveniles collected in 1972 were examined for stomach contents. Remains of amphipods and other small crustaceans common to the habitat were recognizable, in addition to remains of juvenile fishes which we identified as *Micropogon* sp., *Mugil cephalus*, and *Leuresthes sardina*. Within the limits imposed by size, the diet of juvenile totoaba as small as about 6 cm standard length is comparable in these items with the diet of the large adults.

Decline of the Fishery

We have traced the growth and decline of the totoaba fishery and discussed its present status and methodology. We have presented data on aspects of totoaba life history and raised questions concerning possible reproductive behaviors which may have a bearing on reproductive potential. Although these have significance, if we consider the resource from a management perspective one fact becomes clear: the annual breeding migration to the mouth of the Colorado River emerges as the primary source of vulnerability for this declining population. It serves to concentrate adults in a predictable small area where they may be fished with efficiency during a critical phase of their life cycle. To recruit, the juveniles must traverse an area of intense shrimp trawling activity which artificially increases juvenile mortality and leads to further reduction of this already-depleted stock.

The precise factors responsible for the decline of the totoaba stock cannot be identified with certainty, but we can enumerate the three most probable causes as: degradation of the spawning grounds, degradation of the nursery grounds, and overfishing. The first two are a result of replacement of brakish waters by saline waters in and around the mouth of the Colorado River. Both alternatives may be explored by examining Colorado River flow data and annual totoaba yield over the critical period of declining catch and significant flow reduction. We might expect a relationship to exist between flow and annual yield if the density of the resident breeding population (as measured by catch) varies with some unknown but flow-related quality of the spawning ground. Relation between flow and catch n years later (with n years corresponding to age at recruitment) would indicate the importance of some flow-related quality of the nursery ground. Although tests of overfishing using these data are ambiguous, if catch is statistically related to catch n years later we might expect a depletion of the breeding population resulting from lowered recruitment levels.

The decline in catch with declining, erratic flow is evident for the 1942-58 period (Figure 7). Following 1958, the catch increased to a secondary peak and then crashed to the present all-time minimum, though flow varied little in the same period. For reasons given earlier, we discuss separately the pre-1958 and post-1958 periods.

For the years 1942-58 we have plotted catch against flow (Figure 8). Linear regression of the data reveals a highly significant correlation of annual flow and catch for this period ($P < 0.001$). However, the river flow data are derived from a different base after 1951; analysis of these data in two segments, before and after this change point, shows no significant relationship between catch and flow for either the 1942-50 period or the 1951-58 period. These results suggest that the highly significant correlation of flow and catch for the total 1942-58 period may be spurious and due only to the artificial pairing of declining catch and declining flow functions. Despite these results, we cannot ignore the fact that the totoaba congregate only in the Colorado River estuary (so far as known), and the salient feature distinguishing this from other estuaries in the northern gulf is the (former) discharge of large quantities of fresh water from the Colorado River. Therefore, accepting the tentative nature of the flow-catch relationship, we explore its possible biological basis.

The mechanism could lie in olfactory cues from the river system (physiological responses to either fresh water or substrate "odor"). Given the present agricultural scene, such cues may no longer be present. The present Colorado River surface flow to the Gulf of California is close to zero for all practical purposes and this situation is likely to continue in the future. A conspicuous bar now exists across the channel upstream from the delta

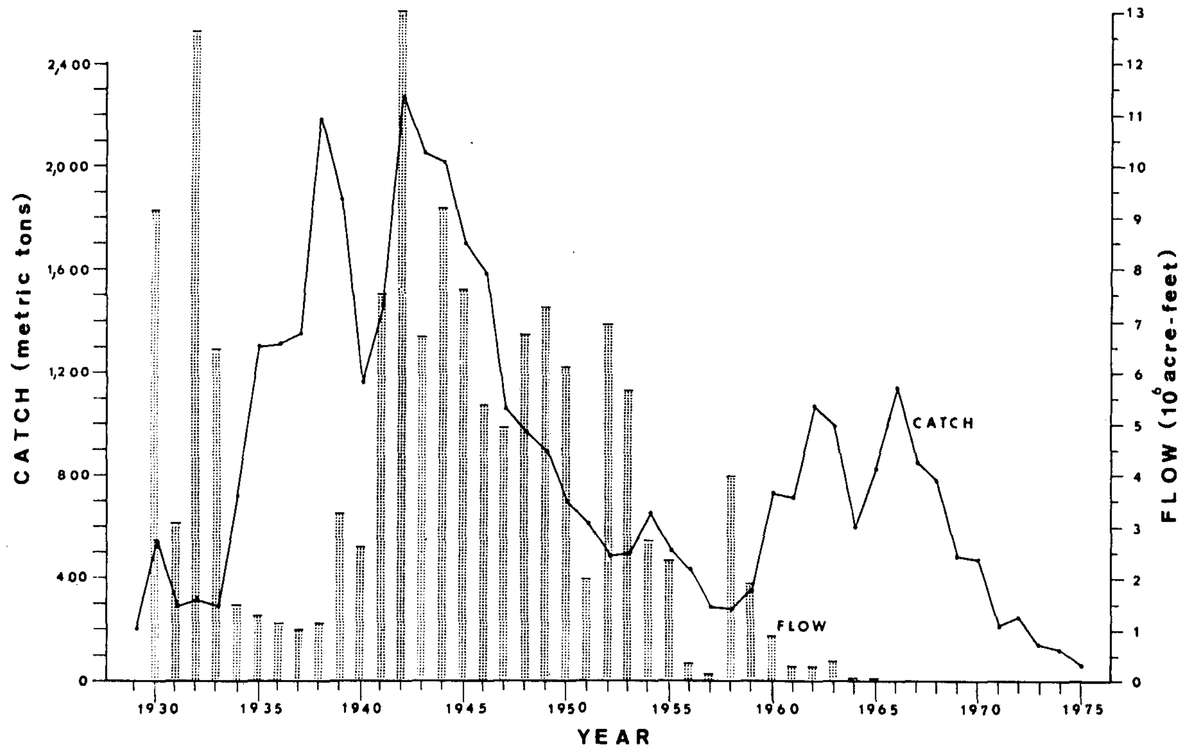

FIGURE 7.–Colorado River flow in thousands of acre-feet and totoaba fishery annual yield in metric tons for the 1930-75 period. Totoaba annual yield data are those of Figure 1. Flow data were calculated from records published in Water Supply Papers 1313, 1733, and 1926 (U.S. Geological Survey, respectively, 1954, 1964, and 1970). Flow data for 1966-75 are not shown but we do not expect them to deviate beyond the 1960-65 variation above. We have calculated the flow delivered to Mexico at the southerly international boundary (near San Luis, Ariz.) as follows (data sources are cited only on first mention): 1930-36: Colorado River at Yuma (1954:710) + Yuma Main Canal Wasteway (1954:717) + Calif. Drainage Canal (1954:723) – Alamo Canal (1954:724) + Eleven-mile Wasteway (1954:726) + Cooper Wasteway (1954:726); 1937-50: Colorado River at Rockwood Gate, Calif. (1954:712) - Alamo Canal + Eleven-mile Wasteway + Twenty-one Mile Wasteway (1954:727) + Cooper Wasteway; 1951-65: Colorado River at southerly boundary, near San Luis (1964:563; 1970:519-521).

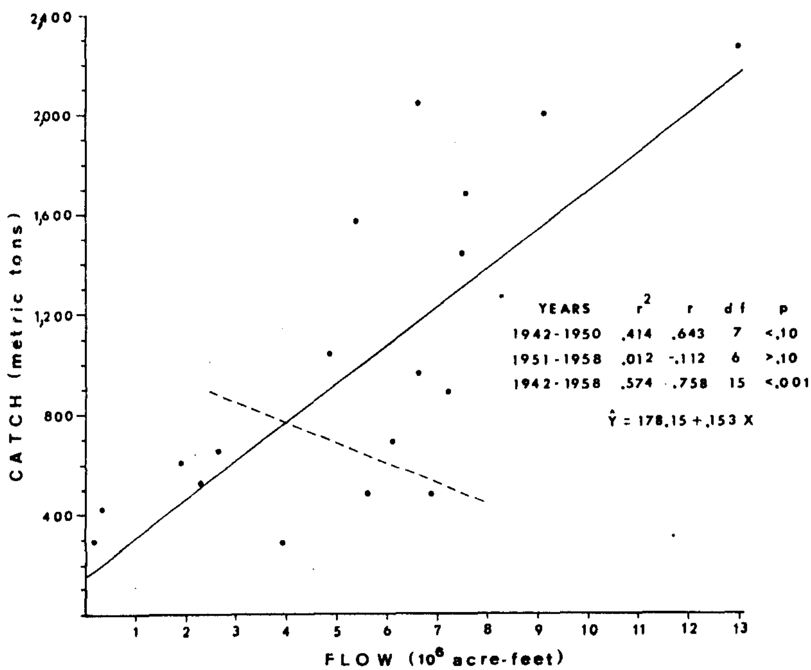

FIGURE 8.–Plot of annual totoaba yield and annual Colorado River flow for the 1942-58 period. Data are those displayed in Figure 7. The points below the dashed line represent the 1951-58 flow years. Though the relationship between catch and flow for the 1942-58 period are highly significant, the disparity between the r^2 levels for the component periods 1942-50 and 1951-58 invites caution in interpretation of these results.

islands, and flow measurements at the southernmost Mexican hydrographic station known as El Marítimo, formerly considered the best single index of actual surface input to the gulf (Schreiber 1969), were discontinued in 1968 for lack of meaningful data.[6] Further, the extensive use of all available water from the lower Colorado River drainage system for irrigation has resulted in hypersalinity of return flows and is a major problem on both sides of the international boundary. Water returned to the river channel which may reach the gulf is now likely to be at least as saline as the marine water it joins. Thompson (1968:8), summarizing the history of Colorado River flow and effects of exploitation on detrital loads, concluded, "Probably little river detritus has reached the northwestern Gulf of California in the last 55-60 years." Thus, if odor is not carried beyond upstream dams and fields where the detrital load stops, it must originate from reworking of the massive deltaic deposits by the strong tidal currents of the uppermost gulf. If Thompson's estimate is correct, this may have been occurring during the developing years of the fishery; the rate of decay of such a process is unknown.

The post-1958 flow and catch data (Figure 7) contrast with those of the previous period. We feel that the secondary peak in totoaba production may be attributable to extraneous factors such as changes in effort or efficiency (availability of nylon gill nets?) which produced a temporary increase in catch. Another possible reason may have been the enforcement of the 1955 breeding preserve regulations which offered some temporary relief from exploitation. If fishing in the sanctuary were to resume after a period of time, the yield might recover and fall in the observed manner.

We now consider the second hypothesis, that the cause of stock depletion is degradation of the nursery ground. When annual totoaba yield is compared with river flow in earlier years (e.g., the 1951 totoaba catch compared with the 1942 river flow, etc.), lag times ranging from 6 to 10 yr all give significant negative correlations ($P<0.05$) using standard linear regression techniques. The relationship is most distinct (Figure 9) when the lag time is 9 yr ($P<0.01$). The 6- to 10-yr periods correspond with estimated ages of recruitment employed below.[7] We find this negative relationship of flow and (lagged) totoaba yield highly interesting, though puzzling. The relation could be taken to imply that survival of young stages is a critical factor, since it couples increased river flow in any one year with reduced recruitment of that year class to the population. This interpretation discounts hypotheses of larval and juvenile physiological dependence on waters of lowered salinity (Berdegué 1955, 1956; Cannon 1966; Gause 1969; Sotomayor 1970). An alternate analysis using flow data only for the March-July period over the years of catch decline would be a better test of the effect of flow on larvae and small juveniles.

We know that successful reproduction still continues in the northern gulf as demonstrated by our ability to find juvenile fish on the nursery grounds. Despite searching, we have found no conspicuous subsurface freshwater seeps which might have provided local areas for limited successful spawning. We believe that reproduction occurs over the entire ancestral spawning grounds. Thus, we conclude that adverse effects of salinity changes must operate in a relative and not an absolute manner. The advantages realized by potential recruits on the nursery ground may be those of reduced predation and abundant food

[6]Nishikawa-Kinomura, K. A. 1973. Flow of the Colorado River into the Gulf of California. *In* S. Álvarez-Borrego et al., Preliminary report to the Secretariat of Hydraulic Resources on the second stage of the chemical study on insecticide contamination at the mouth of the Colorado River, p. 15-19. Unpubl. rep. Mar. Sci. Unit, Inst. Oceanol. Res., Univ. Baja Calif., Ensenada, Mex.

[7]The senior author has reviewed the published estimates of growth curves and ages of recruitment (see Arvizu and Chávez 1972, for a summary of this literature). Apparent discrepancies between reported lengths at different ages and serious disagreement between Berdegué's (1955) growth estimates and the distribution of lengths in observed commercial catches in 1963 (Arvizu and Chávez 1972) encouraged closer scrutiny of these data. The variation in lengths at particular ages and in maximum lengths reported by different authors and summarized by Arvizu and Chávez appear to derive from use of both standard length and total length measurements without discriminating between the two. The senior author calculated von Bertalanffy growth curves using a resolved maximum standard length of 1,600 mm and the intermediate lengths reported by Berdegué (1955). The new growth curves indicate that the best estimate of recruitment age is 6 or 7 yr; they also produce a length series which corresponds well with that observed in commercial catches. Male and female totoaba may vary significantly in growth rates and therefore may recruit at different ages. This variation allows extension of the possible recruitment age to 10 yr. J. E. Fitch (pers. commun.) has examined totoaba otoliths and concluded that totoaba first spawn at age 8. If totoaba do not accompany the migrant population until reproductively mature, his results are consistent with the ages of recruitment used here. However, his overall ages as read from otoliths indicate that these new growth curves may contain a wide margin of error in terms of predicted age at length observed. Fitch has also found that totoaba scales are of little use for growth studies after about age 8; this may explain the maximum lengths at age 8 or 9 reported by Nakashima (Jordan 1916), which we now believe to be erroneous. It also may account for errors in Berdegué's (1955) estimates, since he relied heavily on age determinations from scales.

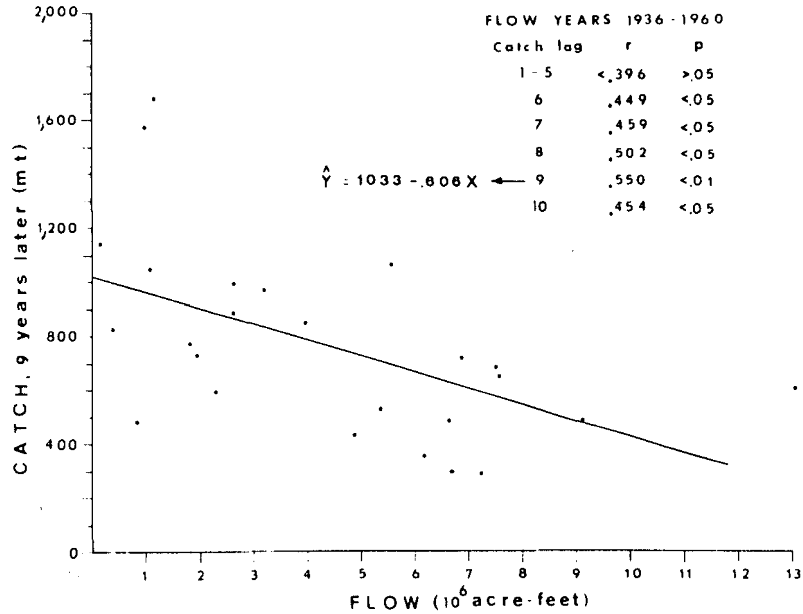

FIGURE 9.—Plot of annual totoaba yield (metric tons) 9 yr following the annual recorded flow, for the 1936-60 period. This plot displays the suggested relationship between flow and recruitment level. Linear regression calculations employing lag times from 1 to 10 yr are significant only for those years corresponding to estimated ages of recruitment (6-10 yr).

resources, both of which are directly related to substrate and shallowness, and indirectly related to flow.

The final cause suggested for the decline in totoaba stock is overfishing of the breeding population. We have examined the relationship of catch with catch n years later. If catch is a good indicator of population size, then we would expect a linear, positive relationship between population size and the size one recruitment age later. Alternatively, if catch is partially a function of sociopolitical constraints (e.g., enforcement of a preserve area and closed season resulting in a catch which significantly underrepresents the population size), we might expect a more complicated plot with a distinct cluster of years corresponding to periods of fishing regulations. We have analyzed plots of catch against catch for recruitment periods ranging from 6 to 10 yr and have found significant relationships which satisfy both of the above predictions. Graphs for all estimated ages of recruitment from 6 to 10 yr showed essentially the same pattern (Figure 10). However, we note inconsistencies which advise against drawing strong conclusions of either overfishing or the demonstrated worth of enforced regulatory measures. For example, increases in catch occur 2-3 yr earlier than is consistent with our assumption that regulatory measures were not enforced until 1955, given that the minimum age of recruitment is 6 yr. The question of a change in gear efficiency, effecting a realized increase in effort, serves to confound the analysis; although catch would increase, this factor alone could not explain recovery of catch to such high levels. We can visualize a combination of factors giving rise to the significant second peak in totoaba production (increase in gear efficiency acting on an increased population size following the period of regulation) but lacking effort data throughout the period, our hypothesis must remain speculative.

Support for the overfishing hypothesis may lie in the recent trend of the relative catches of the three main totoaba fishing fleets. Historically, the

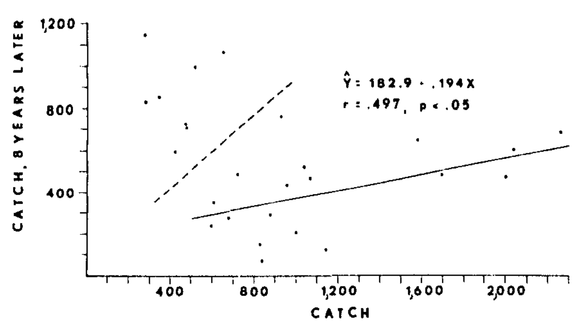

FIGURE 10.—Totoaba catch plotted against catch 8 yr previous. This examines for evidence of reduction in breeding stock by overfishing. All data are from Figure 1, in metric tons. Points above dashed line are for the 1952-59 period. The breeding sanctuary was established in 1955 and the points corresponding to the years 1955-59 may reflect enforcement of this regulation (see text).

TABLE 2.–Prime season catch,[1] in metric tons, of the three principal totoaba fishing ports, 1964-75. Data for 1965-70 period are from Arvizu and Chávez (1972). Data for 1971-75 were provided by H. Chávez (pers. commun.). The 1974-75 data are preliminary but are not expected to increase by more than 10% from these figures.

Year	Puerto Peñasco	Golfo de Santa Clara	San Felipe
1964	72.7	128.4	277.7
1965	97.0	561.2	57.0
1966	177.5	388.6	488.7
1967	188.3	173.4	334.7
1968	37.9	385.7	290.0
1969	60.2	213.8	160.9
1970	27.2	248.7	169.4
1971	69.0	46.0	95.0
1972	52.0	86.0	104.0
1973	88.0	21.0	37.0
1974	51.0	17.0	52.0
1975	49.0	4.0	5.0

[1]Catch is calculated by adding January-April yields as recorded in the official statistics.

Puerto Peñasco fleet catches fewer totoaba than either the San Felipe or Golfo de Santa Clara fleets (Table 2). This is a logical result of the fishing methods and areas worked by the three fleets. However during the last 3 yr, Puerto Peñasco has equalled or exceeded the other ports in recorded totoaba yield despite no apparent increase in effort. Our interpretation of this new trend is that the migrant population, encountered first by the Puerto Peñasco fleet along the Sonora shore, is being decimated before reaching the spawning grounds.

CONCLUSIONS

Our review of the history of exploitation of the stock, our data on spawning concentrations, breeding migration, and juvenile habitat, and our analyses of proposed hypotheses for the decline of the fishery have emphasized points of population vulnerability. Fleets of the three major ports are highly skilled at finding the migrant schools of totoaba. They have, in a sense, specialized to exploit the ascent, resident, and descent phases of the breeding migration, both by nature of their vessels and their port facilities, and by consequence of their geographic locations. This level of exploitation is possible only because the fishers are able to predict with accuracy the migration pattern. In the past, the commercial population level was high and the temporal nature of the port specializations was not a factor in the ranking of port yields. Now, when the population level has reached an all-time low, the Puerto Peñasco fleet seems to have some new advantage.

The totoaba breeding behavior we describe serves to render the resident spawning population especially vulnerable to fishing effort. Frenzied spawning in dense aggregations following a period of behavioral stimulation insures that when a net is encountered, the capture rate will be particularly high. Our capture incidence, daily catch, and gonadal maturation data confirm the consequences of these attributes. The bathymetry of the delta restricts the spawning schools to highly limited areas. These areas, or channels, are the prime fishing sites for the Golfo de Santa Clara fleet. They appear to lie (by our estimate) partially within the breeding sanctuary established by the Mexican Government.

We reiterate here the artificial fishing mortality suffered by juveniles in their forced crossing of the near-delta waters as they make their way south from the nursery grounds. We have documented some known nursery sites and have suggested characteristics of the juvenile habitat which may have predictive value in future surveys of the area.

We have examined the three most probable factors responsible for the decline in totoaba stock. Subject to the limitations of our catch and flow data, our results suggest that overfishing has played the most significant role during the pre-1958 catch period. We speculate that the low yields of the 1956-59 period may have been due to enforcement of the breeding sanctuary regulation and that this partial temporary relief from exploitation may, together with increased gear efficiency, have been responsible for the second peak in totoaba production. If this is true, then the power of regulatory measures for recovery of this commercial stock has been demonstrated. The correlation of annual yield with annual Colorado River flow, though weakened by statistical irregularities, attests to the importance of some flow-related quality of the spawning grounds. Degradation of the spawning grounds, possibly in the ability to provide olfactory cues, also may have resulted in a decline of the commercial population. According to our results, degradation of the nursery grounds, through deterioration of some unknown flow-related quality, has probably not played a significant role in the fishery's decline.

Although it may be possible to ignore statistical analyses and the conclusions therefrom, one cannot deny that the annual yield in 1975 was the minimum recorded in the history of the fishery, a mere 2.5% of the highest recorded catch. The area of the fishery has shrunk to a small fraction of its former size, and catch events have become sporadic and undependable. The span of the breeding period has been reduced from several months to a period of only 18 days within the open season of 1972. Of those 18 days, a majority of the catch occurred on 21 and 22 March. Although data are scarce, the average size of adult fish is reduced and in recent years most commercially caught individuals have probably been first- or second-year spawners. These harsh facts are indications of a fish population struggling unsucessfully for survival under pressure.

The future of the species is uncertain. Until the recent action of the Mexican Government in establishing a total closed season, the outlook was bleak, indeed. While the commercial fishery was ready to crash before its legal cancellation (a number of financial failures were reported to us), and would presumably never have hunted down and eliminated the last reproductive pair of these magnificent animals, the continued rising prices for totoaba in a seller's market would have guaranteed continued maximum pressure. If there are behavioral elements in the reproductive pattern of the species which require mutual stimulation in large schools for reproductive success, a threshold may have already been crossed which will drive the totoaba the way of the passenger pigeon. The trends produced by irreversible change of the spawning ground may prove more important than we have speculated. In either of the last two circumstances, the ability of the stocks to rebound upon release of fishing pressure may be critically impaired.

We suggest three meaningful measures at this stage: 1) Continuation of the total closed season which has been imposed, until intensive studies document a strong and vigorously increasing population. We suggest an enforcement period of about 1½ times our estimated 6-yr minimum recruitment age, or 10 yr. 2) Action by the U.S. Government (the major market area) complementing the Mexican action by declaring the totoaba an endangered species, to facilitate enforcement of the neighbor country laws by removing much of the stimulus for poaching and smuggling. 3) Intensive scientific investigation to provide knowledge of the species' autecology and behavior with potential application to all facets of management, ranging from environmental manipulation to hatchery techniques. Failing these, we conclude that the probability of extinction of *Cynoscion macdonaldi* by the year 2000 is high.

ACKNOWLEDGMENTS

Various research grants and contracts contributed to the support of this work and are here gratefully acknowledged: International Union for the Conservation of Nature and Natural Resources/World Wildlife Fund Project No. 623; National Science Foundation Grants GB29101 and GB34675; National Aeronautics and Space Administration Contract NAS5-21777; and a special University of Arizona Foundation Grant. We acknowledge with sincere appreciation the support and professional participation of Mexican authorities and scientists in this work. Luis Kasuga Osaka, Director of the National Institute of Fisheries, Mexico, and Pedro Mercado Sánchez of the Subsecretariat of Fisheries, Ministry of Industry and Commerce, helped us obtain necessary permits (3977, 5344, 8202, and 12183) for work in the field and in other ways provided important support and encouragement. Among the many members of the National Institute of Fisheries who gave freely of their time and efforts, special mention must be made of Joaquín Arvizu and Humberto Chávez, who cooperated in field work and data analysis. We are particularly indebted to Biologist Chávez, Head of the Institute's Department of Fisheries Resources, for important contributions and professional advice from inception of field work to manuscript preparation. The Fishery Inspectors of San Felipe, Baja California Norte, and Puerto Peñasco, Sonora, rendered valuable assistance in making contacts with fishers and made date available. Francisco Aguilera Grijalva, Fishery Inspector at Golfo de Santa Clara, Sonora, made particular efforts on our behalf and was of invaluable assistance in collection of detailed catch data. We thank all the students of the University of Arizona who rendered assistance on field trips, and all the staff and students of the Institute of Oceanologic Investigations, Autonomous University of Baja California, who have been such productive partners in most of our work in the northern Gulf of California. Special recognition is due L. T. Findley for his field and museum contributions and enthusiastic interest. We greatly appreciate the time spent by D. A. Thomson, J. Tash, and G. Pyke who read the manuscript critically and consulted on matters of data analysis and interpretation (all responsibility for errors is ours). It is impossible to overvalue the contribution of Lupe P. Hendrickson in clerical, translation, and editorial functions throughout the entire course of the project. Lastly, a particular expression of gratitude is due to Javier Ramírez of Golfo de Santa Clara, master fisher and astute student of nature, who was frequently the key to success in field projects.

LITERATURE CITED

ARVIZU, J., AND H. CHAVEZ.
1972. Sinopsis sobre la biología de la totoaba, *Cynoscion macdonaldi* Gilbert, 1890. FAO (Food Agric. Organ. U.N.) Fish. Synop. 108, 21 p.

BERDEGUE, A. J.
1955. La pesqueria de la totoaba (*Cynoscion macdonaldi* Gilbert) en San Felipe, Baja California. Rev. Soc. Mex. Hist. Nat. 16:45-78.
1956. Peces de importancia comercial en la costa noroccidental de Mexico. Secre. Mar., Dir. Gen. Pesca Ind. Conexas, 345 p.

BREDER, C. M., JR., AND D. E. ROSEN.
1966. Modes of reproduction in fishes. Natural History Press, Garden City, N.Y., 941 p.

CANNON, R.
1966. The Sea of Cortez. Lane Magazine and Book Co., Menlo Park, Calif., 283 p.

CHAVEZ, H.
1973. Descripción de los ejemplares juveniles de totoaba, *Cynoscion macdonaldi* Gilbert. Rev. Soc. Mex. Hist. Nat. 34:293-300.

CHUTE, G. R.
1928. The totuáva fishery of the California Gulf. Calif. Fish Game 14:275-281.
1930. Seen Kow, a regal soup-stock. Calif. Fish Game 16:23-35.

CRAIG, J. A.
1926. A new fishery in Mexico. Calif. Fish Game 12:166-169.

CROCKER, R. S.
1932. The white sea-bass and related species that are sold in California fish markets. Calif. Fish Game 18:318-327.

FITCH, J. E.
1949. Mexican corbina and totuava. *In* The commercial fish catch of California for the year 1947 with an historical review 1916-1947, p. 83-84. Calif. Dep. Fish Game, Fish Bull. 74.

GABRIELSON, I. N., AND F. R. LAMONTE.
1954. The fisherman's encyclopedia. Stackpole Co., Harrisburg, Pa., 730 p.

GAUSE, C. I.
1969. A fish threatened. Underwater Nat. 6:28-31.

GILBERT, C. H.
1891. Scientific results of the explorations by the U.S. Fish Commission steamer Albatross. No. XII–A preliminary report on the fishes collected by the steamer Albatross on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. Proc. U.S. Natl. Mus. 13:49-126.

GUEVARA, S.
1974. Sobre le eclogía de los juveniles de totoabe *Cynoscion macdonaldi* Gilbert. (Abstr.) *In* Resûmenes Quinto Congreso Nacional de Oceanografıa, 22 Oct. 1974, p. 7. Guaymas, Sonora, Mexico.

JORDAN, D. S.
1916. Notes on the totuava (*Cynoscion macdonaldi* Gilbert). Copeia 1916:85.

JORDAN, D. S., AND B. W. EVERMANN.
1898. The fishes of North and Middle America. Bull. U.S. Natl. Mus. 47, Part 2:1241-2183.
1902. American food and game fishes. Doubleday, Page & Co., N.Y., 573 p.

JORDAN, D. S., B. W. EVERMANN, AND H. W. CLARK.
1930. Check list of the fishes and fishlike vertebrates of North and Middle America north of the northern boundary of Venezuela and Colombia. U.S. Bur. Fish., Rep. U.S. Comm. Fish. 1928. Part II. Append. 10, 670 p. (Doc. 1055.)

LANHAM, U.
1962. The fishes. Columbia Univ. Press, N.Y., 116 p.

SCHREIBER, J. F., JR.
1969. Changes in Colorado River flow. *In* D. A. Thomson et al. (editors), Environmental impact of brine effluents on Gulf of California, p. 83-87. U.S. Dep. Int., Off. Saline Water, Res. Dev. Prog. Rep. 387.

SOTOMAYOR, C.
1970. La totoaba, una especia que se extingue lentamente. Téc. Pesq. 3:22-25.

THOMPSON, R. W.
1968. Tidal flat sedimentation on the Colorado River Delta, northwestern Gulf of California. Geol. Soc. Am., Mem. 107, 133 p.

THOMSON, D. A.
1969. The commercial fisheries industry. *In* D. A. Thomson et al. (editors), Environmental impact of brine effluents on Gulf of California, p. 100-103. U.S. Dep. Int., Off. Saline Water, Res. Dev. Prog. Rep. 387.

U.S. GEOLOGICAL SURVEY.
1954. Compilation of records of surface waters of the United States through September 1950. Part 9. Colorado River Basin. [U.S.] Geol. Surv. Water-Supply Pap. 1313, 749 p.
1964. Compilation of records of surface waters of the United States, October 1950 to September 1960. Part 9. Colorado River Basin. [U.S.] Geol. Surv. Water-Supply Pap. 1733, 586 p.
1970. Surface water supply of the United States 1961-65. Part 9. Colorado River Basin. Vol. 3. Lower Colorado River Basin. [U.S.] Geol. Surv. Water-Supply Pap. 1926, 571 p.