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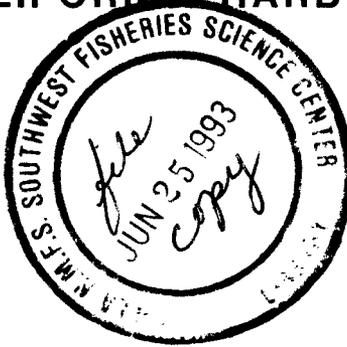
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SOUTHWEST FISHERIES CENTER

DECEMBER 1986

NATIONAL MARINE FISHERIES SERVICE

## FACTORS AFFECTING THE RECOVERY OF *Phocoena sinus*, THE VAQUITA OR GULF OF CALIFORNIA HARBOR PORPOISE



By

Jay Barlow

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FACTORS AFFECTING THE RECOVERY OF PHOCOENA SINUS,  
THE VAQUITA OR GULF OF CALIFORNIA  
HARBOR PORPOISE

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ABSTRACT

The vaquita (Phocoena sinus) is a small porpoise found only in the northern Gulf of California. This species may have been subject to high levels of mortality in the gill-net fishery for totoaba (Totoaba macdonaldi) in the 1960s and early 1970s (prior to a ban on totoaba fishing). Incidental fishing mortality continues to be associated with shark gill-net fishing and illegal totoaba fishing. Based on its limited range and history of incidental mortality, several national and international organizations have concluded that P. sinus is in danger of extinction, and the species is included in the list of U.S. Endangered Species. Little is known about the species. Food sources include small fish and squid. Sightings have occurred most commonly in water from 13 to 18 m deep. No population estimates have been made to date, and the present and historical range of the species is currently the subject of debate. Researchers who have conducted surveys agree, however, that the species is rare. Insufficient information exists to estimate population growth rates, but based on comparisons to closely related species, the maximum annual rate is probably less than 10%. The actual rate of growth is less (and may be much less) due to continued fishing mortality and possible habitat modifications. Given available information and current survey technology, it will be many years before researchers can determine whether population size is increasing or decreasing.

INTRODUCTION

The vaquita or Gulf of California harbor porpoise (Phocoena sinus Norris and McFarland 1958) has the most limited range of any marine mammal. This species appears to be limited to the northern region of the Gulf of California (Brownell 1986). Although some sightings have been claimed south of this area, no specimens have been found outside of the northern Gulf, and the sightings from the central regions of the Gulf and southward have

been questioned (Brownell 1986). Within its limited range, P. sinus is described as rare (Hoz and Colmenero 1985). Prior to 1986, only 20 sightings of P. sinus have been described in scientific literature (Silber, in press), and many of these lack sufficient details to be substantiated (Brownell 1986). Since 1986, 12 sightings were made on one expedition (Silber, in press). Four previous expeditions resulted in only 7 probable sightings of P. sinus (Villa 1976; Wells, Würsig and Norris 1981; Vidal et al. 1985; Turk et al. 1986; Vidal et al., in press).

P. sinus is vulnerable to incidental mortality in commercial fishery operations. Historically, P. sinus has been taken in the gill-net fishery for totoaba (Totoaba macdonaldi), a large sciaenid (Norris and Prescott 1961; Robles, Findley, Vidal, Brownell, and Manzanilla 1986; Brownell, Findley, Vidal, Robles and Manzanilla, in press), in shrimp trawls (Norris and Prescott 1961; Robles, Vidal, and Findley, in press), and in shark and other gill net fisheries (Brownell 1982; Robles et al. 1986; Robles et al., in press). P. sinus was taken in a small experimental fishery for totoaba during 1985 (Robles et al. 1986), and is also taken in illegal fishing for totoaba (Robles et al. 1986; Robles et al., in press).

Given its limited range, low apparent abundance, and susceptibility to fishing mortality, P. sinus is vulnerable to depletion and possibly extinction. In 1978, Mexico listed P. sinus in its list of wildlife species that are rare or in danger of extinction (Villa 1978). In the same year the International Union for the Conservation of Nature and Natural Resources (IUCN) included P. sinus in the classification of "vulnerable species" in the Red Data Book (Brownell 1983). In 1979, P. sinus was included in Appendix I of the Convention on International Trade in Endangered Species (CITES) (Brownell 1983). In February 1985, P. sinus was listed as an endangered species under the U.S. Endangered Species Act (U.S. Federal Register, Vol. 50(6):1056-1059).

As a consequence of listing P. sinus as an endangered species under United States laws, the U.S. Congress has requested that the National Marine Fisheries Service (NMFS) review information regarding the species and consider factors influencing or promoting its recovery. This document has been written as a contribution towards fulfilling this requirement. In this report, I review the available biological information on P. sinus, comment on the weaknesses and gaps in our current knowledge, and make suggestions for filling these gaps.

#### BEHAVIOR AND ECOLOGY

Given the few sightings that have been made by scientists to date, little is known about the behavior and ecology of P. sinus.

It is related (most closely) to Phocoena spinipinnis (Burmeister's porpoise) and (less closely) to Phocoena phocoena (harbor porpoise) (Norris and McFarland 1958; Brownell 1983). The behavior and food habits of P. sinus may be similar to those of the two congeners. From stomach contents of two specimens found on the beach 20 km north of San Felipe, Baja California Norte, P. sinus are believed to feed on small (20-25 cm) fish, including the bronze-striped grunt (Orthopristis reddingi) and croaker (Bairdiella icistia) (Fitch and Brownell 1968), as well as several other species of fishes and squids (Brownell 1982; L. T. Findley, pers. comm.). Both the grunt and the croaker are found throughout the Gulf of California (Thomson and McKibbin 1981).

Like P. phocoena, P. sinus occurs in small groups of 1 to 4 (Norris and Prescott 1961; Silber, in press), although loose aggregations of up to 8-10 individuals have been reported (Silber, in press). Ventilation patterns have been observed for two cow-calf pairs (Silber, Newcomer, and Barros, in prep.). The general pattern they describe is for a series of 3 to 5 rapid surfacings followed by a long dive of approximately 45 or 80 seconds (respectively for calves and cows). For the adults, surface time was estimated to be approximately 20% of total observation time (Silber et al., in prep.). These patterns are very similar to those of P. phocoena (Watson and Gaskin 1983; Taylor and Dawson 1984; Barlow, Oliver, Jackson, and Taylor, in prep.). P. sinus has been described as "elusive" (Silber, in press) and avoids vessels. Individuals have been sighted most frequently in water 13-28 m deep (Silber, in press), although they have also been caught in totoaba gill nets that were set in less than 10 meters (A. Robles, pers. comm.). Recent information has been gathered on vocalizations of P. sinus (Silber and Barros 1986), but this information is not yet analyzed or available.

Several gaps exist in information on behavior and ecology of P. sinus. Detailed information on food habits is relatively old and is based on data from only two specimens. It would be desirable to add additional information and to determine their dependence (if any) upon commercially harvested fish and invertebrate species. L. T. Findley, A. Robles, and R. L. Brownell, Jr. are currently analyzing the wider spectrum of dietary items taken from recently obtained specimens (L. T. Findley, pers. comm.). Current data on ventilation patterns are limited to cow/calf pairs; additional observations of other sex and age classes may be essential for designing efficient survey methods for this species and in extrapolating survey results to a population estimate. Likewise, additional information on depth distribution could contribute to the design of a survey. Collection of additional vocalization data is planned (G. Silber, pers. comm.) to evaluate the feasibility of using passive acoustic surveys to estimate abundance.

## INCIDENTAL MORTALITY

Little information exists for estimating the current or historical levels of incidental mortality in fishing operations. The highest levels of kill were associated with the gill-net fishery for totoaba (Brownell 1983). The totoaba fishery developed ca. 1929; the predominant mode of fishing changed from spearing, handlines, and dynamite to modern nylon gill nets (Flanagan and Hendrickson 1976). The peak commercial catches were recorded in 1942 (2,261 metric tons) with other peak years including 1934, 1962, and 1967 (Flanagan and Hendrickson 1976). Norris and Prescott (1961) made the first mention of incidental mortality of P. sinus in totoaba gill nets. This fishery was largely limited to the totoaba spawning grounds in the far northern regions of the Gulf of California during their spawning season (January to May) (Flanagan and Hendrickson 1976). The typical areas fished commercially are shown in Fig. 1. Brownell (1982) estimated that the incidental kill of P. sinus was in the range of tens to hundreds of porpoise per year in the early 1970s; however, this estimate was not based on statistical sampling. The totoaba fishery was closed in 1975 by the Mexican government as a result of marked declines in the totoaba stock (Arvizu and Chávez, 1972; Flanagan and Hendrickson, 1976).

Despite the closure, illegal fishing for totoaba has continued in recent years, and it is still possible to buy fillets in regional markets (Robles et al., in press). Currently the totoaba may still be in danger of extinction due to illegal fishing and possible habitat degradation (Robles et al., in press); however, some fishing cooperatives in the northern Gulf claim that stock levels have recovered and that the totoaba fishery should be re-opened (A. Robles, pers. comm.). A small-scale experimental fishery for totoaba was allowed in March and May 1985 and in February 1986 near El Golfo de Santa Clara, Sonora. That experimental fishery was monitored, and a minimum of 14 porpoise deaths was attributed to gill nets (Robles et al. 1986); however, at least 6 of these individuals were probably taken in shark gill nets (Brownell et al., in press).

Incidental mortality in fisheries for other than totoaba is believed to include mortality in shrimp trawls and in other forms of gill netting (Norris and Prescott 1961; Brownell 1982; Robles et al., in press). No estimates are available for the magnitude of this source of mortality.

The most direct way to promote the recovery of P. sinus would be to reduce the level of human inflicted mortality. Better information is needed on the magnitude of incidental

mortality, especially in the growing shark gill net fishery in the northern Gulf (A. Robles, pers. comm.). Also, in order to interpret the relative magnitude of incidental mortality, per-capita mortality rates are needed (for which an estimate of population size is required, see below). Methods should be investigated for reducing the entanglement in gill nets. Methods that have shown promise include implementing local area closures (for sea birds, California State Senate Bill 2266, June 1984), implementing depth closures (for sea otters, California State Senate Bill 1475, June 1982), and making nets more acoustically "visible" (for Dall's porpoise, Jones, Breiwick, Bouchet, and Turnock, in prep.).

#### POPULATION DISTRIBUTION AND SIZE

Although all researchers do not agree, most believe that the distribution of P. sinus is limited to the uppermost Gulf of California. The collection locations of all known specimens are shown in Figure 1. The location of the sightings that were accepted by Brownell (1986) and the subsequent sightings by Vidal et al. (1985) and Silber (in press) are also shown in Fig. 1.

No reliable estimates exist for the population size of P. sinus. Several independent expeditions have recently surveyed more than 4500 linear kilometers in the Gulf of California with limited success: Villa (1976) reported 3 probable sightings during a 15-day trip; Wells, Würsig and Norris (1981) surveyed 1959 km with 2 probable sightings; Vidal et al. (1985) made 1 (possibly 2) sightings in 1665 km (O. Vidal, pers. comm.); Turk et al. (1986) surveyed at least 300 km and made one probable sighting; and Silber (in press) made 12 sightings while surveying a 843 km. Given the limited range (Brownell 1986) and the paucity of sightings during recent expeditions, the population is probably very small. Rough lower limits may be placed on the current abundance based on recent observations. Silber (in press) saw a total of 30 individuals in 11 different locations in the northern Gulf of California. In recent experimental gill netting for totoaba, 14 were caught incidentally (Robles et al. 1986; Brownell et al., in press). Based on these observations, a lower limit on population size might be 50-100 individuals. It is not possible to estimate a reliable upper limit on population size based on available information.

An intensive survey would be required to provide population estimates for P. sinus. Such a survey has been recommended as a high priority research topic by the Sub-committee on Small Cetaceans of the International Whaling Commission's Scientific Committee (IWC 1984). Funds for such a survey have not been appropriated to date. Previous experience with another porpoise (P. phocoena) has shown that surveys using large research ships

are less subject to changes in weather than are estimates based on aircraft surveys (Barlow, in prep.; Barlow et al., in prep.). Conditions are such in the northern Gulf of California that both ship and aircraft surveys would be difficult. The water is commonly very turbid, limiting aerial observations to the few seconds when some part of the porpoise actually breaks the surface. Ships move much slower, thus the chance of observing a surfacing porpoise is greater, but much of the northern Gulf is too shallow for operation of large vessels. The possibility exists of using multiple small boats working in tandem (A. Robles and O. Vidal, pers. comm.).

#### REPRODUCTION, NATURAL MORTALITY, AND POPULATION GROWTH RATES

Given age-specific estimates of reproduction and mortality it would be possible to calculate the population growth rate for P. sinus. This information is essential for estimating the equilibrium harvest (ie., the rate at which individuals may be removed from a population without affecting the number that would be present in the subsequent year). Research has shown that, in general, the maximum population growth rates for cetaceans are very low (Reilly and Barlow 1986). Unfortunately, almost nothing is known about the rates of reproduction, natural mortality, and population growth for P. sinus. In this paper, I will estimate limits on the population growth rate for P. sinus based on what is known about reproductive rates and natural mortality rates of closely related species. These results should be accepted with caution, however, because taxonomic affinity does not necessarily imply similarity in life history traits (Brownell 1984).

Little is known about reproduction in P. sinus or its putative closest relative, P. spinipinnis, (Gaskin, Smith, Watson, Yasui, and Yurick 1984). For P. sinus, Silber (in press) noted the presence of 6 calves out of 31 individuals observed. Because maturity and sex ratio information is lacking, it is not possible to estimate reproductive parameters from this sample. Instead, estimates of reproductive parameters for P. sinus must be taken from analogy to a related species, P. phocoena, for which more information is available. Females of this species mature at approximately 3 to 5 years (Gaskin et al. 1984). Age determination is, however, difficult for most cetacean species in general (Myrick and Perrin 1980) and specifically for porpoises (Gaskin et al. 1984); hence, this range in estimates may reflect variation in aging techniques rather than true variation in maturation rates. Most estimates of gestation time range from 10-11 months for all porpoise species (Gaskin et al. 1984). A female that matured at age 3 could first give birth at age 4. Reproduction in P. phocoena is strongly seasonal with mating occurring in middle to late summer and with parturition occurring in late spring and early summer (Gaskin et al. 1984). Except in very rare cases, the maximum litter size for delphinoids is 1

(Perrin and Reilly 1984), and this rule appears to hold for phocoenids as well. Lactation in P. phocoena continues after birth for a period of up to 8 months (Gaskin et al. 1984). Simultaneously pregnant and lactating females have been found in samples from several populations (Gaskin et al. 1984), indicating that mature females can give birth every year. This is verified by cases where individually recognizable females were accompanied by different calves in consecutive years (Watson 1976; Taylor and Dawson, manuscript). In most studies, however, the percentage of mature females that were simultaneously pregnant and lactating was less than 100% (Gaskin et al. 1984), indicating an average calving interval greater than 1 year.

Even less information is available about natural mortality rates. Most researchers have agreed, however, that porpoises are relatively shorter lived than delphinid cetaceans, and P. phocoena probably lives to a maximum of 13-15 years, with few individuals living longer than 7-8 years (Gaskin et al. 1984). This short life span is indicative of a high mortality rate in adults. Studies of general mortality patterns in mammals indicate that first year mortality rates are typically greater than that of adults (Caughley 1966; Siler 1979). Although precise estimates of natural mortality in adults are difficult to determine, it is possible to determine likely maximum values for mortality rates from knowledge of longevity. For example, if the calf mortality rate were 0.50 and the average adult mortality rate were 0.10, approximately 10% of a population would live to an age of 15 years. Based on a longevity of 15 years, it is likely that true mortality rates are higher than these values. In fact, mortality rates of porpoises probably change with age, as they have been found to do in other mammals (ie. a decrease during the juvenile period followed by a monotonic increase with age) (Caughley 1966; Siler 1979). Insufficient information exists to determine age specific mortality rates for porpoises.

I estimate maximum limits on the rate of population growth for P. sinus based on ranges of values for reproductive and mortality rates. Growth rate is reported as the annual finite rate of increase,  $\lambda$  (Birch 1948), or the multiplicative factor applied to the population size at one year to obtain the population size the next year. I used the methods and computer programs that were previously used by Reilly and Barlow (1986) to model growth in delphinid cetaceans. Different ranges in input parameters were used to more closely model phocoenid biology. Population growth rate was estimated as the principal eigen value of a Leslie matrix (Reilly and Barlow 1986). This method calculates an equilibrium growth rate and assumes that the population is in a stable age distribution (Caughley 1966).

Parameters used to calculate finite rates of increase included adult and calf survival rates, age at attainment of sexual maturity for females, and calving interval for mature

females. These parameters were re-expressed as elements of a Leslie matrix. Adult survival rates were allowed to vary between 0.71 and 0.90. Calf (first year) survival rates were allowed to vary from 0.50 to the square of the adult survival rate (the latter has been used to approximate the maximum value of first year survival when young are totally dependent on their mothers, Reilly and Barlow 1986). Ages at first parturition of 4, 5, and 6 years were considered (corresponding to ages of sexual maturity ranging from 3 to 5 years). Calving intervals of 1 and 2 years were included; however, it should be remembered that a 1-year calving interval is the biological maximum, and given natural infertility, spontaneous abortions, and occasional disease, this value is not likely to be attained as the average value in any natural population.

The resulting population growth rates based on the above ranges in reproductive and mortality rates are shown in Figures 2, 3, and 4 (for ages at first birth of 4, 5, and 6 years, respectively). In all cases, a 2-year calving interval is not consistent with population growth rates above 1.0. Within the limit of 0.90 for adult survival, and given an age at first parturition of 4 years, the maximum rate of population growth was 1.10, or 10% growth per year. The corresponding values with first parturition at 5 and 6 years are 7% per year and 4% per year (respectively). These values are the maximum rates that are possible given the parameter values that were deemed reasonable here; these rates of increase do not allow for human-inflicted mortality and, because they depend on an average calving interval of 1 year, are not likely to be attained in any natural population.

The broad range of parameter values used to estimate the maximum growth rate of the P. sinus population results from lack of sufficient information. Additional data will be limited to those which can be taken from occasional specimens found along the beaches of the northern Gulf of California and, possibly, a few specimens recovered from fishing nets. Given the limitations on future data gathering, refinements in mortality estimation are not likely from samples of aged specimens. Samples of aged individuals may, however, be useful in verifying the longevity estimate which is used to indirectly place limits on natural mortality rates. The causes of natural mortality in P. sinus are not known, but may include predation by sharks and killer whales Orcinus orca, parasites, disease, and starvation. Methods of reducing natural mortality may become apparent if more information becomes available. Necropsies should therefore be performed on beach-cast specimens to determine causes of death and on gill-net specimens to look for signs of disease.

A greater opportunity exists to narrow the estimates of reproductive rates from the collection and analysis of additional specimens. Age at attainment of sexual maturity can be estimated

from relatively small samples if the variance in maturation rates is small. Also, the calving interval might be more precisely estimated from field studies of the fraction of calves in the population or by observing individual females over successive years. Given the paucity of sightings to date, the likely success of both of these types of field studies is doubtful unless areas can be identified in which P. sinus regularly occurs and can be consistently found. Aerial surveys immediately after the parturition season might be useful to refine estimates of the fraction of calves in the population.

#### HABITAT AND HABITAT MODIFICATION

Given the limited range of P. sinus, habitat quality may play a major role in determining whether recovery is possible and how rapidly it may occur. Habitat degradation may take the form of pollution with organic compounds, reduced productivity due to the reduction of fresh water and nutrients from the Colorado River, reductions in food supplies due to commercial fishing operations, or catastrophic accidents such as a large oil spill. Each of these potential factors will be considered below.

The reproductive potential of coastal marine mammal populations can be reduced by the presence of high concentration of pollutants, specifically PCB, DDT, and their derivatives. Porpoise have been shown to accumulate very high concentrations of these organic pollutants (Otterlind 1976; O'Shea, Brownell, Clark, Walker, Gay, and Lamont 1980; Gaskin, Holdrinet and Frank 1982; Gaskin, Frank, and Holdrinet 1983). Reproductive disorders and population declines in European populations of P. phocoena have been attributed to high PCB concentrations (Otterlind 1976; Wolff 1981). Concentrations of DDT and PCB residues in P. phocoena in California are within the range of values associated with reproductive impairment in pinnipeds (O'Shea et al. 1980). Analysis of tissue samples from P. sinus could determine whether pollutants might be adversely affecting the recovery of this species. Blubber samples are available from 13 net-caught specimens collected in 1985 (R. Brownell, pers. comm.).

Water flow into the Gulf of California from the Colorado River has been greatly reduced by dams and water projects in the southwestern United States. This may affect P. sinus (Brownell 1982). The Colorado River may have been a major source of nutrient input to the northern Gulf of California. With the loss of this input it is possible that general levels of biological productivity could be reduced, reducing the levels of food resources for P. sinus (and other natural populations). In the most extreme case, this could cause increased "natural" mortality via starvation or increased susceptibility to disease. In a less extreme case, it could cause a reduction in reproductive

potential or a reduction in carrying capacity (ie., the number of porpoise that could be supported by ecosystem at equilibrium). Additional information about fat levels or other indices of general health from specimens recovered from gill nets might be useful in assessing the impact of general reductions in productivity. Also, oceanographic studies might be able to more precisely define the link between rates of water input from the Colorado River and general productivity in the northern Gulf.

Although the fishery for totoaba has declined, other fisheries have continued to develop in the northern Gulf of California (A. Robles, pers. comm.). Important commercial fisheries exist for penaeid shrimp and sharks. The shrimp trawl fishery also catches large numbers of "trash" fish which are not kept. It is not possible to predict with any precision the effect of commercial fishing on this or any other marine mammal population. Again the best way to assess potential effects might be to assess the physiological health of P. sinus specimens that are recovered from gill nets. Additional studies of stomach contents might help establish or rule out competition between commercial fisheries and P. sinus.

Exploratory drilling for oil reserves has begun in the northern Gulf. In the early 1980s, two drilling platforms were erected near Puerto Peñasco and one near El Golfo de Santa Clara (A. Robles, pers. comm.). Oil reserves were reportedly found in the northern Gulf, but exploration has currently stopped and two of the drilling platforms have been removed (A. Robles, pers. comm.). Future development of oil production in this area raises the possibility of a large oil spill which could affect P. sinus. It is difficult to assess the potential danger of oil spills to this species.

#### RESEARCH AND INFORMATION NEEDS FOR MANAGEMENT

Accurate information is needed for the intelligent management of any species. Little is known about P. sinus, hence the information needs are great. Below I list items which, if known, would contribute significantly to management of this species. No attempt has been made to set priorities within this list.

- 1) Additional information on food habits.
- 2) Information on behavior as it might relate to survey design.
- 3) Knowledge of which fisheries are currently taking P. sinus and knowledge of the current status of those fisheries (declining, stable, or increasing).

- 4) Accurate estimates of the annual rate of incidental fishing mortality.
- 5) Estimates of the area inhabited by the species.
- 6) Estimates of population size.
- 7) Knowledge of the age at sexual maturation, the calving interval, and longevity of females.
- 8) Information on sources of natural mortality.
- 9) Analysis of tissue samples for pollutant concentrations.
- 10) Studies of productivity in the northern Gulf and the effect of restrictions in Colorado River flow on productivity.
- 11) Information on plans for future oil exploration and development, and information on the possible affect of oil spills in the northern Gulf.

#### CONCLUSION

The survival of P. sinus is not certain. In ecology, the Allee effect (Allee et al. 1949, p. 347) and minimum viable population (MVP, Gilpin and Soulé 1986) have been used to describe the tendency of some populations to continue to decline if their population size is reduced below a critical value. It is not possible to say whether such a critical value exists for P. sinus and, if so, whether it has been reached. It is certain, however, that to promote the recovery of this species, human impacts must be minimized. The most immediate need is to reduce incidental mortality in fishing operations. The possible adverse affects of habitat degradation are more difficult to deal with, but some assessment of its impact may be gleaned by examining the pollutant levels and physiological indices of any specimens that become available.

It is certain that recovery, if it occurs, will be slow. Based on analyses presented here, the maximum rate of growth for P. sinus is less than (and may be much less than) 10% per year. Only a handful of new individuals may be added to the population each year. This rate of change will not be noticeable unless accurate surveys can be executed on a regular basis to monitor the population. Currently the methodology for such surveys does not exist. Estimates of maximum rates of population growth may be refined with the accumulation of additional knowledge of the life history of the species; however, actual rates of increase

will probably remain immeasurable for the foreseeable future. Because of this, the results of any conservation efforts will not be recognized for many decades. The most conservative management scheme for this species would be predicated on the assumption that the species is continuing to decline, unless an increase can be documented. Any other management approach, if applied to a slow growing species like P. sinus, can result in extinction before researchers have the time and technology to document a decline.

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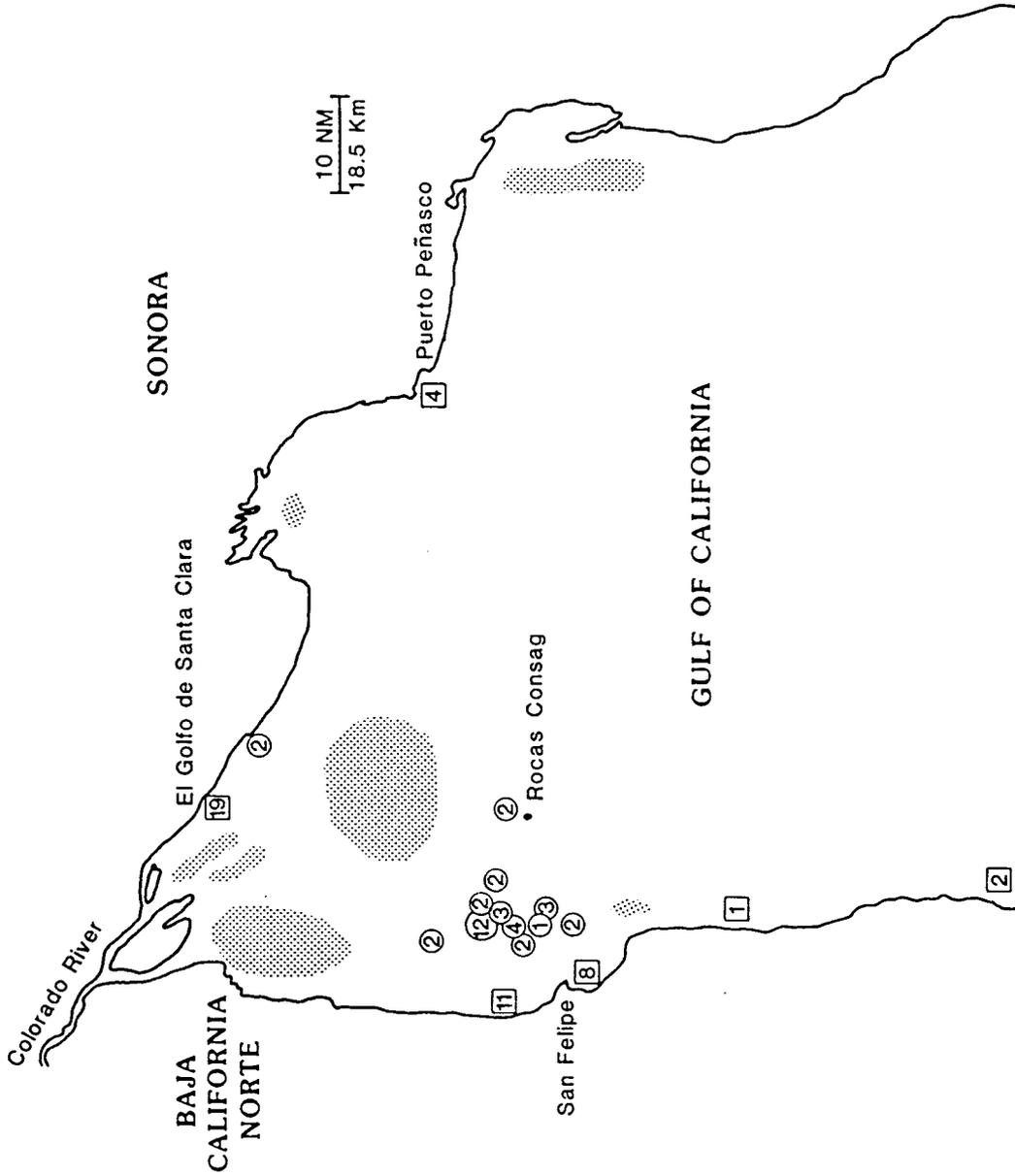


Figure 1. Distribution of validated sightings of *P. sinus* (circles) (Vidal et al. 1985; Brownell, in press; Silber, in press) and sites from which physical specimens were obtained (squares) (Brownell, in press). Numbers indicate the group size or number of specimens from a given site. Shaded areas denote principal locations of totoaba commercial catches in 1972 (Flanagan and Hendrickson 1976).

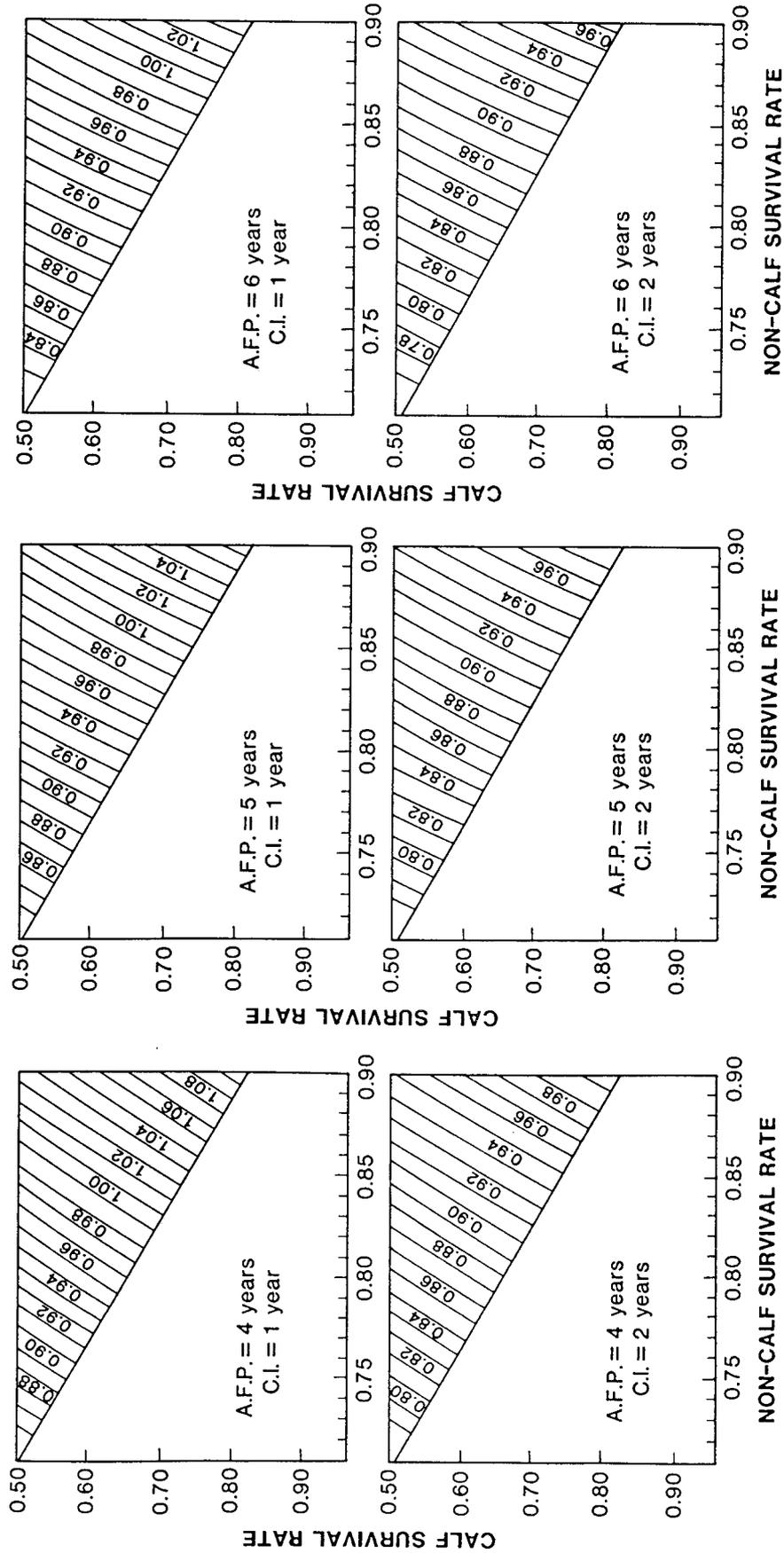


Figure 2. Annual finite rates of population growth,  $\lambda$ , assuming non-calf survival rates ranging from 0.71-0.90 and calf survival rates ranging from 0.50 to the square of the non-calf survival rate. Each panel represent a different combination of maturation age and calving interval. Age of first parturition (A.F.P.) ranges from 4 to 6 years (left to right) and calving intervals (C.I.) range from 1 to 2 years (top to bottom).