Silber 90

UNIVERSITY OF CALIFORNIA

SANTA CRUZ

DISTRIBUTIONAL RELATIONS OF CETACEANS IN THE NORTHERN GULF OF CALIFORNIA, WITH SPECIAL REFERENCE TO THE VAQUITA, *PHOCOENA SINUS*

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Gregory Keith Silber

June 1990

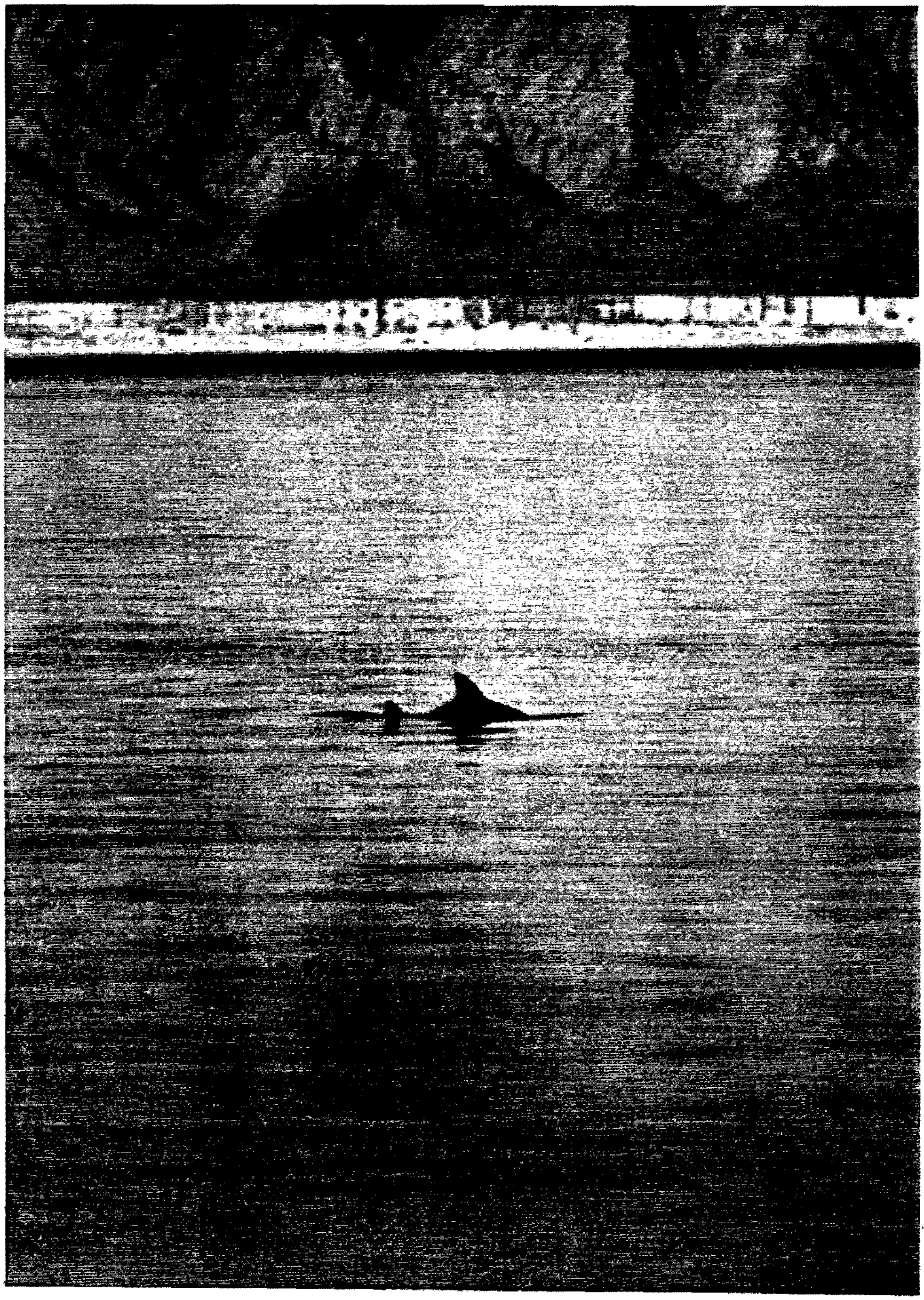
The dissertation of Gregory
Keith Silber is approved:

Dean of Graduate Studies and Research

Tom -

Thank you for your contributions to this work.

Greg



DISTRIBUTIONAL RELATIONS OF CETACEANS IN THE NORTHERN GULF OF CALIFORNIA, WITH SPECIAL REFERENCE TO THE VAQUITA, *PHOCOENA SINUS*

Gregory Keith Silber

ABSTRACT

My objective was to describe habitat utilization and distribution of cetacean species of the northern Gulf of California, with an emphasis on the vaquita, *Phocoena sinus.* I provide an overview of the marine environment of the upper Gulf and relate aspects of the oceanographically unique region to features of the morphology, distribution, range, and acoustic behavior of *P. sinus,* including ecological interactions of this species with other cetacean species common to the northern Gulf. I review currently available information on *P. sinus* and I present the first description of phonations produced by *P. sinus.*

A total of 4,216 km of boat and aircraft surveys was conducted for cetaceans in the Gulf of California in 1986 - 1989. Seven cetacean species were seen on a total of 306 occasions, including 58 sightings (110 individuals) of vaquita. Bottlenose dolphins, common dolphins, and fin whales were the most abundant species in the upper Gulf. Bottlenose dolphins were found almost exclusively in extreme nearshore, shallow water habitats, and common dolphins primarily inhabited deep water. In contrast, vaquita occurred in narrowly defined habitats of moderate depth (13.5 - 56.0 m) in small groups of three or less individuals. The principal range of *P. sinus* is apparently limited to the northern Gulf of California, Mexico, and its distribution is tightly clumped within well-mixed, turbid, highly productive waters. The species probably inhabits the northern Gulf year-round, and the population is held at low levels by incidental mortality in large mesh gillnets. *Phocoena sinus* vocalizations were similar to those of other members of the family, and the high frequency, narrow-band nature of the sounds may act to confine the species to turbid water habitats. Large numbers of sympatric cetaceans of the upper Gulf apparently are able to coexist by occupying different ecological niches.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

APPENDIX

ACKNOWLEDGEMENTS

This study would not have been possible without dedicated assistance in the field by M. Newcomer, T. Silber, H. Pérez-Cortés, G. Ellis, G. Barros, T. Jefferson, D. Breese, L. Torrez-M., A. Valezquez-R., and A. Robles. These people endured the rigors of field work and the high expectations of a demanding captain. I extend thanks to K. Norris, B. Villa-R., R. Wells, and K. Marten who provided encouragement and advice. I am grateful to D. Aurioles and H. Pérez-Cortés for interviewing fishermen in La Paz and San Felipe, respectively, and to G. Notarbartolo di Sciara for allowing me to use his observations. My work received financial and logistical support from the Nature Conservancy (International Program), the Center for Marine Conservation, Project Lighthawk, the Homeland Foundation, the American Cetacean Society (Los Angeles Chapter), the Center for the Study of Deserts and Oceans, and the West Coast Whale Research Foundation. The study was conducted under Scientific Research Permit numbers 301856, 300422, 400036 issued by the Secretaría de Pesca, Mexico.

The thesis is dedicated to Trish Silber who provided me with a constant source of encouragement and strength, and whose confidence in me never faltered.

DISTRIBUTIONAL RELATIONS OF CETACEANS IN THE NORTHERN GULF OF CALIFORNIA, WITH SPECIAL REFERENCE TO THE VAQUITA, *PHOCOENA SINUS*

Gregory Keith Silber

"It is hardly necessary to say, that any person taking up the study of marine mammals, and especially the cetaceans, enters a difficult field of research, since the opportunities for observing the habits of these animals under favorable conditions are but rare and brief. My own experience has proved that close observation for months and even years, may be required before a single new fact in regards to their habits can be obtained."
- Charles Melville Scammon
The Marine Mammals of the
Northwestern Coast of North America, 1874

"We made a trip into the Gulf; sometimes we dignified it by calling it an expedition"
- John Steinbeck
The Log from the Sea of Cortez, 1941

INTRODUCTION

The northern Gulf of California, Mexico presents a paradoxical environment to its inhabitants. Nutrient-rich, well-mixed waters make the upper Gulf one of the most biologically productive regions of the world, and yet its large tidal amplitudes and dramatic annual temperature ranges make it one of the most physically demanding habitats of the world's ocean basins (Alvarez-Borrego 1983). The shallow upper Gulf is ecologically isolated from the remainder of the Gulf to the south by temperature gradients and a system of deep basins and sills; features that have contributed to a high degree of endemism within the Gulf (Walker 1960).

The oceanographically unique region supports several populations of cetacean species, most common of which are bottlenose dolphins (*Tursiops truncatus*), common dolphins (*Delphinus delphis*), fin whales (*Balaenoptera physalus*), and the vaquita or Gulf of California harbor porpoise, *Phocoena sinus* Norris and McFarland 1958 (Fig. 1a & b, frontispiece) (Wells et al. 1981).

Cetacean Surveys in the Upper Gulf

There have been a number of cruises, beginning as early as 1958, that described the cetacean fauna of the northern Gulf, however, none of these studies involved repeated or multi-year surveys. In most cases, cruises were conducted on only several days.

Four cetacean species have been previously reported north of the midriff islands, which include bottlenose dolphins, common dolphins and fin whales (Balcomb et al. 1979, Wells et al., 1981, Vidal et al., 1985). Van Gelder (1960) reported only fin whales, and a number of sightings of vaquita have been reported (Norris and McFarland 1958, Norris and Prescott 1961, Wells et al. 1981, Vidal et al. 1985). I saw these species in addition to Bryde's, *Balaenoptera edeni*, gray, *Eschrichtius robustus*,, and killer whales, *Orcinus orca*

Phocoena sinus

Phocoena sinus is endemic to the Gulf, and its range is apparently limited to the northern third. Norris and McFarland (1958) theorized that a population of porpoises of the Genus *Phocoena* transgressed the equator during one of the interglacial periods of the Pleistocene, became essentially trapped in the Gulf, and subsequently diverged from an ancestral Southern hemisphere form. Based on records that were available to them, Norris and McFarland (1958) described the range of *P. sinus* as occurring in the upper Gulf of California and probably extending south along the Mexican coast, and more recently Brownell (1986) suggested that the range is limited to the upper Gulf of California. However, the actual range remains unsubstantiated, and it is difficult to be certain that the species is not more widespread since phocoenids can be wary and move in small numbers. If vaquita are limited to the northern third of the Gulf, it represents the most restricted range of any marine cetacean species (Barlow 1986, Brownell 1986). Because of its limited range and small population size, the vaquita is one of the least understood of the World's cetaceans.

When this study began, 45 records of *P. sinus* existed (Brownell 1986). These records, gathered between 1958 and 1984, consisted of beach cast specimens and osteological material (Norris and McFarland 1958, Orr 1969, Noble and Fraser 1971, Magatagan et al. 1984), and about 20 reported sightings of vaquita (Norris and McFarland 1958, Norris and Prescott 1961, Villa 1976, Wells et al. 1981). However, Brownell (1986) argued that only four of the sightings were valid. Based on the descriptions and locations of some of the sightings, I also believe that some reported sightings may be of other species of marine mammals. There is a paucity of information with respect to living vaquita.

Research Objectives

The objectives of this study were 1) to survey cetacean species of the northern Gulf of California, and 2) to describe the distribution and habitat utilization of these animals. Much of the study focused on *P. sinus* because the species is little known, whereas other cetacean species which inhabit the upper Gulf are well-studied in other locations. I hoped to provide baseline data to facilitate future study and management of the depleted vaquita population.

I experimented with a technique whereby *P. sinus* might be censused acoustically. Other marine mammal species have been successfully counted using underwater vocalizations, including for example, humpback (*Megaptera novaeangliae*) (Winn et al. 1975) and bowhead whales (*Balaena mysticetus*) (Clark and Ellison in press), and various pinniped species (Stirling et al. 1983). Due to their small body size and a typically small group size, vaquita are difficult to census visually. I reasoned that if vaquita produced sounds like those of their congeners (high-frequency and narrow band), the sounds could be detected above ambient noise, the origins of the sounds could be easily ascertained, and they could therefore, have utility as a means to census the population. However, I detected and recorded *P. sinus* phonations only when the porpoises were very close to the boat. While the technique warrants further experimentation, it appears not to be useful as an approach to census the species. Nonetheless, the sounds (described briefly here) are an important component in influencing the distribution of the animal, because phocoenid phonations and habitat utilization are apparently inter-related.

Data were collected on the vaquita and other cetacean species in the northern Gulf of California while conducting a total of 4,216 km of ship-based and aerial survey transects during four field seasons (1986, 1987, 1988, and 1989). My observations include a total of 306 sightings of cetaceans of the upper Gulf. Fifty-eight of these sightings were of *P. sinus*.

I present a description of the distribution and habitat utilization of cetaceans of the northern Gulf of California. This information has been positioned within a broad framework emphasizing the ecology and physiography of the upper Gulf, because these components influence the modern distribution of cetaceans of the northern Gulf. Most of the cetacean species that inhabit the northern Gulf are also common to other locations worldwide and in most cases there is a considerable amount of literature on these species. In contrast, *P. sinus* is endemic to the Gulf of California and relatively little is known about the species. And although a few papers have emerged in recent years pertaining to various aspects of *P. sinus* natural history (for example, Brownell et al. 1987, Silber et al. 1988), there have been no summaries written on the species. Therefore, I focused my study on *P. sinus* and I provide here a compendium of currently available information on the species derived from the literature and from data gathered during field work in the northern Gulf. This represents the first attempt to assemble, in a single document, a summary of all that is presently known about *P. sinus*, including its habitat usage and ecological relationships to sympatric cetaceans. However, many gaps remain.

MATERIALS AND METHODS

Vessel Surveys

I conducted boat surveys for cetacean species in the northern Gulf of California with an 8 m Boston Whaler. A total of 1,715 km of survey transects were traversed on 71 days during the three years (Fig. 2). All vessel surveys were conducted north of of 30° 30' N Lat (Fig. 3).

Surveys were limited primarily to the spring months for the following reasons. My principal interest was with *P. sinus*, and it appeared at the outset of my study that the vaquita may have been present (or at least much more abundant) in the upper Gulf only during spring. This was seemingly the case as indicated by the initial stages of field work (in 1986) in which only one sighting of the porpoise occurred during six weeks of surveys in February and mid March. In contrast, 11 sightings were made in the last week in March. Although Norris and Prescott (1961) reported seeing vaquita in the northern Gulf in January 1958, the majority of previous sightings of the species in the upper Gulf were made in spring (Norris and McFarland 1958, Wells et al. 1981). And finally, fishermen in El Golfo de Santa Clara told me that vaquita were present only in March through May. Limited funding caused me to restrict the survey work in some manner.

Because initially I was more interested in studying the distribution of *P. sinus* than in its seasonal abundance, I restricted the work to the period when I believed I would most likely encounter the animal. In addition, the spring was a period when I could optimize the field time by increasing the likelihood of experiencing good weather and sighting conditions. In the latter stages of the study, the question of the vaquita's seasonal abundance became more important (after I demonstrated that it was possible to locate the animal), and efforts were made to survey in winter and summer. I attempted to conduct vessel surveys in winter (November/December 1989), but they were thwarted by several weeks of high winds. Ultimately, aircraft time was donated to the project and aerial surveys were made in late summer/early fall, in an attempt to determine the seasonal occurrence of cetaceans. Therefore, many of the conclusions made here with regard to distribution of cetacean species pertain mostly to spring. However, sightings of vaquita and other cetaceans also were made in early fall 1989, and these data have been included.

During vessel transects, two to four observers positioned 3.5 m above the water surface, searched with unaided eyes and with 7 and 10 power binoculars on either side of the vessel's track. The area in front and about 200 - 300 m to either side of the vessel was searched thoroughly, while more distant waters were also scanned. During all surveys, the vessel traveled consistently at 10 - 11 km/hr.

Transects conducted in 1986 were non-random and restricted primarily to nearshore areas. In subsequent field work inshore surveys were augmented by randomly allocated transect lines. Fifteen randomly selected transect lines were planned that were oriented east - west and 22.5 km in length. Five lines began from the eastern coast, five from the western coast, and five intersected a N - S line bisecting the middle of the study area. Actual track lines were plotted on a chart using "deadreckoning" (known speed and heading) and by obtaining positions at the beginning and termination of a given transect. Some survey lines deviated from planned lines due to displacement of the boat by tidal currents. Additional visual searches for marine mammals were conducted when making passage to or from an anchorage, between transect lines, and in areas where *P. sinus* density was relatively high.

For each sighting of cetaceans, number of individuals was estimated and sighting locations were determined by triangulation from landmarks. Water depths were obtained with a JRC color video depth sounder or from a nautical chart. Water clarity (using a Secchi disc) and temperature (using a bucket thermometer) were measured at most sighting locations. Sea states were obtained by visual estimate according to the Beaufort scale. No surveys were conducted when sea state exceeded Beaufort three, and the majority were conducted in a sea state of one (Fig. 4).

I am confident about the our ability to correctly identify vaquita when they were seen, because 1) the appearance and behavior of *P. sinus* was very different from other marine mammal species found in the upper Gulf, 2) all observers had extensive experience surveying and identifying cetacean species from ships, and they had previous experience with various phocoenid species, 3) two of our earliest sightings of the species (in the first year of field work) consisted of following and observing the animals for periods in excess of three hours, which provided a good opportunity to acquaint ourselves with a search image and the behavior of the species, 4) the majority of sightings of *P.*

sinus consisted of a series of sequential surfacings, which usually provided sufficient time to alert the other observers, give them an opportunity to see the porpoise(s), and to discuss and confirm the sighting, and 5) sightings were rejected if the observer(s) was not absolutely sure that he/she had seen vaquita. Nonetheless, because vaquita are small and surface inconspicuously, it is likely that some porpoises along the track line went undetected.

Aerial Surveys

Two opportunities arose, one in spring and one in early fall, to fly a series of sighting transects for cetaceans. Spring flights, taken 3, 4, and 5 May 1988, sampled the upper Gulf before water temperatures in this region attained summer levels. Fall flights, taken 2, 4, and 5 September 1989, searched the Gulf at a time of maximum sea surface temperatures. This allowed a rough assessment of whether nor not the distribution of vaquita and other northern Gulf cetaceans changed with season. In both spring and fall study periods, aircraft surveys were flown south along the Baja peninsula to 29° 34' N Lat. (Fig. 5), but survey effort was concentrated on the upper Gulf. A total of 1,521 km was flown in spring, and 980 km were surveyed in fall.

In addition to providing an opportunity to increase the range of our searches for *P. sinus*, the primary objectives of aerial surveys were 1) to determine if vaquita could be spotted from aircraft, and 2) to determine seasonal presence/absence of the species in the upper Gulf. Therefore, I decided to fly intensive searches in the areas where I had seen *P. sinus* from the boat. I planned a series of transect lines that focused on the area between the island of Rocas Consag and the Baja California peninsula. The transects were oriented north-south, approximately 30 km in length, and 4 - 10 km apart (Fig. 5). Another set of transects was flown near the coast between El Golfo de Santa Clara and Punta Borrascosa, Sonora, where transect lines were roughly 30 - 40 km long and spaced about 8 - 15 km apart. In addition, two to four lines were searched south along the eastern coast of the Baja California peninsula in both spring and fall (Fig. 5).

All surveys were flown at an altitude of 152 m above the sea surface, except one (4 May 1988) that was flown at 213 m. The latter flight was an attempt to determine if vaquita could be seen from an altitude greater than 152 m. No vaquitas were seen during this survey, however, sea states were also greater (Beaufort scale of 4) than in previous surveys; a condition that makes the porpoise difficult to spot.

Three observers, who had previous experience with aerial surveys, conducted observations. These observers had also seen each of the northern Gulf cetacean species from the boat. Two observers were positioned on the left side of the aircraft and one on the right side. Untrained observers (ie. pilots and other passengers) also searched. Surveys were made with naked eye, and observers concentrated their efforts within an estimated distance of 200 - 500 m of the flight path, although they also scanned to greater distances. When marine mammals were sighted, binoculars (7 to 10 power) were used to confirm species identity and for subsequent behavioral observations. For each marine mammal sighting, species identity, group size, and location were determined. Water depths were determined later from a chart.

Fishermen Interviews

Fishermen were interviewed, using a questionnaire (Appendix A), in San Felipe, Baja California Norte (November 1988) and in the vicinity of La Paz, Baja California Sur (July 1987) in an attempt to obtain general qualitative information with regard to the natural history, range, and distribution of the vaquita. We inquired about years of employment, type of fishing, target species, location of fishing, and marine mammals seen while fishing. The men were asked if they recognized vaquita after viewing photographs of living and dead *P. sinus*, and other odontocetes common to the area. A few times I also spoke to fishermen of Puerto Peñasco and El Golfo de Santa Clara, Sonora about vaquita, but men in these communities were not interviewed systematically. Interviews were intended to produce general information about local knowledge to direct future study of *P. sinus*, and contribute to an assessment of fishing effort and vaquita mortality rates in fisheries. Information derived from interviews with fishermen has been presented here, although the survey sample was small and allows me to make only a few general statements with respect to probable vaquita distribution, seasonality, range, and fishing impact.

Phonations of *Phocoena sinus*

Attempts were made to record the underwater phonations produced by *P. sinus*, with the hope that the sounds might be used to census the population. However, sounds were detected only when the porpoises were very close to the boat. Therefore, while the technique warrants further experimentation, it appears to have little utility as a means to census the species. Nonetheless, the type of phonations produced by *P. sinus* are likely related to the animal's distribution. The sounds are described here because they have not been described before and they are treated as an important component in influencing the distribution of the animal.

High frequency recordings of *P. sinus* were obtained from the research vessel, using a Racal Store 4DS reel-to-reel tape recorder, an ATC high-frequency hydrophone, and University of California fabricated pre-amplifier. High-pass filters were used to filter out noise in the sonic frequency ranges. When used at a tape speed of 30 ips, the system had a flat frequency response from 50 Hz to 150 kHz, and at 60 ips the frequency response was flat from 100 Hz to 300 kHz. During all recordings the hydrophone was deployed at a depth of 2 m.

Seventy-three high frequency recordings were made throughout the study area in circumstances when the porpoise was not sighted (including at night), in an attempt to detect *P. sinus* phonations. But these recordings did not contain *P. sinus* sounds. Seven recordings were attempted within 200 m of *P. sinus*, and phonations from *P. sinus* were detected on only three of these. The relative success of the latter instances in obtaining recordings of *P. sinus* phonations probably resulted from the proximity of the porpoises to the boat during recording sessions, because in each instance the animals were within an estimated 50 m of the hydrophone. One recording, obtained when a vaquita adult/calf pair were seen within 50 m of the boat, was made on 25 March 1986. The location (31° 07' N; 114° 42' W) was within 10 km of San Felipe, Baja California Norte, in 15.0 m of water. The second recording was made on 27 March 1986, 9 km NE of San Felipe, (31° 05' N; 114° 45' W) also in a water depth of 15.0 m. During the recording session, a vaquita adult/calf pair surfaced within 20 m of the vessel, while swimming toward us. Both of these recordings were made at 30 ips and a 500 Hz high-pass filter. A third recording was made 16 km ENE of San Felipe (31° 03' N; 114° 40' W) on 7 May 1987 when at least two adult *P. sinus* were seen less than 30 m from the vessel. The water depth was 29.0 m and recordings were made at 60 ips, using a 20 kHz high-pass filter.

Several hundred individual *P. sinus* sonar clicks were detected aurally when the tapes were played at slow speeds. Those with superior signal-to-noise ratios were analyzed on a Hewlett-Packard 5451C Fourier Analyzer and Hewlett-Packard 5466 analog to digital converter.

Statistics

An analysis of variance (ANOVA), and Scheffé's F-test (for intergroup comparisons) were used to determine if differences existed in water depth, distance from nearest shore, water clarity, and water temperature distributions for all cetacean species.

RESULTS

Cetacean Species of the Northern Gulf

Seven cetacean species were seen in the northern Gulf of California: common dolphins, bottlenose dolphins, vaquita, fin whales, Bryde's whales, gray whales, and killer whales (Table 1). I am concerned primarily with the three most commonly seen species, common dolphins, bottlenose dolphins, and vaquita, particularly with respect to habitat utilization by these animals.

Relative abundance

The sighting rate was highest for bottlenose dolphins, followed by vaquita and common dolphins (Table 2). Common dolphins were numerically dominant and were seen in large schools that contained up to 1,100 individuals (Table 1). The number of common dolphins was an order of magnitude greater than the number of bottlenose dolphins, which were in turn about ten times more abundant than the vaquita. Gray, Bryde's, and killer whales were the least common species, and they were seen < 7 times each. Unidentified balaenopterid whales were seen four times.

Habitat Utilization

There appeared to be a general (but not absolute) segregation by area and water depth among the three most common odontocetes, suggesting that they utilized different habitats. The distribution of *P. sinus* overlapped that of *Delphinus*, but its distribution overlapped relatively little with that of *Tursiops* (Fig. 6).

Water depth and distance from nearest shore

With regard to the three most common odontocetes, mean water depths and distances to shore were greatest for common dolphins, least for bottlenose dolphins, while vaquita were sighted at intermediate distances (Figs. 7 & 8, Table 1). The range of water depths utilized by common dolphins (5 - 105 m) was greatest, while those used by vaquita (14 - 56 m) were the most narrowly defined. Differences in water depths ($p < 0.001$, $F = 87.04$, $df = 2$) and distances from shore ($p < 0.001$, $F = 109.5$, $df = 2, 238$) utilized by *P. sinus*, *T. truncatus* and *D. delphis* were highly significant (Figs. 7 & 8); however, distances from shore where common dolphins occurred did not not differ significantly from those of vaquita ($p > 0.25$, $F = 0.467$).

There appeared to be little spatial segregation among rorqual species in the northern Gulf (Fig. 9). There was no significant difference in water depths at locations where fin and Bryde's whales were sighted ($p > 0.05$, $F= 0.808$, $df = 1$) (Fig. 10), but distances to shore differed significantly ($p < 0.05$; $F= 5.94$, $df = 1$) for these two species (Fig. 11). However, conclusions regarding habitat utilization in these species are tenuous because the number of sightings of Bryde's whales was small.

Water clarity measurements obtained at sighting locations differed significantly between all odontocete species ($p < 0.0001$, $F = 11.8$, $df = 2, 70$) (Table 1, Fig. 12); however, differences were not significant between common dolphins and vaquita ($0.25 < p < 0.10$, $F = 1.677$). In addition, water temperatures differed significantly when the three odontocetes were compared ($p < 0.0001$, $F = 12.925$, $df = 2, 90$) (Fig. 13) but differences were not significant between water temperatures at locations of common dolphin and bottlenose dolphin sightings ($p > 0.25$, $F = 0.256$). My observations regarding cetacean distribution with respect to water temperature should be viewed with caution, because the observations are limited primarily to spring, and because water temperatures in the upper Gulf vary a great deal seasonally.

In short, odontocete cetaceans of the upper Gulf of California utilized habitats that can be described in the following manner: Bottlenose dolphins were observed in highly turbid, inshore waters, generally < 15 m deep, and < 10 km from shore (Table 1), and densities were highest on the eastern perimeter and in the waters of the Colorado River delta. Common dolphins inhabited relatively clear, offshore waters, generally > 30 m deep, and > 15 km from shore, and most sightings occurred in the central portions of the upper Gulf. Vaquita were seen in narrowly defined water depths, (between 14 and 56 m), approximately 15 - 20 km from shore, in waters that in general were turbid, although clarity varied greatly. Near the Baja California peninsula, vaquita exhibited an areal distribution that was highly restricted and was intermediate between those of bottlenose and common dolphins.

Seasonal Occurrence

During September 1989 aerial surveys, relative abundance and distribution of bottlenose dolphins, vaquita, and fin whales appeared to be consistent with spring surveys. Bottlenose dolphins were observed in February through May (vessel surveys, 1986 - 1988), November and December (shore-based, 1988), and in September (aerial surveys, 1989). Common dolphins were seen in the same periods, but this species was conspicuously absent during September 1989 aerial surveys. Bryde's whales were not seen in September 1989. The absence of common dolphins in this period may indicate that the species migrates out of the region because of water temperature maxima or to utilize areas of upwelling and/or greater productivity. Gallo and Alessio-Robles (Unpubl. man.) found an increase in common dolphin group size in the mid and southern Gulf in summer and fall, and this may correspond with an evacuation of the species from the upper Gulf, and greater abundances in the south and central Gulf.

Therefore, presence, distribution, and relative abundance of bottlenose dolphins and vaquita appeared to be year around phenomena. Common dolphins may migrate from the upper Gulf in late summer and early fall.

Phocoena sinus Sightings

In this section, I highlight *P. sinus* sightings, differentiated from those of other species. While both data sets (those sightings of all cetaceans and *P. sinus*, exclusively) represent new findings, the information on *P. sinus* is treated separately because it is the first substantial collection of data on living vaquita and the data may be of particular interest to researchers engaged in the study and management of the species. In addition, the two data sets are discussed both separately and collectively in the following sections.

Sightings from the Boat

Vaquita were seen on 58 occasions involving an estimated 110 individuals during boat and aircraft surveys (Table 3). Forty-three porpoises were seen during boat transects, a sighting rate of 2.51 individuals/100 km. The remainder of the sightings occurred when we were not conducting transect surveys. The paucity of sightings emphasizes the rarity of these porpoises.

All sightings of the vaquita occurred north of 30° 45' N Lat., and all but three sightings (96.1%) occurred less than 40 km from San Felipe, Baja California Norte (Fig. 14). Most sightings (94.2%) occurred in sea states 0 or 1 (Fig. 15). In 91.4% (n = 53) of all sightings, porpoises were observed in small groups (< 3 individuals). Mean group size was 1.9 ± s.d. 1.20 individuals (Table 3) and the modal group size was one (Fig. 16). At 70.7% (n = 41) of the locations in which vaquita were seen, water depths ranged from 21 - 35 m ($\overline{X}$ = 26.6 ± s.d. 7.67; overall range = 13.5 - 56.0) (Fig. 17, Table 3), and most sightings occurred 11 - 25 km from the nearest shore ($\overline{X}$ = 18.4 ± s.d. 5.84; range = 2.4 - 32.2) (Fig. 18, Table 3). Water clarity at sighting locations ranged from 0.9 to 12.0 m (Table 3). In general, water in the study area was highly turbid, and I obtained measurements ranging from 0.2 to 12.0 m ($\overline{X}$ = 4.8 ± s.d. 2.99) at a total of 78 stations throughout the upper Gulf. Inshore waters were more turbid than those further from the shore. Turbidity in locations where vaquita were sighted varied greatly.

During four vaquita sightings the boat's depth sounder indicated concentrated layers at 15 (n = 2), 23, and 25 m, which probably represented schooling bait fish or squid upon which the porpoises may have been feeding. Frequently, vaquita surfaced in or alongside surface slicks, consisting of a series of long parallel bands of flat water surrounded by rippled water.

Adult/calf pairs accounted for 15.52% of all sightings, and calves represented 8.18% of all individuals. One very young calf was observed on 9 April 1987. It was estimated at < 2 days old because of its size, a dorsal fin that was not yet fully erect, and the ungainly manner in which it lifted its head from the water with each surfacing. The age of this calf, the relatively high number of calves seen in surveys conducted in March through May, and an absence of calves during September surveys, may indicate that parturition occurs in spring. This hypothesis is in close agreement with Norris and Prescott (1961) who provided anecdotal evidence suggesting that most calves were seen in May and June.

Sightings from Aircraft

Eleven *P. sinus* (five sightings) were seen during the May 1988 aircraft flights, and an estimated 14 individuals were seen in seven sightings during the September 1989 flight series (Fig. 5). Locations of vaquita during these surveys were similar to those obtained during vessel surveys. Sightings obtained in September were noteworthy because they indicated that vaquita occur in the upper Gulf during periods of maximum yearly water temperature (Fig. 19), suggesting that they inhabit the upper Gulf throughout the year. The surveys also provided the southernmost confirmed sighting (at least for this study) of the species (30° 43' N); at a location that was about 20 km south of my previous southernmost observation of vaquita. All sightings of vaquita from the air occurred less than 45 km from San Felipe, and none were made farther south along the Baja peninsula coast, even though some flights went as far south as 29° 50' N Lat. (Fig. 5). However, much less effort was dedicated to this area in relation to the extreme upper Gulf. Aircraft surveys, though very few, serve to support *P. sinus* distribution patterns observed during surface vessel surveys. They failed to yield sightings south of the area surveyed by boat.

This study represents the first attempt to survey vaquita from aircraft. My success in spotting vaquita during aerial surveys suggests that planes are a suitable platform from which to conduct future study.

Unconfirmed Sightings of *Phocoena sinus*

In February and April 1983 I received reports of small cetaceans that may have been *P. sinus*, sighted near Cerralvo Island (24° 10' N; 109° 55' W) (G. Notarbartolo di Sciara, pers. comm., Piazza Duca d'Aosta 4, 20124 Milano, Italy). Notarbartolo di Sciara is a marine scientist with extensive experience with marine mammals and with Gulf of California fauna. In both sightings, the animals were 10 - 50 m from the observer. They were described as being small, possibly possessing a blunt rostral profile, and surfacing "unobtrusively" in small groups. They were "quite distinct from *Tursiops*, *Delphinus*, or *Lagenorhynchus*" (G. Notarbartolo di Sciara, pers. comm.), which are cetaceans common to the area. If true, these unconfirmed sightings of the vaquita occurred in an area > 850 km south of our southernmost sightings, and extend the present known range considerably.

Information from Fishermen

Based on these observations, I decided to carry out interviews with fishermen in the southern Gulf about the presence of the vaquita. In 1987, 17 fishermen from La Paz were interviewed about their fishing practices and their knowledge of the vaquita (Table 4). In most cases the fishermen had spent considerable amounts of time at sea, and they had been engaged in fishing 4 - 6 days/week, 3 - 12 months/yr, for 4 - 51 years ($\overline{X}$ = 20.6 yrs). Fishermen in the La Paz area generally had no knowledge of the vaquita; however, one man was familiar with the porpoise and indicated that he had seen it several times near San Jose Island (25° 00' N; 110° 40' W), 80 km north of La Paz. This man was one of two who had been fishing for over 50 years and unlike others interviewed, he had worked the coast near San Jose Island; an area that appears to be similar, in terms of water depth and bottom topography, to those areas where *P. sinus* occurs in the upper Gulf. In addition, his knowledge of marine mammals was regarded as being accurate by the interviewer (D. Aurioles, Centro de Investigaciones, Biologicas B. C. S., APO Postal 128, La Paz, Baja California Sur, Mexico). Unconfirmed sightings of this nature are of interest, but require further study to establish their validity.

All seven fishermen interviewed in San Felipe expressed a knowledge of the vaquita, and two said that they had entangled the porpoise while fishing for totoaba. Although the taking of totoaba is illegal, three men indicated that they continue to use gillnets for the fish.

Brownell et al. (1987) maintained that fishermen in the upper Gulf referred to *P. sinus* as "vaquita" (a name originally suggested by Norris and McFarland 1958). Therefore, these authors proposed that the vernacular name of the porpoise be changed to vaquita, from "cochito", and vaquita is the common name that is currently used by the scientific community. However, I found that the vernacular name for *P. sinus* tended to vary between communities and individuals. Fishermen in San Felipe referred to *P. sinus* as "cochito", "cochonito", and "vaquita". In contrast, fishermen interviewed in La Paz (using photographs of various marine mammals as references) indicated that "vaquita" refers to *Kogia spp.* or *Phocoena spp.*, whereas "cochonito" refers to *Delphinus delphis*, "cochito" to *Globicephala macrorhynchus*, and "duende", also meaning *P. sinus* in some communities (Norris and McFarland 1958, Magatagan, et al. 1984), refers to *Lagenorhynchus obliquidens* (D. Aurioles, pers. comm.).

Phocoena sinus Phonations

Click Structure

All *P. sinus* sonar clicks were sharp, intense, narrow-band ($\overline{X} = 17.1 \pm$ s.d. 5.38 kHz) signals that ranged in frequency from 122.2 - 146.9 kHz (although a few clicks had energy as high as 160.0 kHz), and dominant frequencies ranging from 128.0 - 139.0 kHz (Table 5, Fig. 20). Click duration ranged from 79 - 193 μsec (Table 5, Fig. 21).

If low frequency components existed in the *P. sinus* sounds, they were not detected in this analysis due to high pass filters that were used during recordings, or to overriding ambient biological noise in the lower frequency registers. Whistles were not detected.

Ambient noise, produced mostly by snapping shrimp, was centered below about 16 kHz, but in some cases the energy was much higher. Because of uncertainties of the position of porpoises with respect to the hydrophone, it was not possible to measure signal strength of clicks.

Repetition Rate

Sounds from *P. sinus* were arranged in trains of pulses, which contained from 3 to 57 individual clicks ($\bar{X}$ = 19.4 ± s.d. 19.23, n = 9). The interclick interval was highly variable and ranged from 0.019 to 0.144 sec ($\bar{X}$ = 0.103 ± s.d. 0.0231 sec, n = 75). The repetition rate also varied, and ranged from 10 to 50 clicks per sec ($\bar{X}$=12.5 ± s.d. 6.91, n = 43) (Table 6).

DISCUSSION

Ecological Relationship of Sympatric Cetaceans in the Northern Gulf

My work represents the first extensive survey of the cetaceans of the upper Gulf. Other work has been conducted in the region, but in brief periods, usually involving only several days. Previous surveys have yielded information on cetaceans beginning as early as 1958. Data from previous survey work suggests that the species composition in the upper Gulf is similar to the present. My evidence suggests that sympatric cetaceans play a role in defining the niche of *P. sinus* through competition for resources.

Four cetacean species have been previously reported north of the midriff islands. Reports were made of bottlenose and common dolphins and fin whales (Balcomb et al. 1979, Wells et al., 1981, Vidal et al., 1985). Van Gelder (1960) reported only fin whales, and a number of sightings of vaquita have been reported (Norris and McFarland 1958, Norris and Prescott 1961, Wells et al. 1981, Vidal et al. 1985).

In addition to these four, the following cetacean species have been reported north of Angel de La Guarda Island, but these species probably occur infrequently in the northernmost Gulf. Gilmore (1957) reported beach strandings of sperm whales (*Physeter sp.*) in the northern Gulf. A beach cast specimen of the pygmy sperm (*Kogia breviceps*) was found north of San Felipe by Brownell (1969) and a live stranding of this species occurred at Puerto Peñasco in 1984 (Vidal et al. 1987). Sightings of humpback whales near El Golfo de Santa Clara and Bahia San Luis Gonzaga were described by Villa (1986), and Heyning (1986) reported a single beach-cast specimen of a rough-toothed dolphin (*Steno bredanensis*) near El Golfo de Santa Clara. Two sightings of pilot whales (*Globicephala macrorhynchus*) were made immediately north of Angel de La Guarda Island (Balcomb et al. 1979).

Ecological Niche Separation

Distribution of the most common cetaceans in the northern Gulf suggests habitat partitioning. The principle that related species coexist by virtue of sufficient difference in ecological niche was demonstrated experimentally by Gause (1934) and re-emphasized by Lack (1947). The concept of ecological niche separation among sympatric species has received considerable attention and has been reported in numerous taxa (for review see Schoener 1982). Resource partitioning has been particularly well described for some social mammals (for example, ungulates: Jarman 1974, primates: Crook and Gartlan 1966, Clutton-Brock and Harvey 1977), in which coexistence is mediated through differences in habitat, food, and occasionally time (Schoener 1974).

Although competition for resources is difficult to quantify in field studies (for example, see Connell 1980), competitive pressures between species may result in a divergence of resource utilization, including that of spatial distribution. Competition for food resources is expected to be acute among predators in the upper trophic levels (Menge and Sutherland 1976, Hairston et al. 1960), such as odontocete cetaceans. Cetaceans of the upper Gulf of California apparently reduce competition by minimizing areal and temporal overlap and by utilizing different prey. In this system, a partitioning of resources and habitats may allow large cetacean populations to coexist. Of mammals that are sympatric with *P. sinus*, the two most common odontocete cetaceans, *Tursiops* and *Delphinus*, may influence distribution of *P. sinus* through competition for resources, and determine niche size and structure.

Resource Partitioning among Cetaceans in the Northern Gulf

Habitat partitioning has been described for cetaceans which occur in relatively protected coastal regions as well as broadly sympatric species inhabiting vast areas of the open ocean. Although there are exceptions, it appears in many cases that odontocete cetaceans partition resources spatially or temporally while sympatric mysticetes are ecologically separated by prey type. In addition, some sympatric cetacean species occupy niches that are segregated by trophic level.

Spatial Separation

Two studies, conducted in different oceans, noted habitat partitioning among odontocete cetaceans, and they provide noteworthy similarities to the findings of this study. Saayman et al. (1972) and Saayman and Tayler (1973) described spatial relationships of *Sousa sp.*, *Stenella coeruleoalba*, and *Tursiops sp.* off the coast of South Africa, in which these species occupied inshore, pelagic, and intermediate habitats, respectively. An analogous situation, involving *T. truncatus* (inshore), *Lagenorhynchus obscurus* (pelagic), and *Phocoena spinipinnis* (intermediate), was described for the coastal waters of Argentina (Würsig et al. 1977, Würsig and Würsig 1979, 1980, Würsig 1984). In addition, Smith (1982) reviewed Soviet data on cetaceans of the Black Sea involving the coexistence of three sympatric species *Delphinus*, *Tursiops*, and *P. phocoena*.

There are interesting parallels among these studies and this one. All of the studies involved bottlenose dolphins, and three of them included porpoises of the Genus *Phocoena*. Each study involved ecological counterparts found in other locations; positions that were filled by the same or different species. In three cases bottlenose dolphins occupied habitats closest to shore, and in one study (Saayman et al. 1972) this species was generally found in areas intermediate between two other species. Walker (1981) and Irvine et al. (1981) suggested that a cetacean species may occupy the same or different ecological niche depending upon geographical location and local conditions found there. The behavior of the bottlenose dolphin is highly adaptable (Shane et al. 1986) and its habitat usage in the Gulf of California has undoubtedly been shaped by local factors, which may include competition with sympatrics. Würsig and Würsig (1979) noted differences in habitat utilization by *Tursiops* in Argentina versus the South African study, and these researchers suggested that competitive exclusion between species may be occurring. The present study provides a third comparison; a situation most analogous in species composition and distributional similarities, to the Argentina study.

Schoener (1982) noted that a small amount of spatial overlap among sympatrics is indicative of a high degree of competition. In the Gulf of California, spatial and temporal overlap of bottlenose dolphins was generally small with respect to those of *P. sinus* and *D. delphis*, whereas the distribution of the latter two species intersected. This suggests that competition between *P. sinus* and *D. delphis* was little, while their competitive interaction with bottlenose dolphins may be relatively greater.

Phocoena sinus may not represent significant competition to the common dolphin due to the high level of biological productivity of the upper Gulf and the modest size of the *P. sinus* population. In addition, the offshore habitat provides patchy but abundant food sources, and it may therefore support both species.

Niche Separation by Prey Type

Odontocetes

In addition to differences in habitat type, vaquita, common dolphins and bottlenose dolphins may also achieve ecological distance by preying on different organisms.

In locations outside of the Gulf, common dolphins reportedly feed opportunistically (Evans 1975), but with a preference for mesopelagic prey (Fitch and Brownell 1968). Evans (1982) reported that common dolphins off southern California fed on anchovies (*Engraulis mordax*), hake (*Merluccius productus*), smelt (Osmeridae), lantern fish (*Seriphus politus*) and squid (*Loligo opalescens*). In the Gulf of California, I sampled fish schools (using "snag" hooks and dip nets) on two occasions while the fish were being preyed upon by *D. delphis*, and the schools contained anchoveta (*Cetengraulis mysticetus*) and the Gulf anchovy (*Anchoa nasus*).

The diet of bottlenose dolphins is highly adaptable to a particular setting, and the species' diet appears to be adjusted to local, sometimes transient conditions (Norris and Prescott 1961, Shane et al. 1986). Habitats occupied by *Tursiops* in the upper Gulf of California suggest that this animal fed mostly on shallow water species. Irvine et al. (1981) reported that bottlenose dolphins near Florida fed on any fish available, but consumed striped mullet (*Mugil cephalus*) primarily, and pinfish (*Lagodon rhomboides*), sheephead (*Archosargus probatocephalus*), and jack crevalle (*Caranx hippos*) secondarily. Norris and Prescott (1961) found that *Tursiops* fed on free-swimming fish and a number of bottom-dwelling fish and invertebrates, including various bivalve, gastropod, and crab species. Therefore, the dolphin must feed, at least part of the time, very close to the bottom layer, or it may actually root in the mud or sand (Norris and Prescott 1961). In an Argentine Bay, *Tursiops* was observed searching for fish among submerged rocks immediately adjacent to shore (Würsig and Würsig 1979, Würsig 1986), and Smith (1982) reported that *Tursiops* in the Black Sea generally fed on benthic organisms.

To date, the meager data available on *P. sinus* diet comes from stomach contents of a single specimen. Squid remains and otoliths from a grunt, *Orthopristis reddingi*, and a croaker, *Bairdiella icistia*, were found in the stomach of that animal (Fitch and Brownell 1968). The latter two species are primarily shallow water, bottom-dwelling fish; they are both abundant in the northern Gulf, and neither is very large (< 25 cm). Fitch and Brownell (1968) concluded that *P. sinus* consumed these fish in water that was < 30 m deep. Therefore, stomach content data suggest that *P. sinus* may feed, at least in part, on or near the bottom. The stomach contents of two *P. sinus* specimens were obtained during this study in 1988. A preliminary examination of these samples indicated the presence of squid beaks, several whole fish < 12 cm in length (probably *Anchoa nasus* or *Sardinops spp.*), numerous unidentified otoliths, and the carapace (about 1 cm) of an unidentified crab (G. Silber pers. obs.). Stomachs from 13 freshly killed vaquitas (Brownell et al. 1987) have been available since 1985, but they have not been analyzed at the time of this writing.

Inferences about the diet of *P. sinus* may be made from extensive data that exist on the diet of a close relative, the harbor porpoise (*P. phocoena*). North Atlantic and North Pacific *P. phocoena* prey has been described as "schooling, soft-rayed fishes" (Prescott and Fiorelli 1980). Gaskin et al. (1974) and Smith and Gaskin (1974) reported that "smooth, non-spiny" fishes, mostly gadoid and clupeoid fishes from 10 - 26 cm long, comprised the main element of the diet of *P. phocoena* in the North Atlantic, although spiny-rayed species are undoubtedly consumed by the porpoise. Recent stomach content analyses of *P. phocoena* which inhabit the Bay of Fundy indicate that this porpoise feeds on pelagic fish as well as benthic forms, including Atlantic herring (*Clupea harengus*), silver hake (*Merluccius bilinearis*), Atlantic cod (*Gadus morhua*), pollock (*Pollachius virens*), mackerel (*Scomber scombrus*), and smelt (*Osmerus mordax*) (Recchia and Read 1989).

In the stomachs of North Pacific harbor porpoises, *P. phocoena*, juvenile rockfish (*Scorpaenidae spp.*), northern anchovy (*Engraulis mordax*), Pacific hake (*Merluccius productus*) and Pacific tomcod (*Microgadus proximus*) accounted for 97% of all otoliths. Invertebrates such as *Loligo opalescens* were also represented (Jones 1981). Tomilin (1957) reported that 70% of the diet of harbor porpoises in the Azov Sea consisted of small bottom dwelling fish, mollusks, and crustaceans.

Fish species that are ecological counterparts or related species to those representing prey of *P. phocoena* are found in the northern Gulf of California and are potentially available as food sources to *P. sinus*.

Although the single *P. sinus* stomach sample analyzed to date contained shallow water forms, it is likely that pelagic schooling fish are also prey items for vaquita. In my study, *P. sinus* was seen in areas where dense layers, probably representing schooling fish or squid, were detected by depth sounder at intermediate depths (15 - 25 m). I believe the porpoises were feeding within these fish schools.

Vaquita were nearly always observed in moderate water depths (14 - 56 m), which suggests that the sea floor and benthic prey were readily accessible to diving porpoises. However, mid-water schooling forms were also seen in these locations. Therefore, *P. sinus* may occupy a niche in which both pelagic and benthic forms are accessible.

Vaquita probably have diets that include both mid-water fish and shallow-water benthic prey. Therefore, the diet of *P. sinus* probably overlaps, to some degree, that of both *Tursiops* and *Delphinus*.

The feeding techniques of these sympatric species also differ. Large herds of common dolphins in the Gulf of California feed via a group process by circling and corralling pelagic fish against the water surface (Wells et al. 1981, pers. obs.), a behavior that is frequently observed among many species of small gregarious cetaceans that feed on small schooling fish (for example, see Würsig 1979, 1986). When feeding close to the shore, *Tursiops* probably fed singly (a behavior also noted by Würsig and Würsig 1979, Würsig 1986) or in small groups. Because of their typically small group size, vaquita probably were not capable of working cooperatively to corral prey.

Therefore, it appears likely that in the northern Gulf of California, common dolphins feed on pelagic schooling fish, the bottlenose dolphin consumed mostly shallow water forms, while the vaquita utilized both benthic and pelagic schooling fish species. The vaquita occupies a habitat that is intermediate to the common and bottlenose dolphins, and its niche, with respect to prey items, probably shares components of both the sympatric delphinids. Its niche, although somewhat generalized, may be narrowly defined by the presence of the vastly more abundant delphinid species. In addition, the niche of vaquita may be turbidity-defined. It is an animal able to stalk individual prey because porpoises can neither be seen nor heard during a predatory approach, in contrast to delphinids that make sounds within the hearing range of their prey.

Mysticete Cetaceans

Sympatric mysticete cetaceans, including those of the northern Gulf of California, probably minimize competition by feeding on different prey. Stomach content analysis conducted on three sympatric balaenopterid species in the North Pacific showed that ecological separation resulted from a specificity to particular prey types (Nemoto 1959, Kawamura 1980, 1982). The study revealed that sei whale (*B. borealis*) diet was diverse; stomachs contained 27 different prey species, including three species of copepods, one species of euphausiid, a sergestid shrimp, and a scombrid fish. In contrast, fin whale and Bryde's whale diets were very specific. Fin whales fed almost exclusively on one or two species of euphausiid, and Bryde's whales were limited to small gregarious pelagic fish. Fin and Bryde's whales exhibit similar dietary patterns in the central Gulf of California (B. Tershy pers. comm., Dept. of Biology, Cornell Univ., Ithaca, NY). A similar circumstance probably exists in the upper Gulf, where Bryde's whale distribution overlapped that of fin whales, but competition is minimized by prey type selection and because the Bryde's whale population size is small in the upper Gulf.

Competition may exist between Bryde's whales and the common dolphin, because their diet and trophic niche appears similar. I have seen Bryde's whales feeding alongside common dolphins on large fish schools, and feeding groups involving these species are common occurrences in the midriff island area of the Gulf (B. Tershy and D. Breese, pers. comm., Dept. of Biology, Cornell Univ., Ithaca, NY).

In sum, cetaceans of the upper Gulf may achieve ecological segregation as a result of competitive exclusion. The upper Gulf may represent a good location to study interspecific competition because of the apparent absence of common dolphins during part(s) of the year. This factor might represent an opportunity to examine the effect of the removal of one species on the ecology and distribution of other cetaceans.

Existing knowledge of *Phocoena sinus*

There is a general paucity of information with regard to life history, biology, and habits of vaquita. Although Brownell (1983) provided a review of some aspects of *P. sinus* biology and several papers have emerged in recent years that describe various features of *P. sinus* natural history (Brownell et al. 1987, Silber et al. 1988, Silber 1990), a general review of current knowledge regarding the vaquita has not been written. In the following section, I review the taxonomy and the scant information that is presently available on *P. sinus* and incorporate my data on the porpoise. The intent is to provide, an updated review of current knowledge on P. *sinus* in a single document, and to present information that is basic to an understanding of distributional and ecological relations between P. *sinus* and sympatric cetacean species. In the subsequent discussion, aspects of P. *sinus* ecology are positioned with respect to distributional and behavioral similarities to its phylogenetic relatives as influenced by adaptations to the oceanographically unique and physically demanding marine environment of the upper Gulf of California.

Phocoenid Taxonomy

True porpoises are a morphologically distinctive and evolutionarily old group of odontocete cetaceans classified as the family Phocoenidae. Barnes (1985) identified two separate lines of descent within the group as the subfamilies Phocoeninae and Phocoenoidinae (Table 7). Modern phocoenids are represented by four extant genera and six species (Barnes 1985).

All phocoenids are characterized by a generally small (< 2.5 m), stout body shape, flat, "spade-like" or tricuspid teeth, and an absence of an elongate rostrum. Most phocoenids inhabit cold-temperate water and they exhibit a coastal, anti-tropical distribution (Barnes 1985, others) (Fig. 22). In general, phocoenid species live in small schools.

Phocoenids have a long fossil history that extends back at least 10 to 11 million years ago to the late Miocene Epoch (Barnes 1976, 1985). The earliest fossil forms were found in rocks around the Pacific basin, and they include the latest Miocene and Pliocene species of *Piscolithax* and the Late Miocene *Salumiphocoena stocktoni* (Barnes 1985).

Different areas of origin for the phocoenids have been postulated by different authors. According to Barnes (1985), the available fossil record suggests that the phocoenids originated in temperate latitudes of the North Pacific Ocean. This area has yielded the oldest known fossil phocoenids and has the greatest diversity of both fossil and living species. However, the immediate ancestry of the family Phocoenidae is not known. The primitive and extinct Miocene family of delphinoids, the Kentriodontidae, is the most likely form from which all modern delphinoids evolved (Barnes 1978).

There are few data regarding phocoenid population sizes and migration patterns, and the natural history and behavior of *P. sinus, P. spinipinnis* and *A. dioptrica* are not well known.

Specimens

A total of 42 whole or partial vaquita specimens were reported by Brownell (1986), and to my knowledge at least four additional specimens have been recovered since 1986. However, a more exhaustive list of specimens is being compiled at the time of this writing by Ing. Omar Vidal (Escuela de Ciencias Marítimas y Alimentarias, Instituto Tecnológico y de Estudios Superiores de Monterrey, Guaymas, Sonora, México), and the total number of specimens is likely considerably greater than the number indicated here. At least 15 (35.7%) of the total reported here died in fishermen's gillnets.

The sites of the majority of recovered *P. sinus* specimens or osteological material, including the type specimen locality, have been either in the vicinity of San Felipe or El Golfo de Santa Clara (Fig. 23). It is noteworthy that there are no records of the vaquita south of Puertecitos on the Baja Peninsula nor south of Puerto Peñasco on the mainland side of the Gulf. This distribution of previous records prompted Brownell (1986) to suggest that the species was limited to the northern quarter of the Gulf. Some of the reported localities of specimens that were obtained on the peninsula side of the upper Gulf may have been incorrectly attributed to the community of El Golfo de Santa Clara, because many of the fishermen from El Golfo de Santa Clara cross the upper Gulf to set nets on the Baja Peninsula coast.

Thirteen of the specimens indicated here as occurring in El Golfo de Santa Clara were collected within a week in 1985. It is likely that a substantial number of porpoises die in nets throughout the upper Gulf, but the 13 animals were recovered at that location because a scientist knowledgeable of the vaquita was working with fishermen (A. Robles, pers. comm., Escuela de Ciencias Marítimas y Alimentarias, Instituto Tecnológico y de Estudios Superiores de Monterrey, Guaymas, Sonora, México).

The distribution of localities of recovered specimens and osteological material are in close agreement with my sighting data; both are restricted to the extreme upper Gulf, and they are clustered primarily on the western side and secondarily on the extreme northeastern coast of the Gulf.

Morphometrics, External Morphology, and Coloration Patterns

Descriptions of *P. sinus* morphology, dentition, and skull structure have been provided by Norris and McFarland (1958), Noble and Fraser

(1971), and Magatagan et al. (1984). Based on similarities in skull morphology and features of post cranial material, Norris and McFarland (1958) hypothesized that *P. sinus* diverged from a Southern hemisphere phocoenid, *P. spinipinnis*, rather than its less distant geographic neighbor, *P. phocoena*. Noble and Fraser (1971) corroborated the Norris and McFarland theory with additional morphometric study of *P. sinus* osteological material.

Brownell et al. (1987) provided the only description of the coloration pattern and external morphology of *P. sinus* based on 13 whole specimens (five male, eight female) that were recovered directly from fishermen's nets in an experimental fishery for totoaba in 1985.

The weights of these specimens ranged from 7.8 (a neonate) to 46.5 kg, and lengths ranged from 70.3 (neonate) to 143.5 cm (an adult female). Three females and one male were physically mature. Three of the females were larger than all of the males. Based on these lengths and previously measured whole specimens (in which one female measured 150.0 cm; Brownell 1983), the authors reported that females attain a maximum length of about 150 cm, while maximum size in males is believed to be about 140 cm. They concluded that these maximum lengths make the vaquita the smallest of the delphinoids. However, a cetacean smaller than *P. sinus*, a dwarf form of the spinner dolphin (*Stenella longirostris*) from the Gulf of Thailand, has recently been described (Perrin et al. 1987).

The external pigmentation of *P. sinus* consists a dark gray dorsal cape, a pale-gray lateral field, and a white ventral field. The porpoise has large black eye and lip patches, the latter of which joins a dorsally located blowhole stripe (Fig. 1a, b).

The shape and size of the dorsal fin is among the most striking external features of *P. sinus*. The dorsal fin is substantially larger in relation to body mass than the dorsal fin of other phocoenids. Most of the specimens described by Brownell et al. (1987) possessed tubercles (or hard raised protuberances) on the anterior edge of the dorsal fin.

Silber et al. (1988) observed that living *P. sinus* are distinctly olive or tawny brown in coloration, and Norris and McFarland described the animal as being brown in color, as opposed to the the pale or slate gray described elsewhere (Norris and Prescott 1961, Brownell et al. 1987). Differences in these descriptions may be related to the presence of diatoms on living animals. The external coloration may change somewhat as diatoms, or other phytoplankters that have adhered to the external surface, slough off or die when porpoises are removed from the water. Living vaquita calves are much darker in appearance than are adults; a color more closely approximating slate-gray (Silber et al. 1988).

Behavior

The few researchers that have seen living *P. sinus* have made few behavioral observations, and these are based on brief encounters with the animal (Norris and McFarland 1958, Norris and Prescott 1961, Villa 1976, Wells et al 1981, Vidal et al. 1987). In general, these sightings include reports of the vaquita's small group size, its low surfacing profile, and its "secretive" nature. Norris and Prescott (1961) reported that the porpoise surfaced unobtrusively in unexpected locations, and it rarely swam in a straight course. In my experience this description is apt.

The only reasonably detailed account of the behavior of the vaquita is from extended observations (> 3 hrs each) on 25 and 27 March 1986 of two adult/calf pairs (Silber et al. 1988). Ventilation patterns of both the young and the adult in each pair were quantified. Average dive time for adults was about 80 sec and average dive time for calves was about 45 sec. Adult porpoises surfaced 4 - 5 times per surfacing sequence, while calves generally surfaced only 2 - 3 times per sequence. The animals traveled an estimated 4 - 8 km/hr while under observation. Although it is generally assumed that *P. sinus* and other porpoises of the subfamily Phocoeninae actively avoid boats, Silber et al. (1988) reported that their relative success in tracking the animals was facilitated by an apparent lack of vessel avoidance by the vaquita, coupled with near perfect sea and sighting conditions.

In each of my encounters with *P. sinus*, and as observed in previously described sightings, the porpoise's surfacing behavior was unobtrusive; this behavior is described as "slow-rolling". Unlike most delphinids, which can be obvious or highly active at the surface, "slow rolling" is typical of those species in the subfamily Phocoeninae. I noted only three exceptions in the vaquita. On one occasion (7 May 1987), several members of a group of about seven individuals, derived from the convergence of two smaller groups, were seen "porpoising" actively at the surface. At the time I thought that these animals were pursuing prey. On another occasion (16 April 1988), a single individual jumped from the water while swimming rapidly, exposing 2/3 of its body. In subsequent surfacings this animal was observed slow-rolling. One additional curious behavior was seen during aircraft surveys (4 September 1988), when a single vaquita was observed (for about 10 sec) very close to the surface, swimming very rapidly, and cutting tight circles (1 - 2 body lengths) and arcs. This porpoise may also have been pursuing prey.

Vocalizations

Phocoena sinus acoustic signals were similar to those described for other members of the family Phocoenidae, particularly with respect to click duration, dominant frequencies, and bandwidth, including those of *Phocoena phocoena* (Dubrovskii et al. 1971, Møhl and Andersen 1973, Kamminga and Wiersma 1981, Kamminga 1988), *Neophocaena phocaenoides* (Kamminga et al. 1986, Kamminga 1988), and *Phocoenoides dalli* (Awbrey et al. 1986, Evans and Awbrey 1988) The sounds are also similar to those of the delphinids, *Cephalorhynchus spp.* (Watkins and Schevill 1980, Kamminga and Wiersma 1982, Kamminga 1988, Dziedzic and De Buffrenil 1989) (Table 6). Among these species, there is apparently considerable inter- and intraspecific consistency in click structure, as well as a great deal of interclick similarity (Kamminga 1988).

However, some aspects of *P. sinus* clicks differed slightly from the click structure in other phocoenid species. For example, the maximum frequency was somewhat greater and the average bandwidth was slightly less in clicks produced by *P. sinus* than in those reported in other phocoenids. Observed differences may represent "real" interspecific variation in echolocation signals, or they may be related to the context, or the manner in which the recordings were made. Alternative reasons for these differences are discussed below, and a larger sample of *P. sinus* recordings might resolve the discrepancies.

In this study and in other descriptions of phocoenid clicks, a relatively small number of clicks was actually measured in each study and click structure may be influenced by the size or age of the individual(s) recorded. Location of the hydrophone relative to the sound beam produced by vocalizing porpoises may result in small misrepresentations of clicks when recordings are obtained at sea (Watkins 1980), whereas recordings made of captive animals provide better control of the acoustic environment and allow direct observation of the animal's orientation with respect to the hydrophone.

Slight differences in *P. sinus* click structure relative to those of other phocoenids also may have been a function of the behavioral context in which they were emitted, because behavioral and environmental contexts influence the type of signal recorded. It is becoming increasingly obvious that delphinid echolocation signals are highly adaptable to a given context. Norris et al. (1967) found that a bottlenose dolphin used signals that emphasized low frequencies for orientation and higher frequency-rich signals for size discrimination of targets. Evans (1973) reported that most energy in bottlenose echolocation clicks were between 35 - 60 kHz in tanks, but during a target detection experiment with bottlenose dolphins in the open waters of a Hawaiian bay, Au et al. (1974)

recorded peak frequencies between 120 and 130 kHz. The bay was acoustically dominated by snapping shrimp in the lower frequency registers, and the dolphins apparently optimized the signal-to-noise ratio by employing sounds that exceeded this noise. Similar flexibility in acoustic behavior apparently exists in phocoenids (although to a much smaller degree), in which behavioral or environmental context may affect the type of signal used. Dubrovskii et al. (1971) suggested that *P. phocoena* tunes its frequency to a certain detection problem, and Møhl and Andersen (1973) suggested that harbor porpoise sonar signals may differ when being used for "ranging" vs. "identifying" (referred to as "navigational" and "inspectional" by Kamminga and Wiersma 1981). In my recordings, *P. sinus* may have shifted the maximum frequency range of its clicks upward in response to considerable ambient noise produced by snapping shrimp, and this may account for the high upper frequency ranges reported here. Ambient noise was broadband and most energy was concentrated below 16 kHz. However, there was also considerable ambient noise energy that was high frequency.

Ecological Contexts

The role of the environment and habitat in shaping features of animal communication has been noted in numerous terrestrial systems (for example, see Morton 1975, Marten and Marler 1977). Apparently, echolocation clicks of marine mammals are also adapted to the physical structure of the habitat being utilized. This hypothesis has received attention by several researchers (Evans and Awbrey 1988). The ecological significance of echolocation in dolphins was first considered by Norris

(1969), addressed briefly by Evans (1973), and subsequently discussed by Wood and Evans (1980) and Evans and Awbrey (1988).

The structure of sounds produced by phocoenids may have important ecological ramifications. Narrow band, high frequency sounds exceed the hearing ranges of both predators and prey, and allow phocoenid porpoises to search for prey in shallow, turbid water habitats. Murky water habitats reduce visual detection by both predator and prey, and further reduction of acoustic detection should have great adaptive value. Andersen and Amundin (1976) reported that sounds of *P. phocoena* exceeded the auditory range of one of its principal predators, the killer whale; thereby limiting the ability of this predator to locate phonating porpoises. Therefore, the nature of these sounds allow porpoises that inhabit turbid water to search for and ensonify prey, while remaining undetected during a predatory rush, and to be "hidden" from potential predators. Furthermore, the use of sounds of this nature limit the species to murky water habitats where avoiding visual detection by predators is paramount.

Relationship Between Acoustic Signals and Habitat

Sounds produced by phocoenids share great interspecific similarity (Table 6), relationships that are probably linked to the utilization of analogous habitats. Interestingly, there are also parallels in both signal character and habitat type between the phocoenids and the distantly related delphinids *Cephalorhynchus spp.*, and several authors contend that similarities among these quite different taxa are linked to the use of similar habitat types (Watkins et al. 1977, Wood and Evans 1980, Evans et al. 1985, Kamminga 1988).

Both species of *Cephalorhynchus spp.* and phocoenids inhabit coastal, turbid water regions, areas that are acoustically complex. Nearshore habitats may be characterized by irregular reverberational surfaces such as rocks and non-uniform sea floor. Topography and composition of the substrate may present surfaces, ranging from soft mud to rock or reef substrates, that vary greatly in relative reflectivity capacity. The acoustic environment is further complicated by biologically and physically generated noise, such as snapping shrimp, fish, or other benthic and epibenthic organisms, and wave action on the shore.

Phocoenid clicks that possess acoustic energy concentrated in a narrow spectral band, are particularly well adapted to pursuing prey associated with the sea floor (Dubrovskii et al. 1971, Kamminga et al. 1986). The detection and recognition of food objects near or against the background of the sea floor requires utilization of acoustic signals whose wavelengths are comparable to or shorter than the dimensions of the food objects. A small wavelength signal permits the echolocating animal to focus the sounds in a manner that minimizes reverberation from the bottom and objects associated with it, and they involve frequency ranges that minimize competition with ambient noise. Therefore, the sounds have features that enable echolocating porpoises to optimize their ability to detect returning signals while minimizing interference by ambient noise.

The sounds produced by *P. sinus* are likely related to the same ecological factors. I have shown that vaquita inhabit murky water of moderate depth, a physically and acoustically cluttered habitat where porpoises can search for prey while remaining undetected by prey and predator. Vaquita sounds are indicative of its phylogenetic affinities with other phocoenids. In addition, the sounds are well adapted to murky water regions. In fact, the characteristics of the sounds may serve to limit *P. sinus* to habitats of this nature.

Vocal Repertoire of Delphinids and Phocoenids Compared

A great deal has been written on the structure and function of delphinid vocal repertoires, and a review is beyond the scope of this work. Nonetheless, a comparison of the probable function of delphinid whistling behavior relative to the absence of whistles in phocoenids warrants brief consideration. In contrast to phocoenids, a number of delphinid species inhabit open-water environments. These habitats are very different acoustically from nearshore areas. Open-ocean environments present situations in which social living is paramount to predator defense and location of prey, and the acoustic behavior of delphinids correspond to these factors. Whistles produced by delphinids have acoustic properties, including the use of sonic frequency ranges and frequency modulated sounds, that allow the sounds to be detected at greater distances than narrowband, unmodulated high frequency sounds. Whistles probably serve important social and behavioral functions, including an indication of identity or behavioral state of the caller, and maintaining group cohesion of large schools in pelagic habitats (Norris et al. 1985, Würsig 1986). While the high frequency phonations of phocoenids may have social facilitating functions in some contexts, they probably do not travel great enough distances to serve as contact calls or act as long range group coordination roles. The relative inability to communicate long distances may have contributed to the evolution of typically small group sizes in phocoenids; however, a myriad of ecological factors undoubtedly led to this characteristic. By relying on high frequency signals, the capacity among phocoenids for long distance signalling may have been sacrificed for the adaptive importance of predator avoidance, a reduction of detection by prey, and prey acquisition in acoustically complex habitats.

The Marine Environment of the Northern Gulf of California and its Relationship to the Distribution of *Phocoena sinus*

Most records for *P. sinus* are from the upper quarter of the Gulf of California. Therefore, it appears to be a species wholly locked within the Gulf. Neither modern understanding of the tectonic history of the Gulf, nor the broader oceanographic history of the Eastern Tropical Pacific have been considered in trying to understand this restricted distribution. Both must have had important parts to play. Therefore, I review here the oceanographic structure of the Gulf and its relations from Pliocene times to the present, as well as the inter glacial episodes of the Pliestocene when the animal is presumed to have reached its present distribution.

Geology

The Gulf of California is an elongate trough (about 1000 km long, and an average of 150 km wide) that is open to the Pacific at its southern end and is bordered by highlands to the west and mostly lowlands on the east. It is situated between the arid Baja California peninsula and the almost equally arid states of Sonora and Sinaloa. The Gulf is oceanographically unique because its long axis and the Baja California peninsula limit moderating influences from the Pacific Ocean circulation. The northern Gulf is an area of extreme tides, shallow depths, and great seasonal temperature fluctuation, which grade to moderate almost oceanic physical conditions and extreme depth in the south. These physical features produce a wide spectrum of spatial and temporal marine habitats, resulting in a high number of endemic species.

According to Rusnak et al. (1964) the Gulf of California evolved as fractured plates of coastal material moved northwestward along the continental plate margin. Spreading of the Gulf began about 4.5 million years ago (Atwater 1970). Several million years prior to the period of rifting, the sea probably invaded parts of the Gulf, creating a proto-Gulf (Moore and Buffington 1968, Karig and Jensky 1972). Subsequent spread of the basin during the Pliocene and Pleistocene created what is now the western part of the Gulf (Gastil et al. 1983), and the original axis was probably east of Angel de la Guarda Island, as the Ballenas Channel (in its current location) appears to be a relatively young structure (Phillips 1964). The motion of the tip of the Baja California peninsula away from the Mexican mainland has been an average of 6 cm/yr^{-1} for the past four million years (Larson et al. 1968).

Oceanographic Provinces of the Gulf

There are four general oceanographic areas in the Gulf (Roden 1964). The southern portion is predominantly oceanic. This region is in open communication with the Pacific Ocean above 2000 m depth and it has water masses similar to the subtropical Pacific, though modified to some degree by surface evaporation (Bray 1988).

The central portion has oceanographic features that are intermediate relative to the areas to the north and south. Basin depths are great (the Guaymas and Carmen basins have depths of 2,000 and 2,700 m, respectively) and the thermocline is well developed (from 30 - 60 m) from April through October, reaching maximum strength in August. Below the thermocline, water is essentially the same as in the equatorial Pacific (that of Antarctic Intermediate Water) (Alvarez-Borrego 1983).

The third area is located near the midriff islands. These waters, particularly those of the Ballenas Channel, are isolated from the central part of the Gulf by a sill about 450 m deep that lies perpendicular to the long axis of the Gulf immediately south of the midriff islands (Rusnak et al. 1964). Above 450 m, exchange of water between northern and central parts is unrestricted, but below sill depth the hydrographic properties are quite different on each side of the sill (Bray 1988). For instance, at 1000 m the temperature north of the sill is 4° C warmer than it is south of the sill, and salinity is 4 $^{o}/oo$ higher (Roden and Groves 1959).

The sill, the islands, and the Ballenas Channel are important to the thermohaline circulation of this area and the rest of the Gulf. These constricting geologic features create strong longitudinal tidal currents that result in a high degree of vertical mixing and anomalously high bottom temperatures, salinities, and dissolved oxygen values. A deep salinity minimum (characteristic of the south) does not occur here (Bray 1988).

Mean monthly surface temperatures in this area are usually the lowest in the Gulf, due to upwelling that is prevalent in both summer and winter (Maluf 1983). The midriff zone, with its deep water Ballenas Basin (to 800 m) harbors a number of animal species typical of the cooler waters of the outer coast of Baja California, such as California spiny lobsters (*Panulirus interruptus*), California sheepheads (*Semicossyphus pulcher*), cat sharks (*Apristurus spp.*), and others (Hubbs 1952).

The fourth area, the northern Gulf between the Colorado River delta and the northern extent of the midriff islands, is characterized by shallow (< 200 m), gently sloping bottom contours, high nearshore turbidity, high salinities, large tidal amplitudes, and strong tidal currents.

In the shallows of the Colorado River delta and extensive intertidal areas of the upper Gulf, salinities are high due to low precipitation and substantial evaporation, particularly in summer. The aerial climate is more continental than oceanic, which leads to large annual and diurnal water temperature ranges (Roden 1964) and strong thermocline development in the summer (Alvarez-Borrego 1983). These combined characteristics have important consequences for the marine flora and fauna inhabiting the upper Gulf and act to exclude many southern forms. Numerous species are "trapped" in the upper Gulf, including fishes with ranges well to the north outside the Gulf (Hubbs 1948). The same factors may also represent ecological barriers to *P. sinus*.

Bathymetry

As a whole, the floor of the Gulf exhibits gross irregularities, a combination of lowlands and highlands with moderate and steep slopes, much like the adjacent continental areas. Rivers originating in the Sierra Madre Occidental have deposited a smooth deep blanket of sediment along the mainland coast, resulting in broad gentle slopes on the eastern shelf. In contrast, there are few rivers on the Baja California peninsula and little sediment is available to smooth bottom contours (Maluf 1983). Therefore, the shelf is generally rocky and narrow around islands and along most of the Baja California peninsula, and the shelf break averages only 5 km from shore except within embayments (Byrne and Emery 1960). Beyond the shelves, slopes lead down to basin depths. These features are indicative of the relatively recent geologic history of the Baja California peninsula, and its movement northwestward away from the Mexican mainland.

Most depressions in the Gulf are submerged valleys or deep submarine canyons (to 2,400 m) which extend to slopes off the southern tip of the peninsula (Roden 1964), and are probably from the Miocene or Pliocene (Shepard 1964). South of the midriff island area the floor is of high relief, featuring polygonal basins, long troughs, high ridges, steep cliffs, and deep water. Polygonal basins and sills result from the tectonic movement of the Baja peninsula northwestward. Basin floors are covered with rock, gravel and an overlying sand layer resulting from current scouring.

The upper end of the Gulf is limited by the Colorado River and the Imperial Valley trough that contains the Salton Sea. The trough is a structural and topographic extension of the Gulf, 250 km beyond the Gulf's present northern limit (Schreiber 1969). The trough once housed the Gulf as far north as Indio, California on occasion. The delta that divides the Salton Sea from the Gulf is almost flat and consists of Pliocene to Recent deltaic sediment (Tarbet 1951, Diblee 1954). The delta region represents the widest shelf in the entire Gulf.

The northern Gulf sea floor is a generally smooth plain which slopes east southeast at an average of 0.05° from mean sea level to depths of about 15 m. This plain is the subtidal continuation of the extensive intertidal mud flats (Thompson 1969b). South of the delta, the sea floor continues on a gradual slope where extensive sedimentation has hidden most dramatic features. There are three small depressions in the upper Gulf - all deeply silted. The deepest basin in this area is the Wagner Basin (180 m) which is situated southeast of Rocas Consag (Maluf 1983) (Fig. 24).

The low-lying coastal plain area between San Felipe, Baja California Norte and the mouth of the Colorado River consists of barren intertidal mud flats whose sediment was derived from the Colorado River (Schreiber 1969). The subtidal plain in this area is characterized by a rippled substrate which consists of low ridges and intervening flat-bottomed troughs that trend approximately parallel to the Gulf axis (Fig. 24). These features are thought to represent "tidal current ridges" which are common in other areas of comparably strong tidal currents where sandy sediment exists (Thompson 1969b). The north-south orientation of the channels and troughs may act to concentrate tidal flow and hence turbidity, localized upwelling, productivity, and intermediate trophic levels. They may therefore be important features in concentrating food sources for the vaquita and other vertebrates that feed in the upper trophic levels.

A prominent channel is also evident in the northeastern Gulf which traces a broad arc from the eastern tip of Isla Pelicano to the north end of the

Wagner Basin (Fig. 24). The V-shaped profile and relatively steep sides (2 - 3°) of this channel suggest that it represents a formerly entrenched course of the Colorado River. Irregular troughs separated by shoal ridges extend virtually to the shoreline, so that water depths of 25 - 30 m are encountered fairly close to shore. In contrast to the western Gulf, the topography in the northeast may reflect the combined effects of river cutting and Recent crustal disturbances along faults which extend into this area from the northwest (Thompson 1969b).

Unlike other areas on the eastern perimeter of the upper Gulf, the shoreline located southeast of El Golfo de Santa Clara has rather deep water areas (to 30 m) close to shore (Fig. 24). Several of my sightings of vaquita occurred in this region, and many other records of vaquita are from this area (Fig. 23). Vaquita are frequently caught by fishermen along this coast (Robles et al. 1986), because the coast is an important corridor for the northward migration of the totoaba. The bathymetry of this area is much like the western perimeter, and I believe that these features - a relatively rapidly sloping seafloor, corrugated bottom contours and moderate depths close to shore - are among the most important traits of the habitat utilized by *P. sinus*.

Suspended sediments

High turbidity levels are a permanent feature of the upper Gulf due to the constant re-suspension of Colorado River silt (Alvarez-Borrego et al. 1975). However, the amount of suspended sediment in this area varies geographically, seasonally, and during tidal cycles. Highest turbidities are always encountered around Isla Montague at the mouth of the Colorado

River and south to San Felipe (Garcia-De-Ballesteros and Larroque 1974), where suspended sediment values of 4 - 400 ppm have been measured (Gayman 1969b).

The nearshore waters of Sonora are relatively less turbid than the western shores, with moderate levels occurring near El Golfo de Santa Clara, Sonora and Bahia San Jorge; patterns that have been attributed to a counterclockwise flow in the northern Gulf, superimposed on semidiurnal tides (Gayman 1969b). According to Gayman (1969b), visibilities rarely exceed 0.3 - 0.6 m in the Colorado River delta and Alvarez-Borrego (1983) indicated that secchi disk readings were in the range of 0.5 m near the Baja coast and 1 - 2 m near the Sonora coast. Thompson (1969a) reported that maximum turbidity in the river delta occurs four hours before low tide, suggesting that a muddy plume of water is pushed back and forth by tidal currents.

During my study, secchi disc measurements varied considerably (0.5 - 12.0 m) in the waters off San Felipe (i.e. areas of "roiled" sediment laden water, occasionally interspersed with windows of relatively clear water). This condition may be a function of substantial vertical exchange that results from tidal mixing, complex current patterns, convergent zones, and internal waves. During aerial surveys, I also observed water masses of dramatically different coloration and turbidity that were juxtaposed, but clearly delineated. Satellite imagery yielded similar results (Hendrickson 1973, Lepley et al. 1975). For instance, I observed reddish-brown plumes covering large areas that were intersected along well-defined convergent zones by other water masses of a relatively lighter tint. These were in turn replaced by relatively clearer, blue-green areas farther from shore. Zones of varying turbidity are influenced by tidal pulses, resulting in complex currents, the re-suspension of sediments and nutrients which contribute to increased productivity.

Vaquita seem clearly to have distributional affinities for areas of high turbidity. The range of the species corresponds to turbid water areas of the upper Gulf, and it is absent or rare farther south where greater depths and relatively clearer waters prevail. This range is analogous to other phocoenids that are generally found in murky water regions. For example, during surveys along the west coast of the U. S., Barlow (1988) found *P. phocoena* in abundance in river deltas, bays, and estuaries, such as the Columbia River delta and in the Monterey and San Francisco Bays. This porpoise is common to various turbid water habitats in the waters in Puget Sound, and coastal regions off Alaska and British Columbia. In addition, the finless porpoise (*Neophocaena phocaenoides*) inhabits the highly turbid estuaries and shallow inland waterways of Asia, such as the muddy Yangtze River. This turbid water habitat is paralleled by the "black and white sonar" of phocoenids, and the type of sounds used by the rather distantly related delphinids *Cephalorhynchus spp.* , which are also turbid water species.

Organic material is very high in the turbid waters of the upper Gulf. The percent of organic matter in suspended sediments is sometimes near 100% (Garcia-De-Ballesteros and Larroque 1974), but usually values are about 30% (Alvarez-Borrego 1983). Consequently areas of greatest turbidity in the extreme northwest region appear to be quite rich in bacteria, zooplankton, and juvenile fishes and crustaceans (Garcia-De-Ballesteros and Larroque

1974). The Colorado River delta zooplankton biomass is apparently consistently high with no clear seasonal variability (Cummings 1977).

The high productivity of the area supports a rich faunal diversity at various trophic levels including shrimp, fish, birds, and marine mammals. The delta is a spawning ground for the totoaba and corvinas, and is also a nursery region for juvenile fish (totoaba, corvinas, mullet, grunion) and shrimp (Berdegue 1955, Thomson 1969, Thomson and Muench 1973). The area supports abundant populations of edible clams and crabs. My observations and those of others indicate that the density of California sea lions, dolphins, and various seabird species is also high in this region, and the highest densities of vaquita are found near the river delta. Due to its importance to reproduction in many fish species, in 1955, the Mexican government established the delta region as a marine sanctuary that is closed to commercial fishing in all seasons. Despite this closure, totoaba fisheries are extensive in areas within and adjacent to the sanctuary.

Sedimentation

Most sediments in the Gulf, and nearly all sediments in the northern third, are alluvial (Roden 1964). Sediments were furnished primarily by the Colorado River, and consist of fine-grained sands, silts and clays (Thompson 1968). Additional inorganic materials come from volcanic and batholithic sources of the Baja California peninsula. These are mostly granitic which have been uplifted and exposed by erosion. But this quantity is low in comparison to stream-borne sediment contributions from the Colorado River and Mexican mainland (Maluf 1983). Thus, most of the fine-grained sediments are deposited in the northern third and the eastern perimeter, and coarser materials are found along the western margin.

Deposited sediment layers in the upper Gulf can attain thicknesses of nearly 5 km in some areas (Phillips 1964), and recent sediments exhibit considerable local variability (Thompson 1969b). Although the introduction of new sediment has virtually ceased, existing Colorado River sediments are re-suspended and sorted according to particle size, primarily by tidal currents. To some degree, the Gulf also receives storm runoff and wind blown terrigenous sediments from both coasts.

In the northernmost Gulf, much of the sediment has been shifted toward the western margin, part has settled in the slightly deeper central Gulf where it occurs mixed with relict Colorado River sand, but most has accumulated in the deeper Wagner Basin and Delfin Basins (van Andel 1964).

Thompson (1969b) reported that fine sand prevails on the crests of tidal current ridges and silty clay is found in the intervening troughs near the mouth of the Colorado River. Farther south muddy sand occurs only on higher ridges, while sand-silt-clay covers the lower ridges and troughs. Fine to medium sand occurs in a continuous belt along the Sonoran coast extending throughout the intertidal and shallow subtidal zone. This belt widens southward and merges with an extensive area of sand covering the shelf north and east of the Wagner Basin. Silty clay predominates over most of the intertidal mudflats north of San Felipe and covers the smooth subtidal plain in the western Gulf, to depths of 10 - 12 m. Modern dispersal of sand appears to be limited to the area of elongate tidal current ridges which extend 20 - 30 km southeast of the river mouth.

Colorado River Effluent

Freshwater and sediment flow into the Gulf has been dramatically (and probably irreversibly) altered by human intervention. Changes in flow of the river have resulted from the construction of dams for storage and diversion to irrigation projects in Arizona, California, and Mexico. Some irrigation water is returned to the Colorado River downstream from the point of diversion, but much is lost to evaporation, and to ground water. Diverted water receives secondary use in municipal and industrial activities (Schreiber 1969).

Between 1905 and 1907 most of the river flow was diverted into the Salton Sea Basin. No clear cut channel to the Gulf has been maintained since 1905, rather the river migrated through a series of channels which terminated flow well north of the Gulf head (Schreiber 1969).

Prior to human intervention, the Colorado River contributed roughly 50% of the total freshwater to the Gulf. Before the Hoover Dam was constructed, the Colorado River provided an annual average flow of almost 18 billion m^3 of water (a rate of 500 m^3/sec), which carried 161 billion kg of sediment. Since 1935 the amount of sediment and alluvial detritus reaching the northern Gulf has greatly diminished (Schreiber 1969). The average flow has been reduced to less than 8 billion m^3, which carries about 12 billion kg of sediment.

Chemical sedimentation of very fine particles (colloids) occurs where fresh and salt water meet, which produces nutrient-rich bottom muds.

Colloid sedimentation and the subsequent enrichment of the substrate has probably been lessened dramatically following the reduction of freshwater input.

The decrease of the Colorado River fresh-water and nutrient input may have altered the productivity levels and ecological conditions of what used to be an estuarine system (Alvarez-Borrego 1983), although there are few data to support this contention. The Colorado River delta is now an area that has some of the highest salinities in the Gulf. The lack of estuarine waters may well have had an affect on the reproduction of totoaba and other fish that use the delta for spawning and the development of juveniles (Alvarez-Borrego 1983, Thomson 1969). This may in turn have resulted in an impact to the entire northern Gulf community, including the *P. sinus* population, through a disturbance of critical habitat and a reduction in available prey.

Salinity

The Gulf is a "negative estuary", in which salinity levels at the head exceed those at the mouth (Carlson and Thomson 1969), and it is the only evaporation basin in the Pacific Ocean (Alvarez-Borrego 1983). Salinities are 1 - 2% higher in the Gulf than salinities in areas of the Pacific at the same latitude (Bray 1988), and Roden (1964) reported that salinity regimes in most areas of the Gulf showed remarkable seasonal stability. Surface salinities in the shallow and extensive Colorado River river delta and in semi-enclosed bays can reach values of 41.0 ^{o}/oo during summer. Salinities become progressively more oceanic toward the south, and are essentially oceanic, mostly between 34 - 35 ^{o}/oo, at the mouth of the Gulf (Alvarez-Borrego et al.

1975). A salinity minimum is present between 500 - 1100 m south of Angel and Tiburón Islands, corresponding to Antarctic intermediate water (Bray 1988).

Evaporation exceeds precipitation and river input in the Gulf by 250 cm/yr (Roden and Groves 1959, Roden 1964). Evaporation is strongest in the north and values of 2.5 - 3.0 m/yr^{-1} have been measured in coastal areas (Roden 1958, 1964).

Precipitation

Throughout the Gulf, precipitation varies substantially by location and between years. Precipitation is restricted primarily to winter, and is slightly higher in the east than the west. Average annual rainfall is 73.5 mm in Puerto Peñasco, and 59.1 mm in San Felipe (Green 1969), and in most years rainfall in the southern Gulf exceeds that of the northern Gulf by an order of magnitude (Bray 1988).

Water Temperature

The Gulf water mass is not large enough to produce a strong influence on the climate of the surrounding land masses in the northern Gulf; in fact, the opposite is the case. Consequently, mean sea surface temperatures, particularly in the upper Gulf, are more continental than maritime and undergo drastic seasonal fluctuation.

At the head of the Gulf, mean monthly sea surface temperatures range from 14° C in January to 30° C in August (Fig. 19). Daily offshore sea surface temperatures in these areas may drop close to 8° C in winter and approach 33° C in summer (Alvarez-Borrego et al. 1975). Summer and winter extreme air temperatures strongly influence surface water temperatures particularly in areas such as deltas and tidal flats in the upper and central Gulf (Maluf 1983). Monthly average air temperatures in San Felipe range from 16.3° C in January to 32.5° C in August (Green 1969).

The central and southern Gulf temperatures are less extreme but follow the same seasonal pattern as those in the upper Gulf. In the Ballenas Channel, monthly average surface temperatures range from 14° C to 30° C, even though 640 km to the south, the annual temperature range at the mouth of the Gulf is 11° C, from 18° to 29° C. From October to June water temperatures at the mouth (monthly mean range = 21 - 29° C) are higher than at the head (monthly mean range = 14 - 28° C) of the Gulf (Robinson 1973).

At 100 m depth, temperature in the upper Gulf ranges from 14 to 24° C and the annual mean is about 18° C (Robinson 1973). These are relatively high values for bottom water, reflecting the degree of solar heating and vertical mixing that takes place (Maluf 1983). In the deeper midriff island area, turbulence caused by tidal currents around the irregular topography keeps bottom temperature about the same as that in the upper Gulf (annual range at 100 m = 13 - 27° C). South from Angel de la Guarda and Tiburón Islands, water temperature decreases regularly with depth, and basin bottom temperatures in the central and lower Gulf are much lower than those in the north. In central basins, bottom temperature is about 4° C, and in the southern basins it drops to < 2° C in deep portions (Sverdrup 1941). Temperatures increase to 14° C along the slopes in both areas (Maluf 1983). The annual temperature range at the mouth of the Gulf at 100 m is small (14 - 17° C).

Waters in the northern Gulf are nearly isothermal in winter, but during late summer the thermocline is strong and temperature differences between the surface and 150 m can exceed 14° C (Alvarez-Borrego 1983). The position of the thermocline has greater range in the north and around the midriff islands (from 15 - 130 m) than elsewhere (from 15 - 50 m) (Robinson 1973). In the northern Gulf, tidal mixing and winter storms cause a reduction of the vertical stratification (Maluf 1983).

Thermal Balance of *Phocoena sinus*

If vaquita do in fact occupy the upper Gulf of California throughout the year as my data suggest, the species must be subjected to very high water temperatures during summer and fall (up to 33° C). If its body temperature is like that of other mammals (near 37° C), very little difference exists during such high temperature periods between its body temperature and its environment, presenting the animal with severe heat balance problems during activity. The species has probably adapted to the environment at least in part, through its body morphology. Relative to its body mass, vaquita fins and flippers are very large, and they represent heat radiating surfaces. The body size of vaquita, which is small relative to other phocoenids and to nearly all of the delphinids, is also likely related to energy balance. For reasons of hydrodynamic efficiency and for additional heat dumping capacity, a reduction in body size probably occurred concurrently with an enlargement of the extremities, especially the dorsal fin which is by far the largest relative to body size of any phocoenid.

Oxygen

Dissolved oxygen levels are generally saturated in surface waters throughout the Gulf because of continuous exchange with the atmosphere and the release of oxygen by phytoplankton as a by-product of photosynthesis. However, in areas near Tiburón and Angel de Guarda Islands undersaturation is common. Around these islands subsurface water depleted in oxygen is brought to the surface by tidal currents or upwelled by wind action. Low oxygen values are also found in some other upwelling areas and in the highly turbid waters in the Colorado River delta (Maluf 1983)

In most areas of the Gulf low dissolved oxygen concentrations occur at intermediate depths (Sverdrup 1941, Roden 1964). This plays and important role in the ecology of the Gulf as it relates to organism distribution patterns and sedimentation regimes. Except in the northernmost regions, oxygen concentrations are >1 ml/l^{-1} in the upper 100 m, are <0.5 ml/l^{-1} from 150 m to 1100 m, but then increase to 2.4 ml/l^{-1} at 3500 m (Alvarez-Borrego 1983). In contrast, there is no oxygen minimum in the upper Gulf, and oxygen decreases gradually from the surface (Sverdrup 1941, Rosenberg 1969).

The absence of a mid-water oxygen minimum in the well-mixed waters of the upper Gulf may allow a number of mid-water species to inhabit the region, whereas mid-water oxygen minimums in the central and lower Gulf limit the distribution of various mid-water fishes (Moser et al. 1974). Productivity at the head of the Gulf is doubtless related to mixing and continuous high levels of dissolved oxygen. These factors in turn lead to overall high productivity in the northern Gulf, which contribute to extensive commercial fisheries for shrimp and other species, and support large populations of top level carnivores, such as marine mammals, including *P. sinus*.

Waves

Surface waves in northern Gulf are low, steep, and short period, and are generated mostly by winds. Sea breezes are most intense in afternoon and travel toward the nearest shoreline around the circumference of the Gulf (Gayman 1969a). The limited fetch produced by land masses bordering the Gulf prevents the occurrence of large, long period wind-driven waves. Waves originating in the open Pacific are rarely noticeable in the northern Gulf, however, occasionally severe storms in the southern or mid Gulf produce relatively large swells (Gayman 1969a). Occasional large storm swell, which increase in amplitude as they enter the shallow upper Gulf, may cause turbulence along the bottom, and they serve to re-circulate local nutrients. However, in the northern Gulf, large scale transport of water by wave action is negligible relative to water movements induced by substantial tidal forces.

Phocoenid species that are closely related to *P. sinus* are common to coastal areas, shallow bays, and other regions that are largely protected from oceanic swell. The semi-enclosed northern Gulf is generally an area that is protected from large swell and waves, and this may be an important feature of *P. sinus* habitat.

Upwelling

Temporal and geographical patterns of upwelling in the Gulf are complex and result from wind, tidal mixing, and circulation gyres. Upwelling brings high-nutrient water to the surface and these areas are characterized by increased productivity, phytoplankton blooms, and high zooplankton abundances (Maluf 1983).

Wind driven upwelling has two principal components in the Gulf (Gilbert and Allen 1943). In summer and early fall, southeasterly winds result in areas of upwelling near steep slopes and in the lee of islands and promontories on the western margin of the Gulf. In winter, upwelling occurs on the eastern side as a result of northwesterlies (Roden and Groves 1959, Roden 1964). Summer winds are less strong and more humid than winter winds (Bray 1988). Year around upwelling occurs in the vicinity of the island of Angel de la Guarda due to strong tidal mixing.

In addition to wind-driven upwelling, a thermodynamic model of water circulation in the northern Gulf predicts that upwelling occurs at the center of the circulating gyre in the winter, and along the coasts in summer (Maluf 1983). These areas of upwelling are undoubtedly important to vaquita distribution. For example, upwelling associated with the edge of the gyre may account for the number of sightings of vaquita near coasts.

A majority of vaquita sightings have occurred in the vicinity of particularly productive region surrounding the island of Rocas Cosag, and the island itself may cause upwelling. The rock island rises almost vertically from the sea floor, and tidal action near the island results in formation of eddies, current anomalies, and upwelling which act to re-circulate bottom nutrients. Furthermore, upwelling that occurs in conjunction with the edge of the northern Gulf circulating gyre passes between the island and the Baja Peninsula coast; a factor that contributes to the productivity of the area and is undoubtedly linked to the relatively high density of vaquita in this region.

Rocas Consag also hosts tremendous numbers of nesting sea birds and it is an important haul-out site for California sea lions. Guano from these animals contributes to the nutrients of the areas surrounding the island. Nutrient enrichment of the waters surrounding pinniped haul-out sites has been documented in other areas. With respect to elephant seals on Año Nuevo Island, California, LeBoeuf and Kaza (1981) reported that great quantities of nitrogen compounds from pinniped waste products accumulate on the island and eventually wash into the sea. This produces marked increase in ammonium nitrogen content of the waters in the vicinity. Algal growth is promoted, providing increased food for invertebrates, small fishes, seabirds, and eventually the seals themselves. A similar situation must occur near the island of Rocas Consag in the northern Gulf of California, where productivity of the waters surrounding the island is increased as a result of seabird and sea lion waste products. The nutrients are subsequently mixed in the water column by complex current patterns around the island and carried substantial distances by tidal action.

Much like the affinity of *P. sinus* for areas of upwelling, concentrations of *P. phocoena* occur in regions of upwelling in the North Pacific (Huber et al. 1982), and in areas of vertical water exchange in the North Atlantic (Gaskin and Watson 1985).

Tides

Tidal mixing has a significant influence on the thermohaline structure and circulation in the Gulf, particularly in the central and northern portions. Tides in the northern Gulf are among the greatest in amplitude in the world where maximum spring tidal ranges are 9.6 m and the mean range is 6.6 m (Matthews 1968, 1969). Therefore tides are an important factor in influencing the distribution and dispersal of many marine organisms.

The Gulf shows very different patterns for semidiurnal and diurnal tidal wave constituents. The semidiurnal wave enters the Gulf, slows down from the mouth to the middle of the Gulf at about Guaymas, decreasing in amplitude. From the middle to the head at the Colorado River, it accelerates and its amplitude rises to 15 times the values at Guaymas (Filloux 1973). The semidiurnal tide acts as a progressive wave and a virtual amphidromic point exists in the mid Gulf (near Guaymas), as the waters in the Gulf "tip" back and forth. The diurnal tide increases slowly and regularly northward to almost twice its original amplitude at the mouth. Its uniform phase suggests that it acts as a standing oscillation (Filloux 1973). The tidal range and phase indicate the predominance of the semidiurnal tide in most areas of the Gulf with the exceptions of Bahía Concepción and Guaymas, where the diurnal tide is more important during part of the month (Alvarez-Borrego 1983).

Sykes (1937) reported that tides move up the Colorado River estuary as a tidal bore that attained velocities of 3 - 4 m/sec and heights of several meters. However, Thompson (1969a) suggested that this situation prevailed when significant outflow of the river existed, and with the River's reduced flow the bore has decreased to about 0.5 m in height. Nonetheless, slack water periods do not occur, and ebb currents of equal velocity are immediately reversed upon arrival of the bore (Thompson 1969a).

Tidal wave amplitude and gentle bottom slopes create huge intertidal areas (up to 5 km wide) in parts of the upper Gulf. This feature has important implications for flora and fauna that inhabit the area. Outwash from the large intertidal is probably important to nutrification and productivity in the upper Gulf. Sand and mud substrate, heated by solarization, breed algae and bacteria which are swept off the beach by tidal flow. When submerged, vast intertidal plains provide large surface areas for animals that inhabit, graze, or feed on or near the substrate. The large intertidal areas in the upper Gulf are comprised mostly of sandy substrate, and therefore species that are found over sandy bottoms are likely abundant in this region. Many forms that inhabit the benthos or feed upon epibenthic animals represent prey for upper trophic level feeders, including totoaba and vaquita.

Currents and Circulation

Due to its positioning, the Gulf is influenced relatively little by North Pacific circulation, and complex local current patterns develop that are influenced strongly by tidal flow (Maluf 1983). In general, at the mouth of the Gulf, waters exit the Gulf at 50 - 250 m, an inflow from the Pacific occurs between 250 - 500 m, while flow of the surface layer is governed by seasonal changes in wind (Bray 1988).

A counterclockwise circulation gyre is predominant in the upper Gulf (Vonder Haar and Stone 1973, Alvarez-Borrego and Schwartzlose 1979, Lepley et al. 1975). A model of upper Gulf circulation has been proposed by Hendrickson 1973, Lepley et al. 1975). The model involves a thermally-driven current that creates rotary circulation (Maluf 1983). Hendrickson

(1973) proposed a seasonally-reversing heat engine where flow lines are curled by Coriolis force. The principal heat source is the shallow tidal waters of the Colorado River estuary, and shores along the Baja and Sonoran coasts. At the surface, seaward flow of warm water from the coasts and delta are curved right by the Coriolis effect. In winter, the same shallow water cools and sinks, causing a replacement of surface flow shoreward, again curved by the Coriolis force into a counterclockwise gyre. In all seasons, bottom currents are in opposition to those at the surface. As a result of this rotary motion, current velocities in the upper Gulf are greater on the west side of the upper Gulf relative to the eastern border. Greater current velocity on the west coast increases vertical mixing in this region, and may in part account for a vaquita distribution that favors the western shore.

Water exchange between the central Gulf and upper Gulf is believed to take place in a near surface layer of water over a channel that extends from the eastern tip of Isla Pelicano to the northern end of the Wagner Basin (Fig. 24) and a corresponding northward flow of subsurface water (Maluf 1983). This brings central Gulf water to the surface to mix with delta water.

A tongue of cold upwelled water extends northward (in April to June) from the region of Isla Angel de la Guarda (Rosenberg 1969). By August, cold water from the south is no longer apparent, because local heating has reached sufficient depth to warm the cold water (Rosenberg 1969). This wedge of cold upwelled water is manifested primarily along the western coast of the upper Gulf. Vaquita and its prey may associate with this water mass.

Internal Waves

Hendrickson (1973) and Lepley et al. (1977) described the occurrence of "surface slicks" (areas of smooth water surrounded by rippled water) in the upper Gulf which appear in aerial photographs as a series of long parallel bands. The slicks are surface manifestations of tidally-induced subsurface internal waves, which are waves on water discontinuities below the surface (Hendrickson 1973). Surface slicks of this nature have also been reported in coastal regions of various water basins throughout the world (Ewing 1950, LaFond 1959, Cairns 1967, Shea and Broenkow 1982, Chereskin 1983), and the slicks are generally attributed to tidally-induced internal waves.

High levels of biological activity are often associated with internal waves due to their tendency to concentrate small organisms (Norris 1966, Zelids and Jillett 1982, Kingsford and Choat 1986). Pelagic larval invertebrates and fish are transported by the waves (Norris 1966, Shanks 1983, 1988, Shanks and Wright 1987), and fish that are presumably feeding on concentrated plankton are also attracted to internal wave slicks (Kingsford and Choat 1986).

Cetaceans, including vaquita, utilize internal waves as well, presumably to feed on concentrated prey. Vaquita had a tendency to surface in or near these slicks, and internal waves are apparently of ecological importance to porpoises. Harbor porpoises in Monterey Bay, California have been observed spending a significantly greater amount of time milling than traveling while near surface slicks than in interslick areas (Silber and Smultea in press). Like *P. sinus*, these porpoises were probably feeding on higher localized prey densities as a result of the concentrating properties of internal waves. Other cetaceans, such as *Feresa attenuata*, (Pryor et al. 1965), *Steno bredanensis*, and *Pseudorca crassidens* (K. S. Norris, pers. comm., University of California, Santa Cruz, CA), have been observed in association with a related phenomenon: offshore areas caused by convergent zones between water masses and strong currents, which are manifested at the surface as long sinuous slicks and have a tendency to accumulate flotsam and debris. Dolphins seem to patrol them as a source of food.

Similarities exist between habitats utilized by vaquita and those used by its relative *P. phocoena*. For example, harbor porpoises inhabiting eastern coastal Canada were abundant in areas of steep bottom topography and passes between islands (Gaskin and Watson 1985). These areas are characterized by strong tidal currents that result in vertical mixing and increased quantities of deep-water plankton that are in turn fed on by herring (*Clupea harengus*) (Watts and Gaskin 1985). Herring were associated with areas of well mixed water and zooplankton abundance that concentrate along convergent zones (Battle et al. 1936), and porpoises were also drawn to these areas (Watts and Gaskin 1985). This situation is analogous to the physiographic features that influence the distribution of *P. sinus*. In the same way that convergent zones and internal waves influence porpoise distribution in the North Atlantic and North Pacific, similar features affect *P. sinus* distribution in the northern Gulf of California. In my experience, internal wave surface slicks were more apparent in the west and central regions than in the shallow eastern bays of the upper Gulf, and their capacity to concentrate prey may contribute to a vaquita distribution that favors the western coast.

Primary Productivity

The Gulf, the northern region in particular, has features that favor a high level of primary productivity, including numerous areas of upwelling, a euphotic zone that is well mixed by winds and tidal currents, extensive shallow shelves, and an accumulation of terrestrial material from the Colorado River. Primary productivity levels in the Gulf are among the highest in the world, and are comparable to those of the Bay of Bengal, upwelling areas on the west coast of Baja California, and North Africa, and they are about 2 - 3 times greater than those of the open Atlantic of Pacific at similar latitudes (Zeitzschel 1969, Alvarez-Borrego 1983).

Phytoplankton concentrations apparently exhibit patchiness and great variability with time (Allen 1938), and locality (Alvarez-Borrego 1983); and this distribution appears to be linked to upwelling (Gilbert and Allen 1943). Measured concentrations of C_{14} tended to vary the most in the southern part of the Gulf and were consistently highest in the northern portions. Zeitzschel (1969) obtained values that ranged from 0.002 - 0.952, 0.371 - 0.645, and 0.588 - 0.766 g $C/m^{-2}/day$ for the southern, central and northern Gulf, respectively.

Chlorophyll *a* distribution was also patchy throughout the Gulf (Gendrop-Funes et al. 1978). Highest surface values were found near the northernmost coasts of Baja California and Sonora. At 50 m, highest values were found in the Ballenas Channel and near San Felipe. Lowest chlorophyll *a* values were obtained in the north-central Gulf at all depths between surface and 50 m, and relatively low values were found between Angel de la Guarda and Tiburón Islands (Gendrop-Funes et al. 1978).

The upper Gulf is undoubtedly very productive. However, within this system, there appeared to be differences in the levels of productivity relative to location. Although not quantified, it appeared during repeated vessel and aircraft surveys that the western portions of the upper Gulf possessed greater biological productivity and faunal diversity than did the east. During transects across the Gulf, changes in relative abundance of fish, bird, and mammal concentrations were often dramatic as one neared the peninsula side of the Gulf. Among the most biologically active places was the area between Rocas Consag and the Baja peninsula; an area where vaquita were seen most often. I observed greater relative abundance of surface-dwelling marine vertebrates, particularly planktivores and surface feeders in the west than I did in the east. In the western portions, large schools of bait fish and various other fish species such as bat rays (*Myliobatis californica*), manta rays (*Manta birostris*), and numerous sharks (probably *Mustelus lunulatus* and/or *Rhizoprionodon longurio*) were more commonly seen near the Baja peninsula than they were on the mainland Mexico side. Various seabirds, planktivores and shallow divers in particular, were also abundant in the western half, such as the brown booby (*Sula leucogaster*), the blue-footed booby (*Sula dactylatra*), the black storm-petrel (*Oceanodroma melania*), the least storm-petrel (*O. microsoma*), and Bonaparte's gull (*Larus philadelphia*). Unusual sightings (for the northern Gulf) of the Laysan albatross (*Diomedea immutabilis*) occurred on the west, but not on the east (Newcomer and Silber in press).

Several of the above mentioned species were often seen near vaquita; affiliations that probably represent utilization of a similar habitat by two or more species rather than active association. On several occasions, black storm-petrels and Bonaparte's gulls dipped into the wake of surfacing vaquita. Manta rays were seen once near *P. sinus*. Bryde's whales were seen < 1 km from *P. sinus* on two occasions, and three times common dolphins were observed < 1.5 km from vaquita. In contrast, I never saw bottlenose dolphins near the vaquita or common dolphins.

Zooplankton

Most systematic studies on zooplankton have been conducted north of 31° N. Like phytoplankton concentrations, zooplankton biomass in the Gulf is highly variable as a function of location and time. In some locations, zooplankton volumes are as much as seven times greater than values obtained in other subtropical and tropical seas (Alvarez-Borrego 1983). According to Cummings (1977) zooplankton volumes in the upper Gulf were greatest during winter (up to 25 ml of plankton/m^{-3}). Copepods were numerically dominant and euphausiids were found only during winter and spring (Cummings 1977).

Brinton and Townsend (1980) studied the seasonal distribution of six euphausiid species in the Gulf. Most of these were limited primarily to the central and southern portions of the Gulf. However, two species *Nyctiphanes simplex* and *Nematoscelis difficilis,* had the broadest ranges which extended into the northern Gulf during some times of the year. Of these, *N. simplex* was found in very high abundance throughout the upper Gulf in April and May sampling periods.

Ichthyofauna

The Gulf has unique faunal characteristics, which seem to have arisen in response to ecological and physical factors (Walker 1960). The Gulf fish fauna is part of the Tropical American or Panamic faunal province (Moser et al. 1974). Walker (1960) surveyed the fish fauna of the Gulf, and he described 586 species that were divided into four distinct faunal areas that are related to ecological factors. The four provinces are the upper Gulf, the central Gulf, the Cabo San Lucas area, and the southeastern Gulf which includes the low estero-broken shoreline south of Guaymas. Of these, the fauna of the southeastern Gulf is least distinctive and most like the Panamic faunal province, while the fauna of the other areas within the Gulf are more clearly differentiated from the rest of the Panamic fauna. The upper Gulf is the poorest in terms of species diversity as it is in habitat diversity.

Rocky-shore species are particularly well represented in the Gulf. Nearly 3/4 of the shorefish are tropical or subtropical species with principal ranges to the south of the Gulf.

Various physical or ecological barriers prevent southern forms from inhabiting the central or upper Gulf, whereas many species within the Gulf have diverged from northern water forms. About 50 fish species have distributions exclusively to the north of the Gulf, most of which are disjunct from southern California or San Diegan fuanas. Ninety-two species, or 17% of all Gulf species, are endemic to the Gulf. The unusually high degree of endemism is due to an isolation from the outer coast, the extent of semi-isolated rocky habitats (Walker 1960); and environmental extremes in the Gulf such as temperature variation, extreme tidal range, and oxygen minimums (Moser et al. 1974). In the northern Gulf, the fish fauna includes many species that are disjunct temperate fishes that have adapted to warmer waters. Similarly, vaquita are adapted to warmer water temperatures, whereas its congeners are distributed primarily in temperate and subarctic water.

Of the Gulf endemics, 37 range widely throughout the Gulf, 22 species are confined to the upper Gulf, 27 species are found only in the southern sections, and only six species inhabit the area near Cabo San Lucas. Almost all of the species indigenous to the upper Gulf are found only in waters of moderate depth.

Only 259 species are found in the upper Gulf, and this region is depauperate relative to the remainder of the Gulf. There are 19 endemic species from moderate depths, including three sciaenids, three ophidiids, and the remainder from various spiny-rayed families. No sharks or soft-rayed fishes are endemic to the upper Gulf.

The mid-water fish fauna is dominated by warm water species. Apparently some mid-water fishes do not penetrate very far north, and most are limited to southern-most basins. All of the abundant mid-water Gulf fishes have wide latitudinal ranges outside the Gulf and are able to tolerate seasonal temperature changes in the Gulf (Walker 1960).

Moser et al. (1974) sampled fish larvae in the upper Gulf and reported moderate abundance for round herring (*Etrumeus teres*), sierra (*Scomberomorus spp.*), sardine (*Sardinops sagax*), Pacific cutlassfish (*Trichiurus nitens*), rockfish (*Sebastes spp.*), bonito (*Sarda chiliensis*), Gulf opaleye (*Girella simplicidens*), sanddab (*Citharichthys spp.*), Pacific mackerel (*Scomber japonicus*), and representatives of the family Moridae (*Physiculus* *spp.*). Guevana-Escamilla (1973) sampled the fish fauna in the Colorado River delta, north of San Felipe. The collection included 73 species, 18% of which were endemic, 42% San Diegan and 40% Panamic. Except for those species that attain significant size in maturity, most of the fish described above represent potential prey for *P. sinus*.

Although endemic species are numerous in the Gulf, only four endemic genera are represented, all monotypic. The scarcity of distinctive genera indicates that the Gulf fauna has developed in relatively recent times (Walker 1960). Walker theorized that most of the northern Gulf of California disjuncts reached the Gulf through a late Pleistocene seaway in the La Paz region, at a time when water temperatures in the Gulf were slightly cooler that at present. Hubbs (1948) proposed that currently disjunct species within the Gulf arose from faunal communities to the south during one or several periods in relatively recent interglacial episodes of the Pleistocene; the timing of which accounts for varying degrees of differentiation from specific, subspecific to race. Davies (1963) reported that surface water temperature oscillations during the Pleistocene were as great as 6° C, and a particularly cool period occurred about 15,000 years ago. Numerous organisms are believed to have populated the northern hemisphere about this time and now have disjunct antitropical distributions; among them are kelp, *Macrocystis spp.*, a number of cetacean species (Davies 1963), including right whales, *Eubalaena spp.* (Hubbs 1952), *P. sinus* (Norris and McFarland 1958, Barnes 1985), and several other species of sea mammals, such as sea lions (Hubbs 1952). Cold-water species that entered the Gulf of California in this period, were confined within the Gulf as the cool water seaway of the Pleistocene rose once again in temperature.

Fisheries

The Gulf has supported numerous fisheries and commercially valuable species are caught by trawls, long-lines, and gillnets. Brown shrimp (*Panaeus californiensis*) is unquestionably the most important commercial organism in the Gulf (Carlson and Thomson 1969). This species and *P. stylirostris, P. vanamei,* and *P. setigerus* contribute over 95% of the total value of the commercial fisheries in the Gulf. In the northern Gulf, *P. californiensis* and *P. stylirostris* predominate, occurring in commercial quantities throughout the area, including the waters near the Colorado River delta (Carlson and Thomson 1969).

A significant commercial sardine (*Sardinops spp.*) fishery has existed in the Gulf since 1967 (Arvizu 1988). Mathews et al. (1974) reported that the sardine fishery consisted principally of a subpopulation of *Sardinops caerula*, that apparently spends its entire life within the Gulf and has maximum concentrations in the Guaymas area during the winter which is the spawning season. In the upper Gulf, the most important commercial fisheries are those for shrimp, totoaba (Arvizu and Chavez 1970), other corvinas (*Cynoscion spp.*), sea basses (*Epinephelus spp.*), snappers (*Lutjanus spp.*), the sierra (*Scomberomorus sierra*), the striped mullet (*Mugil cephalus*), and the Pacific sand perch (*Diplectrum pacificum*) (Thomson, 1969). Of these, totoaba and corvinas are most abundant along sandy shores from San Felipe and Puerto Peñasco northward.

Over 1,000 tons of totoaba were caught between 1936 and 1946 (Flanagan and Hendrickson 1976), and the fish was formerly harvested using spears while it spawned in the shallows (Hendrickson 1979). The totoaba fishery has been substantial over the last four decades, but it has declined dramatically since 1970 due to a declining population and to restrictions imposed (in 1975) when catch levels threatened the population. Despite closures, totoaba gillnet fisheries continue on a small scale and they remain a threat to the *P. sinus* population (Brownell 1983, Silber 1990) as well as the fish populations. Juvenile totoaba are also caught and killed in substantial numbers by shrimp trawls (Alvarez-Borrego 1983), which further endangers the totoaba population.

Predators

Although killer whales appear to be infrequent inhabitants of the upper Gulf, they may represent significant predators to *P. sinus*. Killer whales have been observed to prey upon other cetacean species in the upper Gulf (Silber et al. in press) and in other regions harbor porpoises and other small marine mammal species comprise at least part of their diet (Heyning and Dahlheim 1988). Several large shark species are common in the Gulf, and they too may represent potential predators of the vaquita.

Range and Distribution of *Phocoena sinus*: An Overview

As suggested by Norris and McFarland (1958), *P. sinus* probably entered the Gulf during one of the interglacial periods of the Pleistocene, became "trapped" in the cul-de-sac of the Gulf, subsequently adapted to the marine environment of the upper Gulf, and diverged from ancestral southern hemisphere stocks. Like various endemic fish species, *P. sinus* may be restricted to the northern portions of the Gulf by oceanographic features which represent physical or ecological barriers that limit dispersal of the species.

It is believed by some researchers that the entire *P. sinus* population is limited to the upper Gulf, which seems to represent the smallest range of any marine cetacean (Barlow 1986, Brownell 1986); however, the actual range remains unsubstantiated. Occasional reports of *P. sinus* have been made outside the upper Gulf (Norris and McFarland 1958, Norris and Prescott 1961, Villa 1976, Silber 1990). These sightings may have been incorrect identifications. Alternatively, these reports may represent "wanderers", or distributional outliers from main concentrations of the population in the northern Gulf; a situation that has been noted for *P. phocoena* along the west coast of the U. S. (Norris and McFarland 1958). The sightings may be indications of a greater historical range. Therefore, while the overall range for *P. sinus* may be relatively large, the principal range (areas where the porpoise is commonly found) is apparently limited to the upper Gulf.

It is noteworthy that sightings of the closely related *P. phocoena* at its southern range limit in California are also restricted to a modest number of localities, the southernmost being Monterey Bay, California. The range of this species, as determined by occasional captures or strandings, extends far to the south of this locality. For example, although the southernmost locality where sightings of *P. phocoena* schools regularly occur is Monterey Bay, specimens have been taken from San Pedro, California (Norris and McFarland 1958), and it may be seldom sighted or identified outside of a principal range. On east coast of North America, the principal range of *P. phocoena* is apparently limited to areas north of Maryland. However, strandings have occurred in northern Florida, over 900 km to the south (T. Polachek, pers. comm., National Marine Fisheries Service, Woods Hole, MA 02540). Apparently the species may move in small numbers far beyond its centers of abundance, and a situation similar to this may exist for *P. sinus*.

Another factor that may limit vaquita range and distribution is the meager population size of the species. The vaquita population is undoubtedly small and numbers may be decreasing. The species may have progressively retreated to the upper Gulf in response to a shrinking population size, due at least in part to incidental mortality in gillnets. This hypothesis may have analogy in the distributional shift of harbor porpoise of the Bay of Fundy and adjacent waters. There, *P. phocoena* is now rare in areas where it was formerly abundant (A. Read, pers. comm., Woods Hole Oceanographic Institute, Woods Hole, MA 02540). Reductions in population size (resulting primarily from gillnet mortality) may have resulted in changes in the distribution of the species, through a limitation in the number of geographic areas utilized, as opposed to distributional shifts for ecological reasons. That is, the amount of dispersal may increase when populations are large, rather than high densities occurring in a few areas. In addition, it is likely that when the population size is large, some individuals are displaced toward, or wander into, less desired habitats near the periphery of the range. For example, the gray whale, a species whose numbers have increased dramatically in recent decades, recently expanded its range to include waters of the Gulf of California and the western Beaufort Sea. Due to apparent reductions in the *P. sinus* population, perhaps only the "best" habitats are utilized, and in this case, they are turbid water, highly productive regions of the northern Gulf.

Although some small segments of the population may range widely, there is no doubt that highest concentrations of the species are limited to the northern most Gulf - probably the area from Puertecitos to Puerto Peñasco, northward.

Phocoena sinus Distribution Within the Upper Gulf

The distribution of *P. sinus* within the northern Gulf is highly clumped. Nearly all sightings in the upper Gulf have occurred in the vicinity of Rocas Consag and San Felipe (Wells et al. 1981, Vidal et al. 1985, Silber 1988, 1990, this study). Of the 58 sightings that I made, 91.4% were made within 30 km of the Baja peninsula, and one sighting occurred within 3 km of the northeastern Sonora coast, southeast of El Golfo de Santa Clara. All previously reported vaquita sightings in the northern Gulf occurred in areas that were similar to sightings that I obtained. The localities of recovered specimens exhibit a distribution that is similar, though somewhat more extended, to that of sightings locations.

Additional indirect evidence of *P. sinus* distribution comes from fishermen. All fishermen interviewed in San Felipe and El Golfo de Santa Clara were familiar with the porpoise and indicated that they had captured vaquita, whereas not all fishermen in Puerto Peñasco were familiar with the animal (Boyer and Silber in prep., G. Silber pers. obs.).

Therefore, I believe that the clumped distribution, inferred from sighting and specimen localities and information obtained from fishermen represent actual distributional characteristics of the porpoise.

Factors Affecting the Distribution of *Phocoena sinus*: A Summary

In my estimation, *P. sinus* distribution is governed by a multivariate interaction between a variety of physiographic and biological components. Among the most important of the interacting factors are moderate water depths that are relatively close to shore, high levels of biological productivity that result from strong tidal currents, substantial vertical mixing, and suspended organic matter; and a level of productivity that is heightened by the capacity of internal waves and convergent zones to concentrate prey. This habitat allows *P. sinus* to exploit a niche that includes a rather generalized diet by feeding opportunistically on pelagic and benthic forms. However, its niche is limited to some degree, through competitive interaction with bottlenose and common dolphins. The shallow turbid water habitat permits the vaquita to search for food while avoiding detection by predators and prey alike, through the utilization of high frequency, narrow band acoustic signals.

The oceanographic features of the waters off San Felipe and southeast of El Golfo de Santa Clara are probably responsible for the propensity of vaquita records that have occurred in those areas. The Baja California coast is unique relative to the Sonoran shore because: 1) it has greater tidal current velocity throughout the year, both along the coast and in the vicinity of Rocas Consag, that results in increased mixing, turbidity, and upwelling, 2) it possesses steeper and more irregular bottom topography, and therefore greater depths occur close to shore, and 3) it receives upwelled waters from the central Gulf, and therefore has slightly lower water temperatures, and higher productivity. Like the Baja peninsula coast, many of these conditions, particularly murky water and a rapidly sloping sea floor, exist along the shoreline southeast of El Golfo de Santa Clara, an area where *P. sinus* also occurs.

The strong tidal mixing, high levels of productivity, steep bottom contours, and murky water are probably the most important characteristics of *P. sinus* habitat. Although these features, particularly upwelling, high turbidity, and high productivity are found in areas outside the upper Gulf, they are highly localized when they occur or they are present only seasonally.

Human Impact on the Northern Gulf

Various forms of human activity may be altering the ecosystem of the northern Gulf, which ultimately affect *P. sinus*, and the semi-enclosed nature of the upper Gulf may serve to magnify the impact of these activities. Pesticides from agricultural practices in the U.S. and Mexico may enter the Gulf in significant quantities. Reported DDT concentrations of 0.122 ppm have been found in the sediments of the upper Gulf, and DDT concentrations of 0.150 ppm were found in the intertidal clam, *Chione californiensis*, obtained from beaches near San Felipe (Guardado-Puentes and Nuñez-Esquar 1975).

Shrimp trawling must severely alter the benthos of the upper Gulf, although data to substantiate this contention are lacking. Mathews (1974) estimated that on average shrimp nets passed over every square meter of the Mexican Pacific shrimp grounds about seven times each year. In the upper Gulf this rate may be significantly greater than elsewhere. On numerous occasions between 1986 and 1988, I counted more than 50 shrimp trawlers in a 6 km^2 area and several times over 80 boats were counted during a single visual scan of the horizon. In these operations, many species, regarded as "trash" fish, are killed and discarded, along with associated invertebrates, and continual disturbance of the sea floor must certainly have an adverse impact on benthic communities.

The greatest influence on the northern Gulf ecosystem may result from the drastic reduction in Colorado River freshwater flow into the Gulf. Although the effect has not been quantified, the absence of freshwater input to this region has probably altered the ecology of the estuary. For instance, Alvarez-Borrego (1983) suggested that the totoaba fishery was adversely affected by the lack of estuarine waters for reproduction.

Each of these factors probably impact a myriad of marine species by disrupting food webs, including an indirect affect on the *P. sinus* population through a removal of potential prey items.

Human impact on *Phocoena sinus*

The vaquita population has been affected by gillnetting activities (Barlow 1986, Brownell 1983) and other forms of habitat degradation in recent decades, but the extent of the impact is not known. The species continues to experience mortality at an unknown rate in gillnets (Brownell 1983; Silber 1988, 1990, Boyer and Silber in prep.) set primarily for totoaba (*Totoaba macdonaldi*) and for various species of sharks.

Mortality rates are apparently greatest in gillnets with large mesh (5 -6"), and mortality is highest in spring (Boyer and Silber in prep.).

Due to temperature extremes in the northern Gulf, *P. sinus* is presented with severe heat balance problems (Silber and Norris in press), and the species may be close to the limit of maximum water temperature that it can tolerate. It has been suggested that large scale changes resulting from human activities such as global warming, may adversely affect animals like vaquita that are limited in geographic range and are adapted to specific water temperature regimes (Soulé 1988). The warming of the water by a few degrees may affect the *P. sinus* population by pushing water temperatures above those the porpoise can tolerate, or it may cause a distributional relocation as a result of rising water temperatures.

The *P. sinus* population may contain as few as several hundred individuals (Villa 1976, Barlow 1986). Populations of this size may experience a "genetic bottleneck" in which genetic diversity is low, thus making the population vulnerable to habitat perturbation, however, theories regarding genetic bottlenecks remain to be adequately substantiated. Because the vaquita is apparently limited to the upper Gulf, it is probably adapted to narrowly defined ecological circumstances, making it further susceptible to habitat disturbance, and a more rapid decline may result from a lack of genetic diversity.

Although illegal under Mexican law since 1975, gillnet fisheries operations for totoaba continue in the northern Gulf. Totoaba nets, lawfully utilized shark nets, and those that are set for other species result in unknown numbers of vaquita deaths. Most gillnet fishing for the totoaba occurs in spring when the species migrates to the northern Gulf to spawn. This may also coincide with the period when parturition occurs in *P. sinus*. The corresponding timing of these two events may increase deleterious effects of gillnetting activities on the vaquita population, because the kill will include calves (Boyer and Silber in prep.) and pregnant females.

Recent attempts have been made to quantify *P. sinus* mortality in gillnets, inferred from interviews with fishermen. Boyer and Silber (in prep.) estimated that an average of 25 - 35 porpoises are killed annually in gillnets. If the vaquita population contains only several hundred individuals, then this estimated mortality rate may represent a substantial portion of the population of the species. In general, the maximum population growth rates for cetaceans are very low (Reilly and Barlow 1986), and using extrapolations from other species, Barlow (1986) estimated that the maximum rate of population growth for *P. sinus* was 10% per year. Therefore, considering normal replacement rates of cetacean populations, such a kill probably cannot be sustained. Nearly all (90.1%) reported porpoise deaths occurred in nets of large mesh size (5 - 6") (Boyer and Silber in prep.). Deaths occurred in all seasons and the highest proportions were reported from San Felipe and El Golfo de Santa Clara. I believe that the vaquita incidental mortality estimates are reasonably accurate, but the subject requires further study.

In sum, the *P. sinus* population is small and is probably held at low levels as a result of incidental mortality in commercial fisheries. Additional impact to the species may occur indirectly from pesticide contamination, diminished fresh-water input to the northern Gulf, the disturbance of the benthos by shrimp trawling activities and other forms of habitat degradation. Increased levels of sport and commercial fishing boat traffic may also be a source of disturbance to the vaquita. A limited range, a clumped distribution within the range, and a small population size may heighten the relative effect of these perturbations. Continued exposure of the depleted *P. sinus* population to current levels of human impact clearly may result in the demise of the species.

MANAGEMENT RECOMMENDATIONS

I suggest that gillnet operations, particularly those involving nets with large mesh, be halted immediately. Gillnet mortality is probably the greatest threat to the vaquita population. Gillnets indiscriminately capture both target species as well as a number of non-target species. These nets pose serious threats to populations of sea birds, turtles, and various fish and mammal species. The totoaba is an endangered species and cannot be legally caught, sold, or exported. Nonetheless, illegal fishing continues due to the inability by authorities in Mexico to enforce restrictions or to provide alternate means of livelihood for fishermen. Large scale work is needed now to explore all possible modifications to the fishing effort, its timing, and the gear and techniques used. These efforts require a concurrent commitment to the economic consequences of limitations to fishing activities. Plans should be made to compensate fishermen if a reduction in their activity is mandated. An introduction of, and education in, alternative sources of income should be encouraged; these may involve various forms of mariculture and the employment of fishermen and their boats to act as guides for sport fishing and various forms of "eco-tourism", such as whale watching.

Vaquita sightings occurred almost exclusively in discrete locations and water depths. If widespread fishing bans are not possible, emphasis should be placed on excluding fishing from these areas. However, because these are also prime fishing locations and maximum catch of totoaba occurs in areas of high porpoise abundance, there will be difficulty achieving compliance by fishermen. Rigorous sanctions on totoaba meat bound for U.S. and Mexican markets is critical and this may reduce the demand for the fish.

An expansion of the existing marine sanctuary in the northern Gulf has been proposed and these plans should be endorsed.

Foremost is the need for additional study to quantify incidental mortality rates and to assess the size of, and monitor changes in, the vaquita population. In addition, I recommend that additional study on the vaquita be conducted to: 1) refine our knowledge of life history parameters, including reproductive and recruitment rates, age of sexual maturity, life span, etc., 2) collect additional information on the ecology, particularly with respect to diet, and 3) assess the overall range to determine if large scale movements occur. This work will be most productive if conducted through joint efforts of U. S. and Mexican scientists and authorities; a cooperation that utilizes the expertise and resources of both nations.

I suggest that conservation groups and international scientific organizations be encouraged to develop needed resources and to impose pressure, where appropriate, on state and federal governments and managing bodies to act on plans to preserve the vaquita and the ecology of the upper Gulf of California.

CONCLUSIONS

The localities of sightings and beach cast specimens and osteological material indicate that the principal range of *P. sinus* is restricted to an area from Puertecitos, Baja California Norte to Puerto Peñasco, Sonora, northward. The species is probably less common south along the Baja Peninsula and Sonoran coasts and is rare or absent throughout the remainder of the Gulf. It seems probable that it is restricted to areas of turbid water wherever it is found.

If this assessment is correct, vaquita are adapted to a unique environment that possess great annual temperature extremes, substantial tidal amplitude and velocity and high turbidity. The species may be limited to the upper Gulf by ecological or physical barriers, or because the diminished (and probably shrinking) population may have retreated to only preferred habitats. The external body morphology and body size of *P. sinus* diverge from its congeners, and its phonations are similar to those occurring in other phocoenids. These features may allow the porpoise to inhabit the upper Gulf, and they may also be of importance in confining it to that region.

Within the upper Gulf, distribution of the vaquita population is clumped; a characteristic which is probably linked primarily to physiographical and ecological features that include well-mixed, turbid, highly productive waters of moderate depth, and strong tidal currents. Bottlenose dolphins and common dolphins are abundant in the upper

Gulf, and competitive interaction with these species may also have a role in defining the ecological niche of vaquita.

When this project began, *P. sinus* was believed to be exceedingly rare, perhaps even extinct. I have shown that a small population continues to exist in the northern Gulf of California. In addition to the size of the population; the limited range, distribution within that range, and the semi-enclosed nature of the habitat, may all contribute to increasing the magnitude of human impact on the species, the most important of which is incidental mortality in large mesh gillnets. Immediate action with regard to 1) gillnet bans, 2) habitat destruction and overfishing, and 3) pollution evaluation and mitigation is imperative to preserve the species.

LITERATURE CITED

Allen, W. E. 1938. The Templeton Crocker Expedition to the Gulf of California in 1935 - the phytoplankton. Trans. Am. Microsc. Soc. 57:328-335.

Alvarez-Borrego, S. 1983. The Gulf of California. *In*: B. H. Ketchum (ed.), Estuaries and Enclosed Seas. Elsevier, Amsterdam, pp. 427-449.

Alvarez-Borrego, S. and R. Schwartzlose. 1979. Masas de agua del Golfo de California. Cienc. Mar. 6:43-63.

Alvarez-Borrego, S., B. P. Flores-Baez, and L. A. Galindo-Bect. 1975. Hidrologia del Alto Golfo de California II. Condiciones durante inverno, primavera y verano. Cienc. Mar. 2:21-36.

Alvarez-Borrego, S., J. A. Rivera, G. Gaxiola-Castro, M. J. Acosta-Ruiz, and R. A. Schwartzlose. 1978. Nutrientes en el Golfo de California. Cienc. Mar. 5:53-71.

Andersen, S. H. and M. Amundin. 1976. Possible predator-related adaptation of sound production and hearing in the harbour porpoise (*Phocoena phocoena*). Aq. Mamm. 4:56-58.

Arvizu, M. J. 1987. Fisheries activities in the Gulf of California, Mexico. CalCOFI Rep. 38:32-36.

Arvizu, J. and H. Chavez. 1970. Sinopsis sobre la biología de la totoaba, *Cynoscion macdonaldi* Gilbert 1890. FAO Fish. Synops. No. 81, 26 pp.

Atwater, T. 1970. Implications of plate tectonics for the Cenozoic tectonic evolution of western North America. Geol. Soc. Amer.

Bull. 81:3513-3536.

Au, W. W. L., R. W. Floyd, R. H. Penner, and A. E. Murchison. 1974. Measurement of echolocation signals of the Atlantic bottlenose dolphin, *Tursiops truncatus* Montagu, in open waters. Jour. Acoust. Soc. Am. 56:1280-1290.

Awbrey, F. T., J. C. Norris, A. B. Hubbard, and W. E. Evans. 1979. The bioacoustics of the Dall porpoise - salmon drift net interaction. Hubbs - Sea World Res. Inst. Tech. Rep. 79-120, 44 pp.

Balcomb, K. C., B. Villa-R., and G. Nichols. 1979. Marine mammals in the Sea of Cortez. Proc. 4th Int. Conf. on Gray Whales, La Paz, February 16, 1979. (Abstract)

Barlow, J. 1986. Factors affecting the recovery of *Phocoena sinus*, the vaquita or Gulf of California harbor porpoise. NMFS/SWFC Admin. Rep. LJ-86-37. 19 pp.

Barlow, J. 1988. Harbor porpoise, *Phocoena phocoena*, abundance estimation for California, Oregon, and Washington: I. Ship surveys. Fish. Bull., U. S. 86:417-432.

Barnes, L. G. 1977. Outline of eastern North Pacific fossil cetacean assemblages. Syst. Zool. 25:321-343.

Barnes, L. G. 1978. A review of *Lophocetus* and *Liolithax* and their relationships to the delphinoid family Kentriodontidae (Cetacea: Odnotoceti). Sci. Bull. Los Angeles Co. Mus. 28:1-35.

Barnes, L. G. 1985. Evolution, taxonomy and antitropical distributions of the porpoises (Phocoenidae, Mammalia). Mar. Mamm. Sci. 1:149-165.

Battle, H. I., A. G. Huntsman, A. M. Jeffers, G. W. Jeffers, W. H. Johnson, and M. A. McNairn. 1936. Fatness, digestion and food of Passamaquoddy young herring. Jour. Fish. Res. Board Can. 2:401-429.

Berdegué, J. A. 1955. La pesquería de la totoaba (*Cynoscion macdonaldi,* Gilbert) en San Felipe, Baja California. Rev. Soc. Mex. Hist. Nat. 16:45-78.

Boyer, P. and G. K. Silber. *In prep.* An estimate of the mortality of the vaquita, *Phocoena sinus,* in commercial fisheries.

Bray, N. A. 1988. Thermohaline circulation in the Gulf of California. Jour. Geophys. Res. 93:4993-5020.

Brinton, E. N. and A. W Townsend. 1980. Euphausiids in the Gulf of California - the 1957 cruises. CalCOFI Rep. 11:211-236.

Brownell, R. L., Jr. 1969. Pygmy sperm whale in the Gulf of California. Jour. Mamm. 50:356-357.

Brownell, R. L., Jr. 1983. *Phocoena sinus*. Mamm. Species. 198:1-3.

Brownell, R. L., Jr. 1986. Distribution of the vaquita, *Phocoena sinus,* in Mexican waters. Mar. Mamm. Sci. 2:299-305.

Brownell, R. L., Jr., L. T. Findley, O. Vidal, A. Robles, and S. Manzanilla N. 1987. External morphology and pigmentation of the vaquita, *Phocoena sinus* (Cetacea: Mammalia). Mar. Mamm. Sci. 3:22-30.

Busnel, R-G. and A. Dziedzic. 1966. Acoustic signals of the pilot whale *Globicephala melaena* and of the porpoises *Delphinus delphis* and *Phocoena phocoena*. *In*: K. S. Norris (ed.), Whales, Dolphins and Porpoises. Univ. of Calif. Press, Berkeley, pp. 607-646.

Busnel, R-G., A. Dziedzic, and S. Andersen. 1963. Sur certaines caractéristiques des signaux acoustiques de Marsouin *Phocoena phocoena* L. Comptes Rendus Acad. Sci. Paris. 257:2545-2549.

Busnel, R-G., A. Dziedzic, and B. Escudie. 1969. Autocorrelation et analyse spectrale des signaux <sonar> de deux espéces de cetacés odontocétes utilisant les basses fréquences. Comptes Rendus Acad. Sci. Paris 269:365-367.

Byrne, J. V. and K. O. Emery. 1960. Sediments of the Gulf of California. Bull. Geol. Soc. Am. 71: 983-1010.

Cairnes, J. L. 1967. Asymmetry of internal tidal waves in shallow coastal waters. Jour. Geophys. Rev. 72:3563-3565.

Carlson, J. S. and D. A. Thomson. 1969. Productivity, plankton, benthic flora, and invertebrates. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 92-94.

Chereskin, T. K. 1983. Generation of internal waves in a Massachusetts Bay. Jour. Geophys. Rev. 88:2649-2661.

Clark, C. M. and W. T. Ellison. *In press*. Numbers and distribution of bowhead whales, *Balaena mysitcetus*, based on the 1986 acoustic study off Point Barrow, Alaska. Rep. Int. Whal. Comm. 39.

Clutton-Brock, T. H. and P. H. Harvey. 1977. Primate ecology and social organization. Jour. Zool., Lond. 183:1-39.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35:131-138.

Crook, J. H. and J. S. Gartlan. 1966. Evolution of primate societies. Nature 210:1200-1203.

Cummings, J. A. 1977. Seasonal and areal variations of zooplankton standing stocks in the Northern Gulf of California. M.S. thesis. Univ. of Ariz., Tucson, 61 pp.

Davies, J. L. 1963. The antitropical factor in cetacean speciation. Evolution 17:107-116.

Diblee, T. W. 1954. Geology of the Imperial Valley region, California. Calif. State Div. Mines Bull. 170:21-28.

Diercks, J. J., R. T. Trochta, R. L. Greenlaw, and W. E. Evans. 1971. Recording and analysis of dolphin echolocation signals. Jour Acoust. Soc. Am. 49:1729-1732.

Dubrovskii, N. A., P. S. Krasnov, and A. A. Titov. 1971. On the emission of echolocation-signals by the Azov sea harbor porpoise. Soviet Physics-Acoustics 16:444-448.

Dziedzic, A. and V. De Buffrenil. 1989. Acoustic signals of the Commerson's dolphin, *Cephalorhynchus commersonii*, in the Kerguelen Islands. Jour. Mamm. 70:449-452.

Evans, W. E. 1973. Echolocation by marine delphinids and one species of freshwater dolphin. Jour. Acoust. Soc. Am. 54:191-199.

Evans, W. E. 1975. Distribution, differentiation of populations, and other aspects of the natural history of *Delphinus delphis* in the northeastern Pacific. Ph.D. thesis. Univ. of Calif., Los Angeles, 164 pp.

Evans, W. E. 1982. Distribution and differentiation of stocks of

Delphinus delphis in the Northeastern Pacific. *In*: Mammals in the Seas. FAO, Rome 4:45-66.

Evans, W. E. and F. T. Awbrey. 1988. Natural history aspects of marine mammal echolocation: feeding strategies and habitat. *In*: P. E. Nachtigall and P. W. B. Moore (eds.), Animal Sonar, process and performance. Plenum Press, NY, pp. 521-534.

Evans, W. E., F. T. Awbrey, and H. Hackbarth. 1985. High frequency pulses of Commerson's dolphin compared to those of phocoenids. H/SWRI Report SC/37/SM, San Diego, 64 pp.

Ewing, G. 1950. Slicks, surface films and internal waves. Jour. Mar. Res. 9:161-187.

Filloux , J.H. 1973. Tidal patterns and energy balance in the Gulf of California. Nature 243:217-221.

Fitch, J. E. and R. L. Brownell, Jr. 1968. Fish otoliths in cetacean stomachs and their importance in interpreting feeding habits. Jour. Fish. Res. Bd. Can. 25:2561-2574.

Flanagan, C. A. and J. R. Hendrickson. 1976. Observations on the commercial fishery and reproductive biology of the totoaba *Cynoscion macdonaldi* in the northern Gulf of California, Mexico. Fish. Bull., U. S. 74:531-544.

Gallo, J. P. and B. Alessio-Robles. Unpubl. man. Ecology of the common dolphin, *Delphinus delphis* (Linnaeus, 1758), in the Gulf of California. 38 pp.

Garcia-De-Ballesteros, G. and M. Larroque. 1974. Elementos sobre la distribucíon de turbidez en el alto Golfo de California. CalCOFI

Rep. 18:81-106.

Gaskin, D. E. and A. P. Watson. 1985. The harbor porpoise, *Phocoena phocoena*, in Fish Harbour, New Brunswick, Canada: occupancy, distribution, and movements. Fish. Bull., U. S. 83:427-442.

Gaskin, D. E., P. W. Arnold, and B. A. Blair. 1974. *Phocoena phocoena*. Mamm. Species. 42:1-8.

Gastil, G., J. Minch, and R. P. Phillips. 1983. The geology and ages of the islands. *In*: T. J. Case and M. L. Cody (eds.), Island Biogeography in the Sea of Cortéz. Univ. of Calif. Press, Berkeley, pp. 13-25.

Gause, G. F. 1934. The struggle for existence. Williams and Wilkens, Baltimore, 163 pp.

Gayman, W. 1969a. Waves and wave action. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 56-71.

Gayman, W. 1969b. Turbidity in the extreme northern Gulf of California. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 88-91.

Gendrop-Funes, V., M. J. Acosta-Ruiz, and R. A. Schwartzlose. 1978. Distribucíon horizontal de clorofila "a" durante la primavera en la parte norte del Golfo de California. Cienc. Mar. 5:71-89.

Gilbert, J. Y. and W. E. Allen. 1943. The phytoplankton of the Gulf of

California obtained by the *E. W. Scripps* in 1939 and 1940. Jour. Mar. Res. 5:89-110.

Gilmore, R. M. 1957. Whales aground in Cortés' Sea. Pac. Disc. 10:22-27.

Green, C. R. 1969. Meteorological conditions. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 7-15.

Guardado-Puentes, J. and O. Nuñez-Esquar. 1975. Concentracíon de DDT y sus metabolitos en especies filtroalimentadoras y sedimentos en el Valle de Mexicali y Alto Golfo de California. M.S. thesis. Universidad de Baja California, Ensenada, 31 pp.

Guevana-Escamilla, S. 1973. Peces. *In*: Estudio quimico sobre la contaminacíon por insecticidas en la desembocadura del rio Colorado. II. Universidad Autonoma de Baja California Rep. a la Dir. de Acuacultura, S.R.H. Ensenada, B.C. pp. 236-262.

Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. Am. Nat. 94:421-425.

Hendrickson, J. R. 1973. Study of the marine environment of the northern Gulf of California. NTIS Pub. No. N74-16008, 95 pp.

Hendrickson, J. R. 1979. Totoaba: sacrifice in the Gulf of California, letter to my grandchildren. Oceans 12:14-18.

Heyning, J. E. 1986. First record of the dolphin, *Steno bredanensis*, from the Gulf of California. Bull. S. Calif. Acad. Sci. 85:62-63.

Heyning, J. E. and M. E. Dahlheim. 1988. *Orcinus orca*. Mamm. Species

304:1-9.

Huber, H. R., D. G. Ainley, and S. H. Morrell. 1982. Sightings of cetaceans in the Gulf of the Farallones, California, 1971-1979. Calif. Fish and Game 68:183-189.

Hubbs, C. L. 1948. Changes in the fish fauna of western North America correlated with changes in ocean temperature. Jour. Mar. Res. 7:459-482.

Hubbs, C. L. 1952. Antitropical distribution of fishes and other organisms. Proc. 7th Pac. Sci. Congr. 3:324-329.

Irvine, A. B., M. D. Scott, R. S. Wells, and J. H. Kaufmann. 1981. Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus,* near Sarasota, Florida. Fish. Bull., U. S. 79:671-688.

Jarman, P. J. 1974. The social organisation of antelopes in relation to their ecology. Behaviour 48:215-267.

Jones, R. E. 1981. Food habits of smaller marine mammals from northern California. Proc. Cal. Acad. Sci. 42:409-433.

Kamminga, C. 1988. Echolocation signal types of odontocetes. *In*: P. E. Nachtigall and P. W. B. Moore (eds.), Animal Sonar, process and performance. Plenum Press, New York, pp. 9-22.

Kamminga, C., T. Kataoka, and F. J. Engelsma. 1986. Investigations on cetacean sonar VII. Underwater sounds of *Neophocaena phocaenoides* of the Japanese coastal population. Aq. Mamm. 12:52-60.

Kamminga, C. and H. Wiersma. 1981. Investigations on cetacean sonar II. Acoustical similarities and differences in odontocete sonar signals. Aq. Mamm. 8:41-62.

Kamminga, C. and H. Wiersma. 1982. Investigations on cetacean sonar V. The true nature of the sonar sound of *Cephalorhynchus commersonii*. Aq. Mamm. 9:95-104.

Karig, D. E. and W. A. Jensky. 1972. The proto-Gulf of California. Earth and Planetary Sci. Letters. 17:169-174.

Kawamura, A. 1980. A review of food of balaenopterid whales. Sci. Rep. Whal. Res. Inst. 32:155-197.

Kawamura, A. 1982. Food habits and prey distributions of three rorqual species in the North Pacific Ocean. Sci. Rep. Whal. Res. Inst. 34:59-91.

Kingsford, M. J. and J. H. Choat. 1986. Influence of surface slicks on the distribution and onshore movements of small fish. Mar. Biol. 91:161-171.

Lack, D. 1947. Darwin's Finches. Cambridge Univ. Press, Cambridge, 208 pp.

LeBoeuf, B. J. and S. Kaza. 1981. Retrospective. *In*: LeBoeuf, B. J. and S. Kaza (eds.), The Natural History of Año Nuevo. Boxwood Press, Pacific Grove, pp. 375-388.

LaFond, E. C. 1959. Slicks and temperature structure in the sea. U. S. Naval Electronics Lab. Res. Rep. 937:1-35.

Larson, R. L., H. W. Menard, and S. M. Smith. 1968. Gulf of California: a result of ocean-floor spreading and transform faulting. Science 161:781-784.

Lepley, L. K., S. P. Vonder Haar, J. R. Hendrickson, and G. Calderon-Riveroll. 1975. Circulation in the northern Gulf of California from orbital photographs and ship investigations. Cienc. Mar. 2:86-93.

Magatagan, M. D., E. H. Boyer, and B. Villa-R. 1984. Revisión del estado que guarda *Phocoena sinus* Norris and McFarland y descripción de tres nuevos ejemplares. An. Inst. Biol. Univ. Nal. Autón. México, Ser. Zool. 55:271-294.

Maluf, L. Y. 1983. The physical oceanography. *In*: T. J. Case and M. L. Cody (eds.), Island Biogeography in the Sea of Cortéz. Univ. of California Press, Berkeley, pp. 26-45.

Marten, K. and P. Marler. 1977. Sound transmission and its significance for animal vocalization. I. Temperate habitats. Behav. Ecol. and Sociobiol. 2:271-291.

Mathews, C. P. 1974. ¿Cuanto resistira el camaron? Cienc. Mar. 1:86-91.

Mathews. C. P., J. L. Granados-Gallegos, and J. Arvizu. 1974. Results of the exploratory cruises of the "*Alejandro De Humboldt*" in the Gulf of California. CalCOFI Rep. 17:101-111.

Matthews, J. B. 1968. The tides of Puerto Peñasco, Gulf of California. Jour. Ariz. Acad. Sci. 5:131-134.

Matthews, J. B. 1969. Tides in the Gulf of California. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 41-50.

Menge, B. A. and J. P. Sutherland. 1976. Species diversity gradients:

Synthesis of the roles of predation, competition and temporal heterogeneity. Am. Nat. 110:351-369.

Mizue, K., A. Takemura, and K. Nakasai. 1968. Underwater sounds of the Chinese finless porpoise caught in the Japanese coastal sea. Bull. Faculty of Fisheries, Nagasaki University 25:25-33.

Møhl B. and S. Andersen. 1973. Echolocation: high frequency component in the click of the harbour porpoise (*Phocoena phocoena* L.). Jour. Acoust. Soc. Am. 54:1368-1372.

Moore, D. G. and E. C. Buffington. 1968. Transform faulting and growth of the Gulf of California since the late Pliocene. Science 161:1238-1241.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. Am. Nat. 109:17-34.

Moser, H. G., E. H. Ahlstrom, D. Kramer, and E. G. Stevens. 1974. Distribution and abundance of fish eggs and larvae in the Gulf of California. CalCOFI Rep. 17:112-128.

Nemoto, T. 1959. Food of baleen whales with reference to whale movements. Sci. Rep. Whal. Res. Inst. 14:149-290.

Newcomer, M. W. and G. K. Silber. 1990. Sightings of the laysan albatross in the northern Gulf of California, Mexico. Western Birds 20:134-135.

Noble, B. A. and F. C. Fraser. 1971. Description of a skeleton and supplementary notes on the skull of a rare porpoise *Phocoena sinus* Norris & McFarland, 1958. Jour. Nat. Hist. (Lond.) 5:447-464.

Norris, K. S. 1966. The functions of temperature in the ecology of the percoid fish *Girella nigricans* (Ayres). Ecol. Monogr. 33:23-62.

Norris, K. S. 1969. The echolocation of marine mammals. *In*: H. T. Andersen (ed.), The Biology of Marine Mammals. Academic Press, NY, pp. 391-423.

Norris K. S. and W. N. McFarland. 1958. A new harbor porpoise of the Genus *Phocoena* from the Gulf of California. Jour. Mamm. 39:22-39.

Norris, K. S. and J. H. Prescott. 1961. Observations on Pacific cetaceans of Californian and Mexican waters. Univ. Calif. Publ. Zool. 63:291-402.

Norris, K. S., W. E. Evans, and R. N. Turner. 1967. Echolocation in an Atlantic bottlenose porpoise during discrimination. *In*: R-G. Busnel (ed.), Animal Sonar Systems. Vol. 1. Jouy-en-Josas, France, pp. 409-437.

Norris, K. S., B. Würsig, R. S. Wells, M. Würsig, S. Brownlee, C. Johnson, and J. Solon. 1985. The behavior of the Hawaiian spinner dolphin, *Stenella longirostris*. NMFS/SWFC Admin. Rep. LJ-85-06C, 213 pp.

Orr, R. T. 1969. An additional record of *Phocoena sinus*. Jour. Mamm. 50:384.

Perrin, W. F., N. Miyazaki, and T. Kasuya. 1987. A new spinner dolphin from Thailand. 7th Bien. Conf. on the Biol. of Mar. Mamm. Miami, FL, p. 53. (Abstract)

Phillips, R. P. 1964. Seismic refraction studies in Gulf of California. *In*: T. H. van Andel and G. G. Shor, Jr. (eds.), Marine Geology of the Gulf of California - a symposium. Am. Assoc. of Petroleum Geologists, Tulsa 3:90-121.

Prescott, J. H. and P. M. Fiorelli. 1980. Review of the harbor porpoise (*Phocoena phocoena*) in the U. S. Northwest Atlantic. NTIS Rep. No. PB80-176928, 64 pp.

Pryor, R. A., K. Pryor, and K. S. Norris. 1965. Observations on a pygmy killer whale (*Feresa attenuata* Gray) from Hawaii. Jour. Mamm. 46:450-461.

Recchia, C. A. and A. J. Read. 1988. Stomach contents of harbour porpoises, *Phocoena phocoena* (L.), from the Bay of Fundy. Can. Jour. Zool. 67:2140-2146.

Reilly, S. B. and J. Barlow. 1986. Rates of increase in dolphin population size. Fish. Bull. U. S. 84:527-533.

Ridgway, S. H. 1966. Dall porpoise, *Phocoenoides dalli* (True): observations in captivity and at sea. Norsk Hvalfangst-Tidende 55:97-110.

Robinson, M. K. 1973. Atlas of monthly mean sea surface and subsurface temperatures in the Gulf of California, Mexico. Mem. San Diego Soc. Nat. Hist. 5:5-97.

Robles, A., L. T. Findley, O. Vidal, R. L. Brownell, Jr., and S. Manzanilla. 1986. Registros recientes y apariencia externa de la marsopa del Golfo de California, o vaquita, *Phocoena sinus* Norris & McFarland, 1958. XI Reunion Internacional Sobre Mamiferos Marinos. Guaymas, Sonora. (Abstract)

Roden, G. I. 1958. Oceanographic and meteorological aspects of the

Gulf of California. Pac. Sci. 12:21-45.

Roden, G. I. 1964. Oceanographic aspects of the Gulf of California. *In*: T. H. van Andel and G. G. Shor, Jr. (eds.), Marine Geology of the Gulf of California - a symposium. Am. Assoc. Petroleum Geologists, Tulsa 3:30-58.

Roden, G. I. and G. W. Groves. 1959. Recent oceanographic investigations in the Gulf of California. Jour. Mar. Res. 18:10-35.

Rosenberg, D. H. 1969. Distribution of temperature, salinity, and oxygen. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 16-40.

Rusnak, G. A., R. L. Fisher, and F. P. Shepard. 1964. Bathymetry and faults of the Gulf of California. *In*: T. H. van Andel and G. G. Shor, Jr. (eds.), Marine Geology of the Gulf of California - a symposium. Am. Assoc. Petroleum Geologists, Tulsa 3:59-75.

Saayman, G. S. and C. K. Tayler. 1973. Social organisation of inshore dolphins (*Tursiops aduncus* and *Sousa*) in the Indian Ocean. Jour. Mamm. 54:993-996.

Saayman, G. S., D. Bower, and C. K. Tayler. 1972. Observations on inshore and pelagic dolphins on the south-eastern Cape coast of South Africa. Koedoe 15:1-24.

Schevill, W. E., W. A. Watkins, and C. Ray. 1969. Click structure in the porpoise *Phocoena phocoena*. Jour. Mamm. 50:721-728.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27-39.

Schoener, T. W. 1982. The controversy over interspecific competition. Am. Sci. 70:586-595.

Schreiber, J. F., Jr. 1969. Geographical and geological features. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 3-6.

Shane, S. H., R. S. Wells, and B. Würsig. 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. Mar. Mamm. Sci. 2:34-63.

Shanks, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13:311-315.

Shanks, A. L. 1988. Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. Fish. Bull. U. S. 86:703-714.

Shanks, A. L. and W. G. Wright. 1987. Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in settling rate of intertidal barnacles. Jour. Exp. Mar. Biol. 114:1-13.

Shea, R. E. and W. W. Broenkow. 1982. The role of internal tides in the nutrient enrichment of Monterey Bay, California.

Estuarine, Coastal and Shelf Sci. 15:57-66.

Shepard, F. P. 1964. Sea-floor valleys of Gulf of California. *In*: T. H. van Andel and G. G. Shor, Jr. (eds.), Marine Geology of the Gulf of California - a symposium. Am. Assoc. Petroleum Geologists, Tulsa 3:157-192.

Silber, G. K. 1988. Recent sightings of the Gulf of California harbor porpoise, *Phocoena sinus*. Jour. Mamm. 69:430-433.

Silber, G. K. 1990. Occurrence and distribution of the vaquita (*Phocoena sinus*) in the northern Gulf of California. Fish Bull. U. S. 88(2).

Silber, G. K. and K. S. Norris. *In press*. The geographic and seasonal distribution of the vaquita, *Phocoena sinus*. Contributions in Mammalogy. Univ. of Mexico Press, Mexico City.

Silber, G. K. and M. A. Smultea. *In press*. Harbor porpoises utilize tidally-induced internal waves. Bull. S. Calif. Acad. Sci.

Silber, G. K., M. W. Newcomer, and G. J. Barros. 1988. Observations on the behavior and ventilation cycles of the vaquita, *Phocoena sinus*. Mar. Mamm. Sci. 4:62-67.

Silber, G. K., M. W. Newcomer, H. Pérez-Cortés M. *In press*. Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). Can. Jour. Zool. 68.

Smith, G. J. D. and D. E. Gaskin. 1974. The diet of harbour porpoises (*Phocoena phocoena* (L.)) in the coastal waters of eastern Canada, with special reference to the Bay of Fundy. Can. Jour. Zool. 52:777-782.

Smith, T. D. 1982. Current understanding of the status of small cetacean populations in the Black Sea. FAO Fish. Series. 5:121-130.

Soulé, M. 1990. The real work of systematics. Ann. Missouri Bot. Gard. 77:4-12.

Stirling, I., W. Calvert, and H. Cleator. 1983. Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the high arctic. Arctic 36:262-274.

Sverdrup, H. U. 1941. The Gulf of California: preliminary discussion on the cruise of the *E. W. Scripps* in February and March 1939. 6th Pac. Sci. Congr. Proc. 3:161-166.

Sykes, G. G. 1937. The Colorado delta. Carnegie Inst. Washington, Pub. No. 460, 193 pp.

Tarbet, L. A. 1951. Imperial Valley. Am. Assoc. Petroleum Geologists Bull. 35:260-263.

Thompson, R. W. 1968. Tidal flat sedimentation on the Colorado River delta, northwestern Gulf of California. Geol. Soc. Am. Mem. 107, 133 pp.

Thompson, R. W. 1969a. Tidal currents and general circulation in the northern Gulf of California. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 51-55.

Thompson, R. W. 1969b. Bathymetry and sedimentation. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 72-82.

Thomson, D. A. 1969. The commercial fisheries industry. *In*: D. A. Thomson, A. R. Mead, J. R. Schreiber, Jr., J. A. Hunter, W. F. Savage, and W. W. Rinne (eds.), Environmental impact of brine effluents on Gulf of California. U. S. Dept. Interior, Office of Saline Water, Res. and Dev. Prog. Rep. No. 387, pp. 100-103.

Thomson, D. A. and K. A. Muench. 1973. Spawning runs of the Gulf of California grunion *Leuresthes sardina*. Jour. Ariz-Nev. Acad. Sci. 8:7.

Tomilin, A. G. 1957. Mammals of the USSR and adjacent countries. Vol 9. Cetacea. Israel Prog. for Sci. Trans., Jerusalem, 742 pp.

van Andel, T. H. 1964. Recent marine sediments of the Gulf of California. *In*: T. H. van Andel and G. G. Shor, Jr. (eds.), Marine Geology of the Gulf of California - a symposium. Am. Assoc. Petroleum Geologists, Tulsa 3:216-310.

Van Gelder, R. G. 1960. Results of the Puritan-American Museum of Natural History expedition to western Mexico. X. Marine mammals from the coasts of Baja California and the Tres Marías Islands, Mexico. Amer. Mus. Novitates 1992:1-27.

Vidal, O., A. Aguago, L. Findley, A. Robles, L. Bourillón, I. Vomend, P. Turk, K. Gárete, L. Maroñas, and J. Rosas. 1985. Avistamientos de mamiferos marinos durante el crucero "*Guaymas I*" en la región superior del Golfo de California, primavera de 1984. X Reunión Internacional para el Estudio de los Mamíferos Marinos, 24-27 de marzo de 1985, La Paz, Baja

California Sur, México. (Abstract)

Vidal, O., L. T. Findley, P. J. Turk, and R. E. Boyer. 1987. Recent records of pygmy sperm whales in the Gulf of California, Mexico. Mar. Mamm. Sci. 3:354-356.

Villa-R., B. 1976. Report on the status of *Phocaena sinus,* Norris and McFarland 1958, in the Gulf of California. An. Inst. Biol. Univ. Nal. Autón. México, Ser. Zool. 47:203-208.

Villa-R., B. 1986. *Megaptera novaeangliae,* la ballena jorobada en El Golfo de Santa Clara, Mar de Cortés, Mexico. An. Inst. Biol. Univ. Nal. Autón. México, Ser. Zool. 57:481-484.

Vonder Haar, S. P. and R. O. Stone. 1973. Oceanographic analysis of orbital photographs of the upper Gulf of California. Photogrammetrica 29:45-61.

Walker, B. W. 1960. The distribution and affinities of the marine fish fauna of the Gulf of California. Syst. Zool. 9:123-133.

Walker, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. NMFS/SWFC Admin. Rep. No. LJ-81-03C, 52 pp.

Watkins, W. A. 1980. Click sounds from animals at sea. *In*: Animal Sonar Systems. R.G. Busnel and J. F. Fish (eds.), Plenum Press, NY, pp. 291-297.

Watkins, W. A. and W. E. Schevill. 1980. Characteristic features of the underwater sounds of *Cephalorhynchus commersonii*. Jour. Mamm. 61:738-739.

Watkins, W. A., W. E. Schevill, and P. B. Best. 1977. Underwater sounds of *Cephalorhynchus heavisidii* (Mammalia: Cetacea). Jour. Mamm. 58:316-320.

Watts, P. and D. E. Gaskin. 1985. Habitat index analysis of the harbor porpoise (*Phocoena phocoena*) in the southern coastal Bay of Fundy, Canada. Jour. Mamm. 66:733-744.

Wells, R. S., B. G. Würsig, and K. S. Norris. 1981. A survey of the marine mammals of the upper Gulf of California, Mexico, with an assessment of the status of *Phocoena sinus*. NTIS Pub. No. PB81-168791, 51 pp.

Winn, H. E., R. K. Edel, and A. G. Taruski. 1975. Population estimates of the humpback whale, *Megaptera novaeangliae*, in the West Indies by visual and acoustic methods. Jour. Fish. Res. Board Can. 32:499-506.

Wood, F. G. and W. E. Evans. 1980. Adaptiveness and ecology of echolocation in toothed whales. *In*: R. G. Busnel and J. F. Fish (eds.), Animal Sonar Systems. Plenum Press, NY, pp. 381-425.

Würsig, B. 1984. Aspects of the natural history of bottlenose and dusky dolphins. Natl. Geogr. Res. Rep. 1975:759-769.

Würsig, B. 1986. Delphinid foraging strategies. *In*: R. J. Shusterman, J. A. Thomas, and F. G. Wood (eds.), Dolphin Cognition and Behavior: A Comparative Approach. Erlbaum Associates, Hillsdale, NJ, pp. 347-359.

Würsig, B. and M. Würsig. 1979. Behavior and ecology of the bottlenose dolphin, *Tursiops truncatus*, in the South Atlantic. Fish. Bull. U.S. 77:399-412.

Würsig, B. and M. Würsig. 1980. Behavior and ecology of the dusky dolphin, *Lagenorhynchus obscurus*, in the South Atlantic. Fish. Bull. U.S. 77:871-890.

Würsig, M., B. Würsig, and J. F. Mermoz. 1977. Desplazamientos, comportamiento general y un varamiento de la marsopa espinosa, *Phocoena spinipinnis*, en el Golfo San Jose (Chubut, Argentina). Physis 36:71-79.

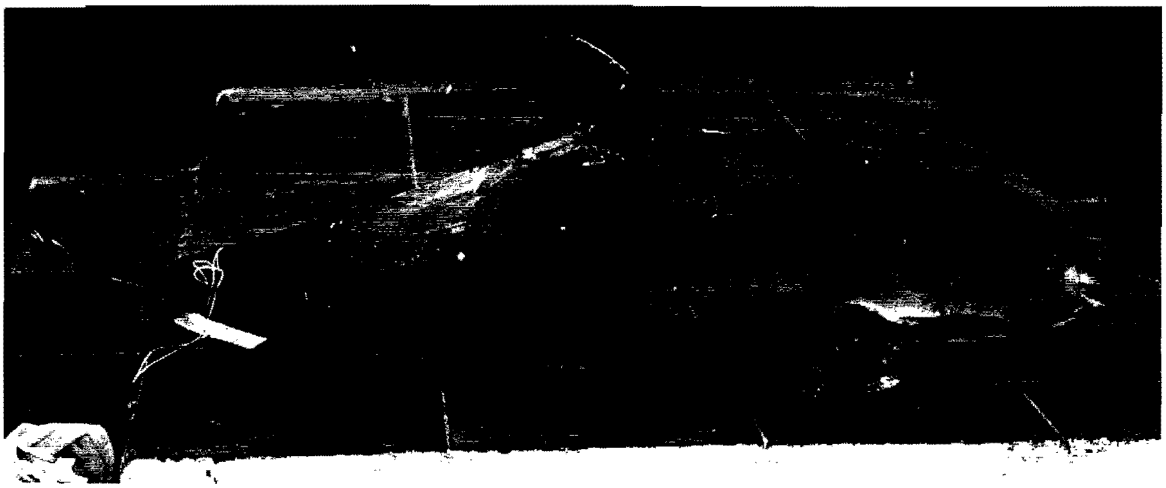
Zaslavsky, G. L., A. A. Titov, and V. M. Lekomtsev. 1969. Investigations of the echolocational abilities of the harbor porpoise (*Ph. phocoena*). Trudy Akasticheskogo Instituta 8:134-138.

Zeitzschel, B. 1969. Primary productivity in the Gulf of California. Mar. Biol. 3:201-207.

Zelids, J. R. and J. B. Jillett. 1982. Aggregation of pelagic *Munida gregaria* (Fabricus) (Decapoda, Anomura) by coastal fronts and internal waves. Jour. Plankton Res. 4:839-857.

Figure 1. Photograph of subadult male *P. sinus* (a) taken by G. Silber at Puerto Peñasco, Sonora, 10 February 1986. Photograph of mature *P. sinus* (b), taken by A. Robles, El Golfo de Santa Clara, Sonora, April 1985.

a.



b.

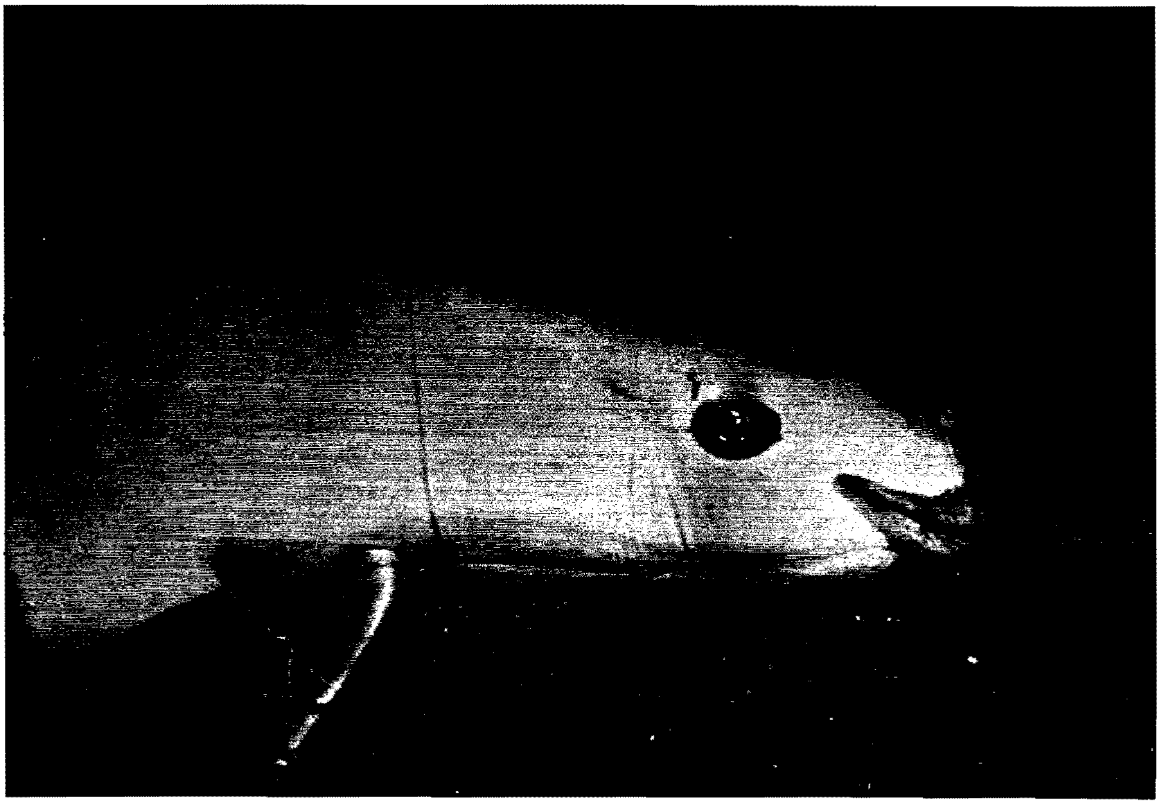


Figure 2. Effort: time spent conducting vessel transects in the northern Gulf of California (1986, 1987, and 1988).

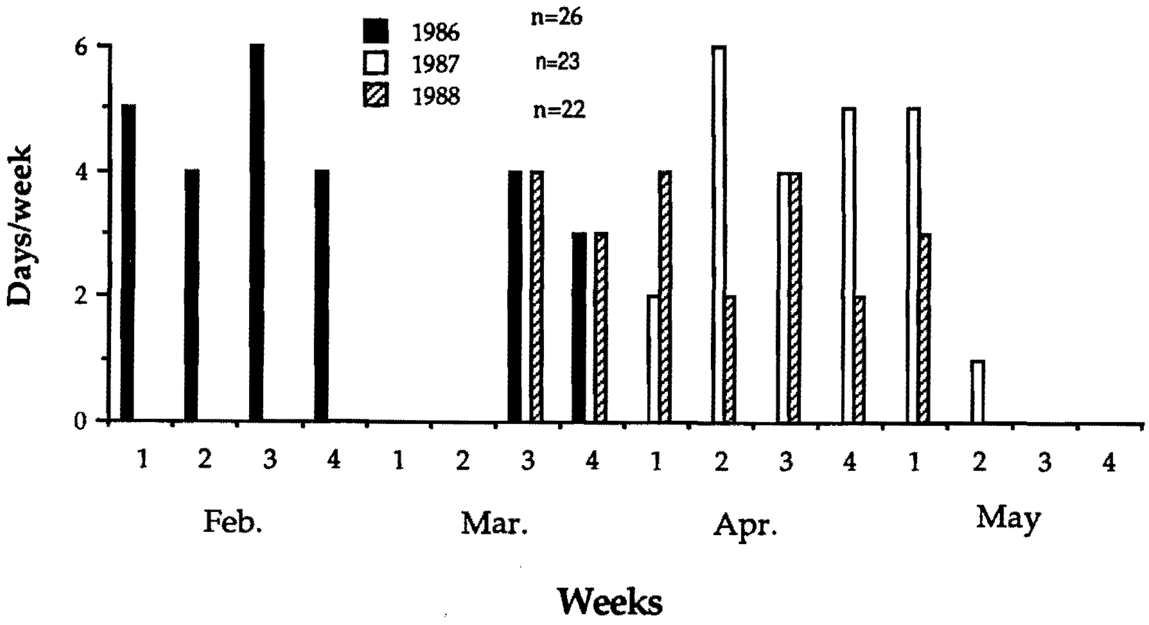


Figure 3. Boat transects (······) in 1986, 1987, and 1988.

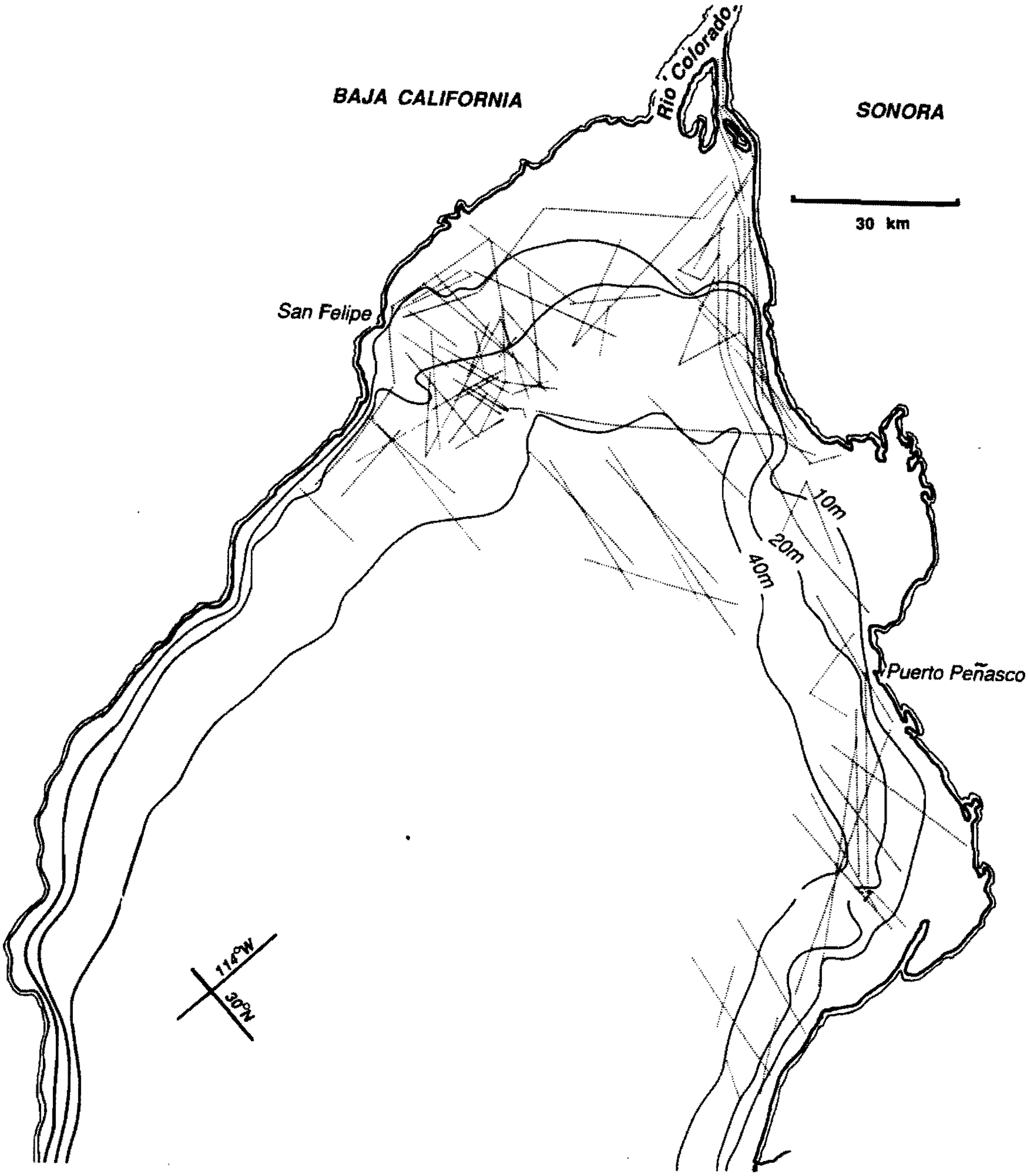


Figure 4. Survey effort relative to sea state.

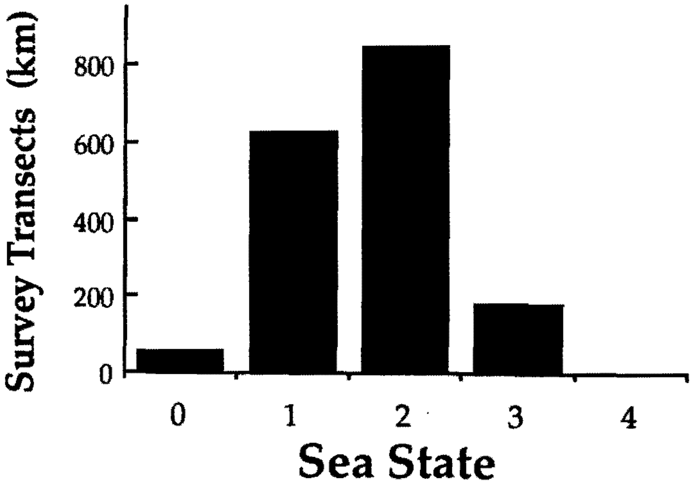


Figure 5. Aircraft surveys on 3 - 5 May 1988 (——) and 2 - 5 September 1989 (- - - -). *Phocoena sinus* sightings from aircraft on May 1988 (◆) and September 1989 (●).

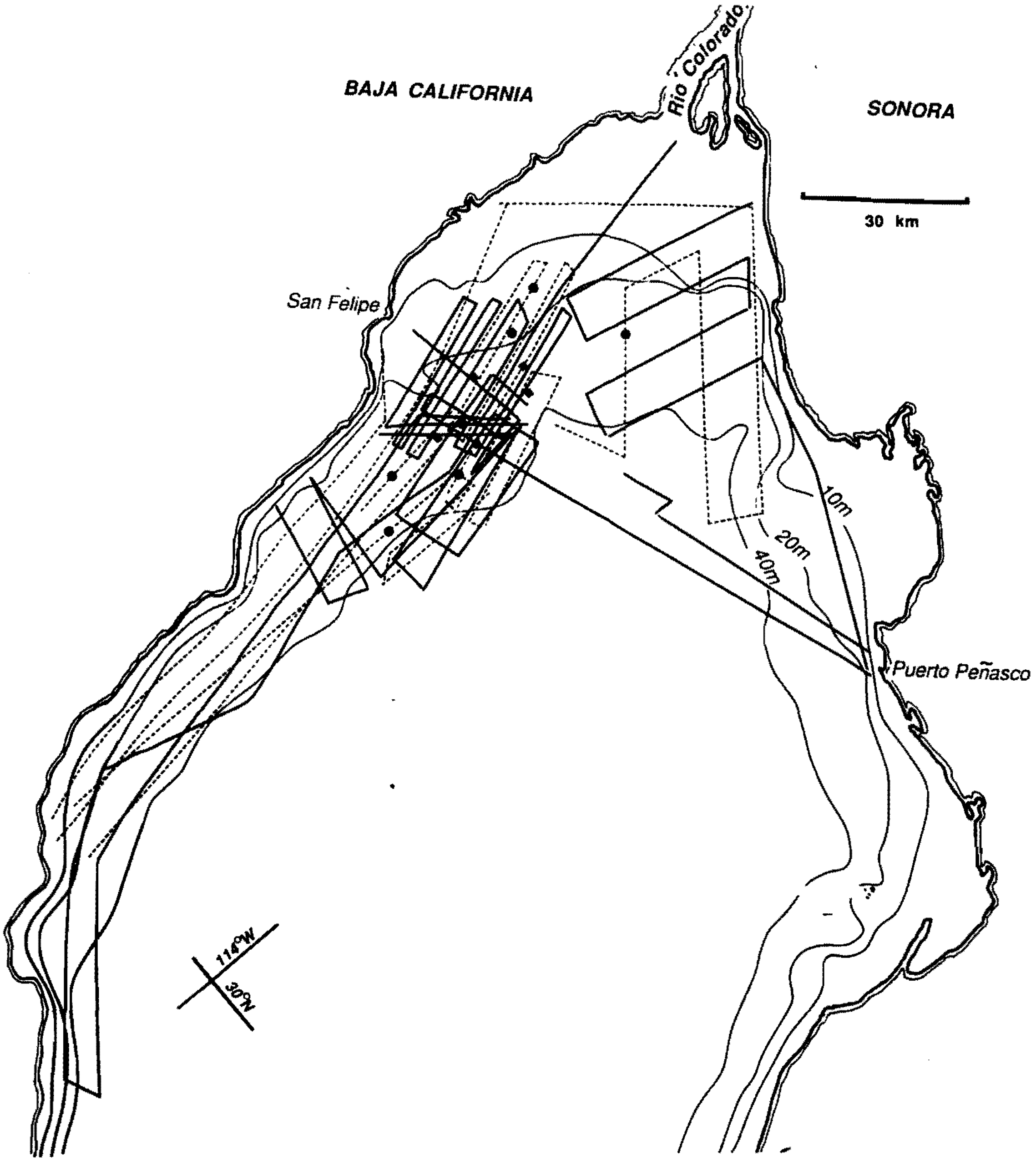


Figure 6. Sightings of *Tursiops* (Δ), *Delphinus* (○), *Phocoena* (●), and *Orcinus* (■) in the northern Gulf of California.

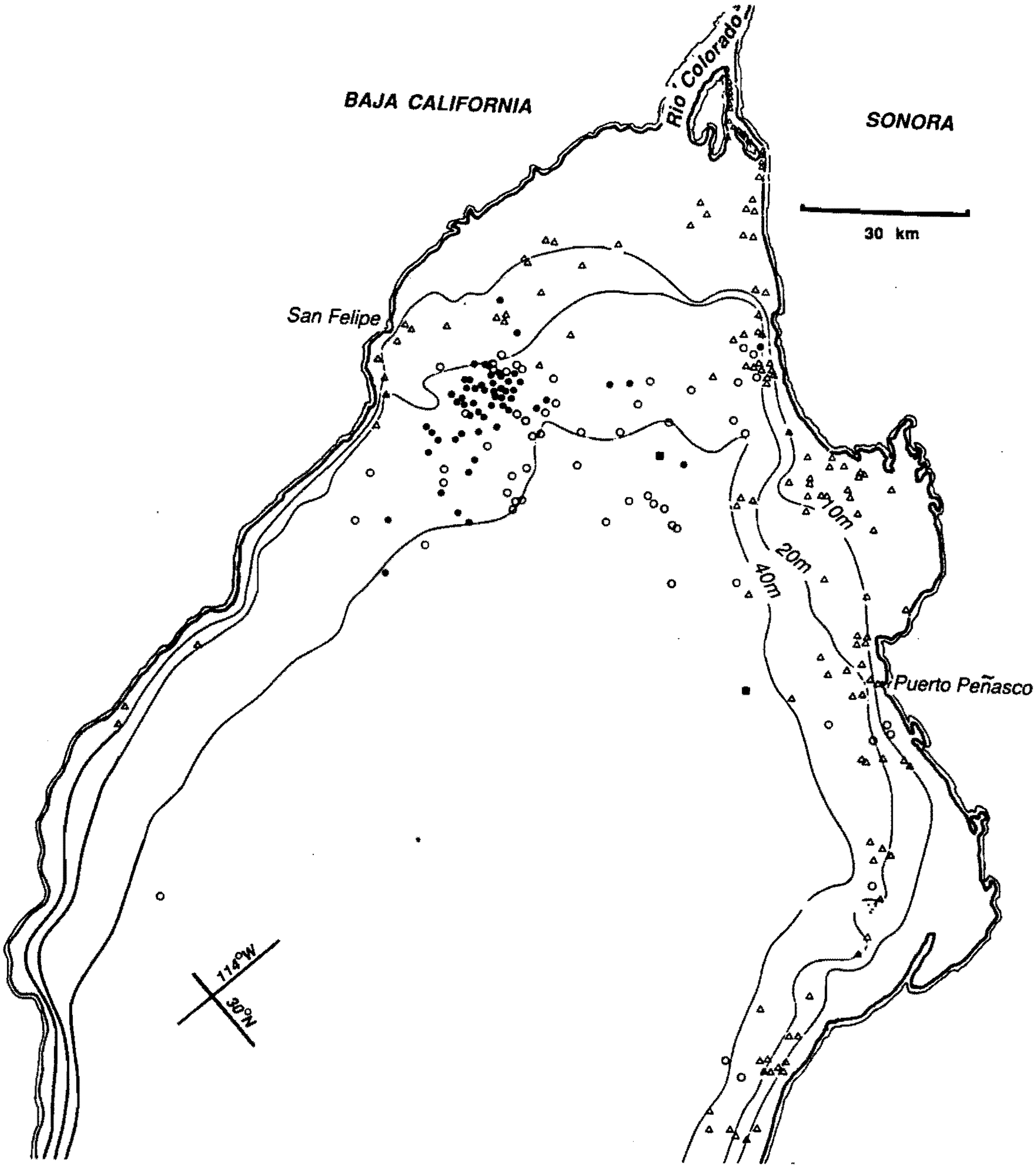


Figure 7. Sighting locations of *Tursiops, Delphinus* and *Phocoena* relative to water depth.

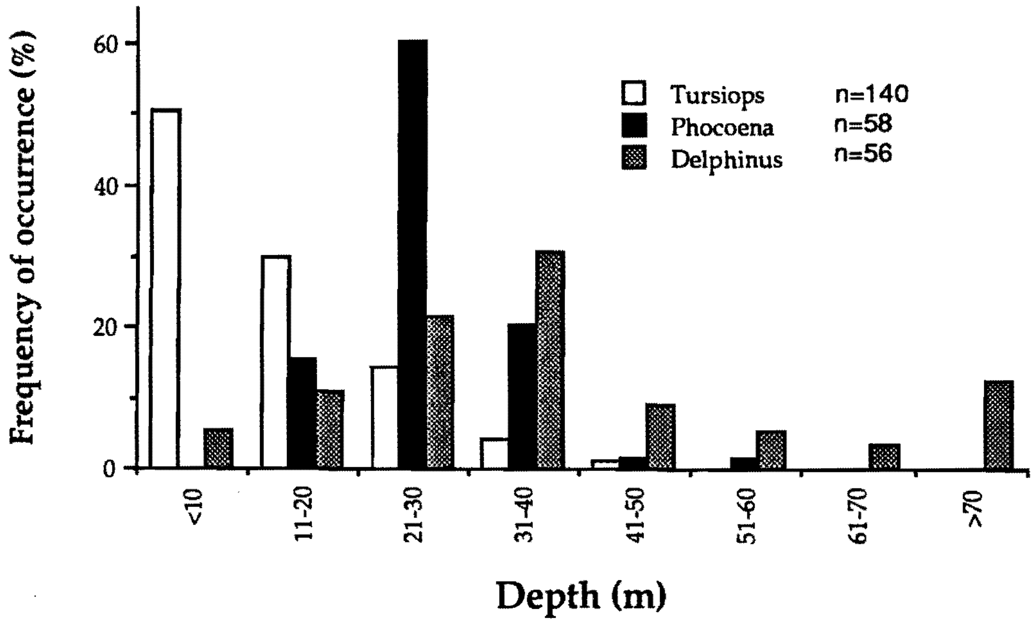


Figure 8. Sighting locations of *Tursiops, Delphinus* and *Phocoena* relative to distance to the nearest shore.

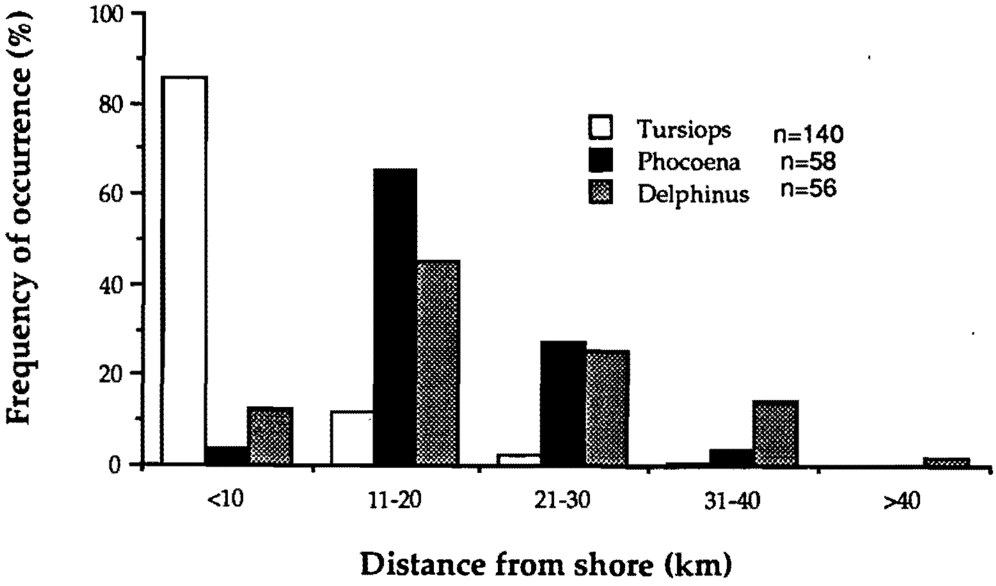


Figure 9. Sightings of *B. physalus* (●), *B. edeni* (Δ), and *Eschrichtius* (■) in the northern Gulf of California.

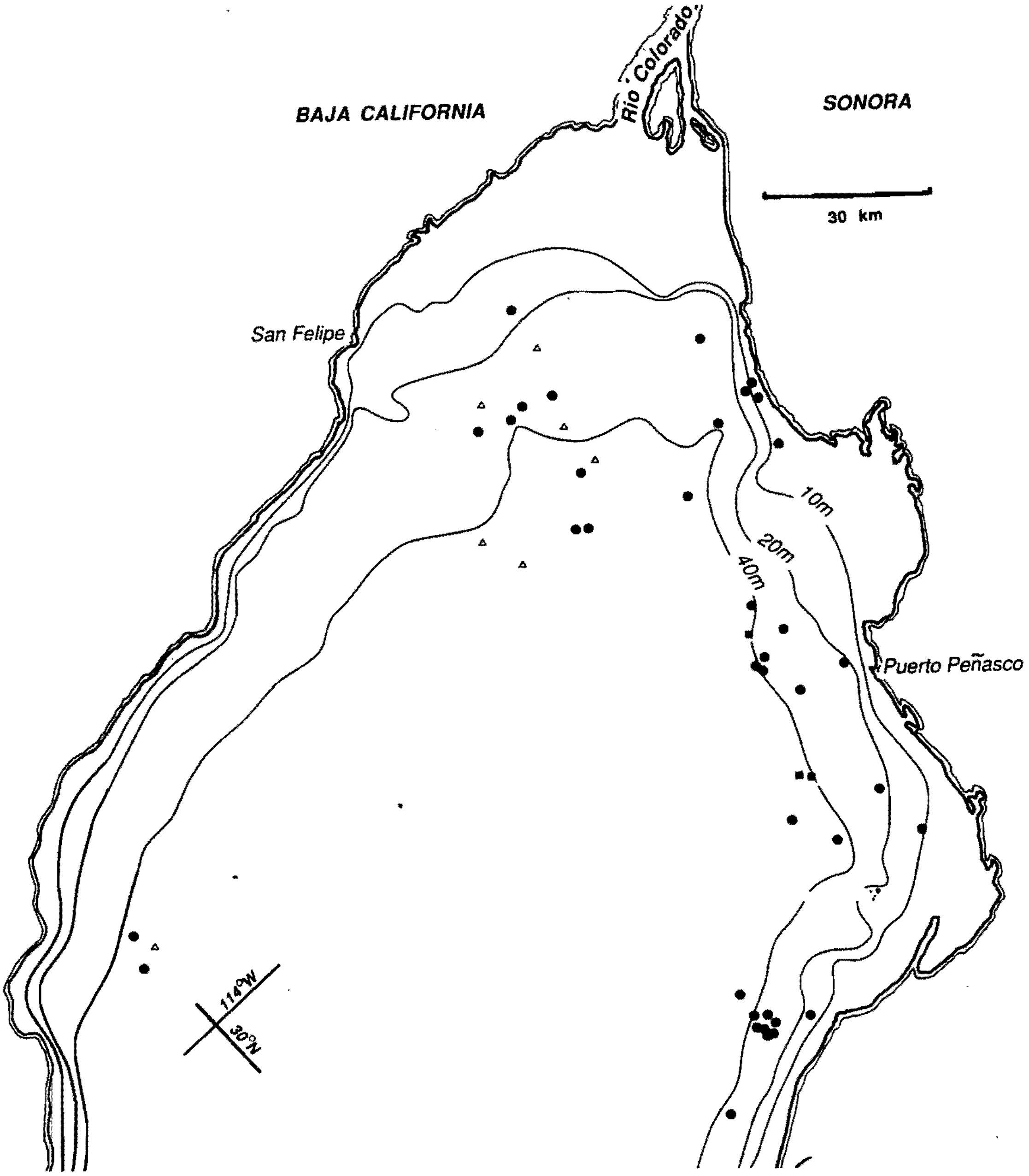


Figure 10. Sightings of *Balaenoptera physalus* and *B. edeni* relative to water depth.

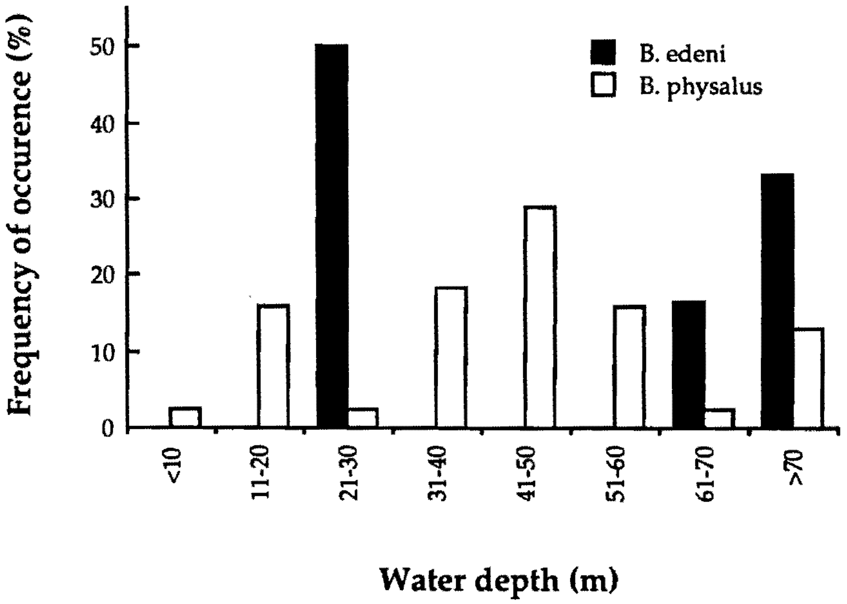


Figure 11. Sighting locations of *Balaenoptera physalus* and *B. edeni* relative to distance to nearest shore.

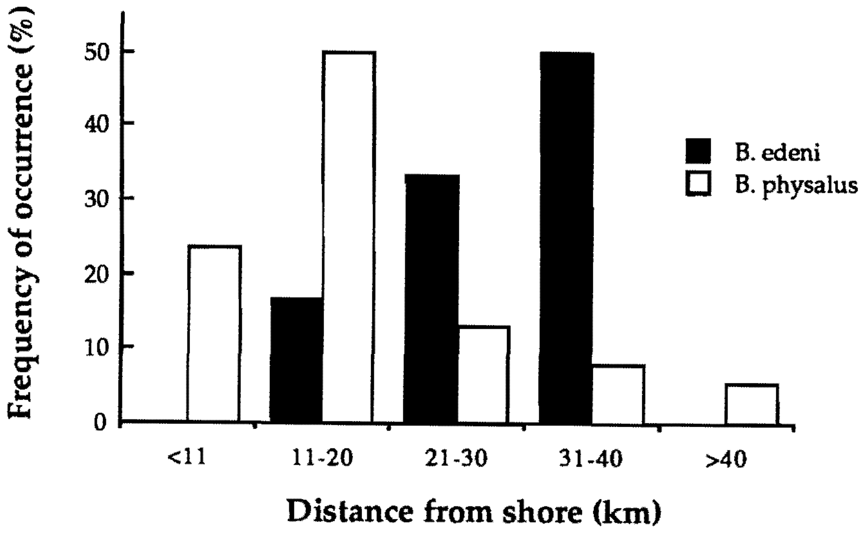


Figure 12. Water clarity values obtained at sighting locations of *Tursiops, Delphinus,* and *Phocoena.* Mean and one standard deviation are represented.

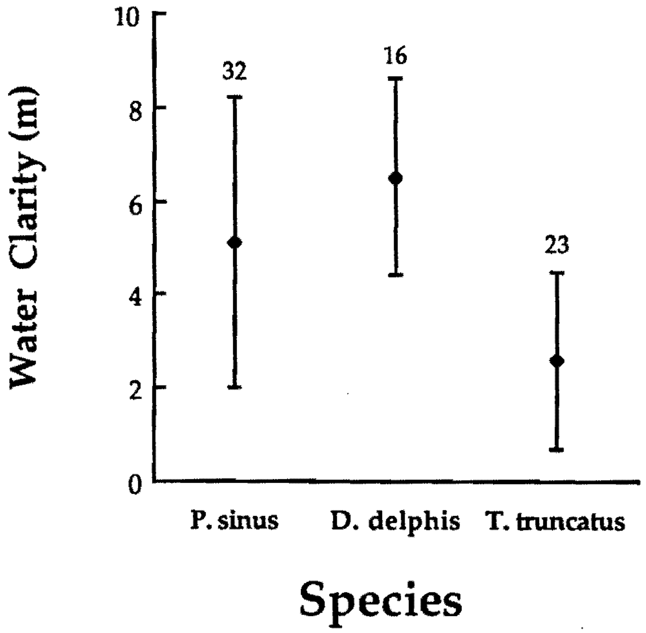


Figure 13. Water temperature values obtained at sighting locations of *Tursiops, Delphinus,* and *Phocoena*. Mean and one standard deviation are represented.

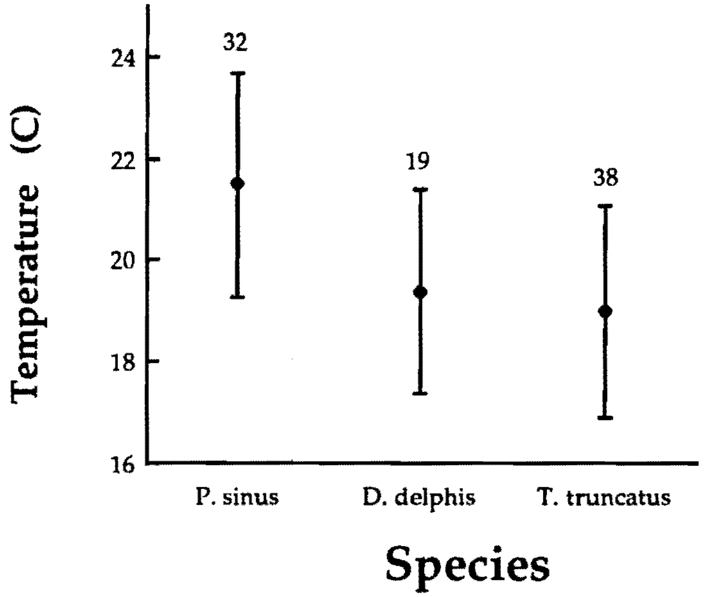


Figure 14. *Phocoena sinus* sightings in 1986 (▲), 1987 (●), and 1988 (■).

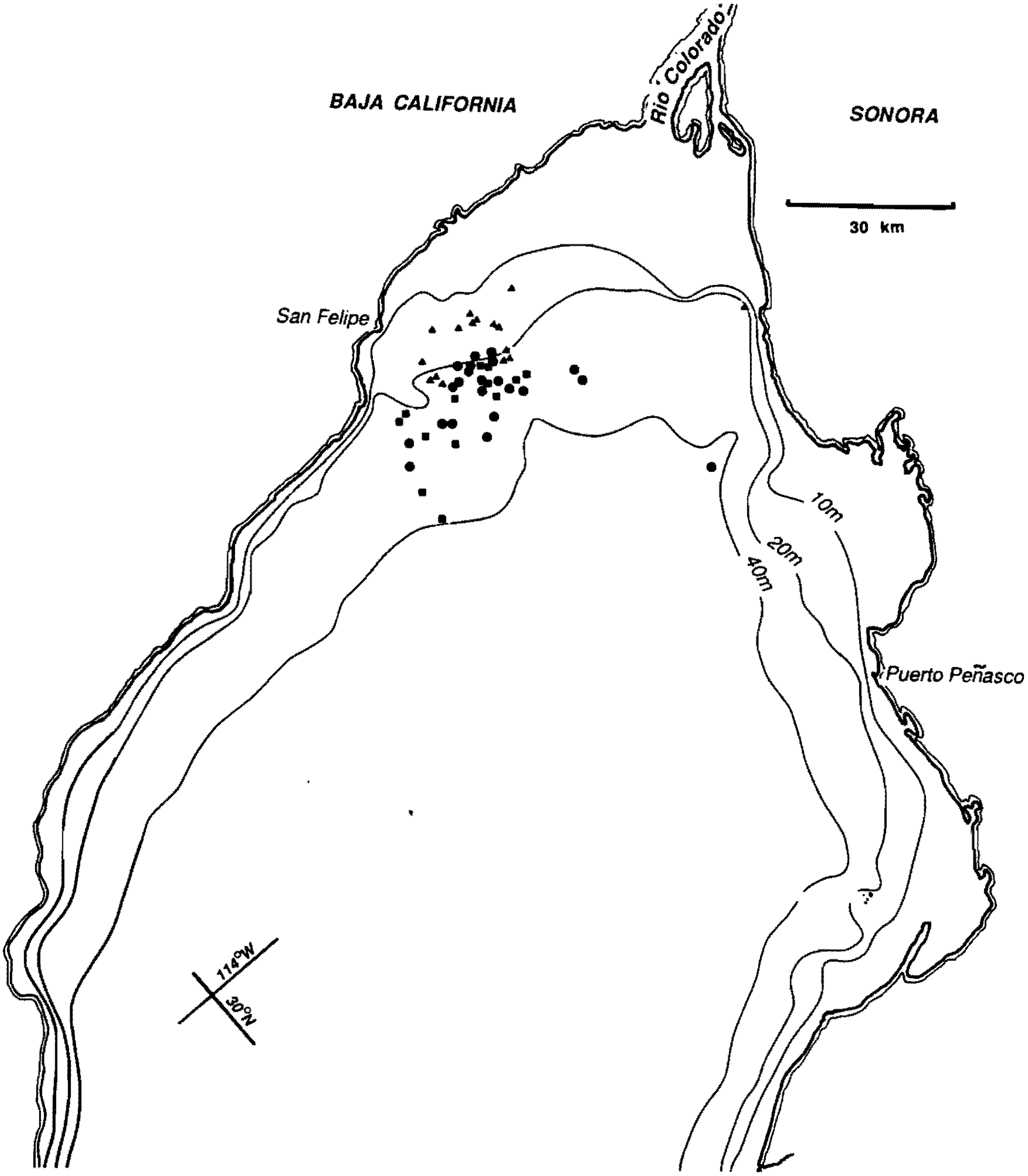


Figure 15. Sighting rate (individuals/100 km) of *Phocoena sinus* relative to sea state.

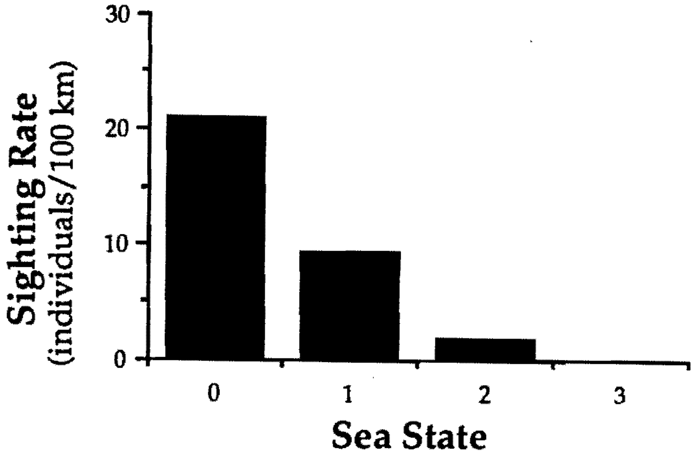


Figure 16. Group size in *Phocoena sinus*.

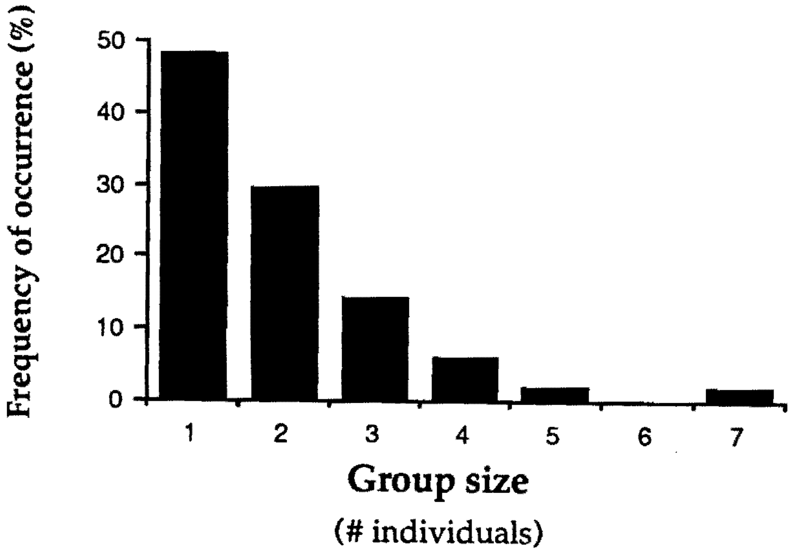


Figure 17. *Phocoena sinus* sightings relative to water depth.

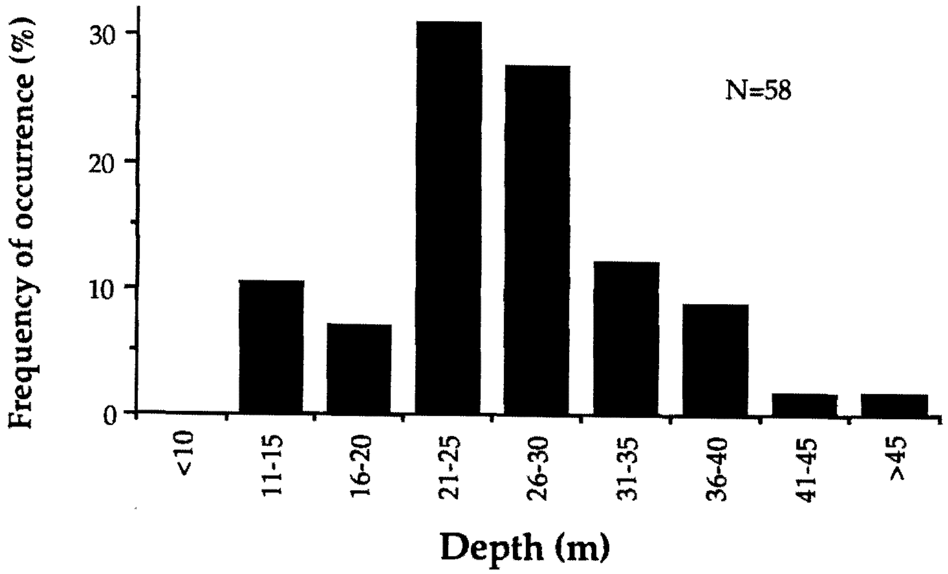


Figure 18. *Phocoena sinus* sightings relative to distance from nearest shore.

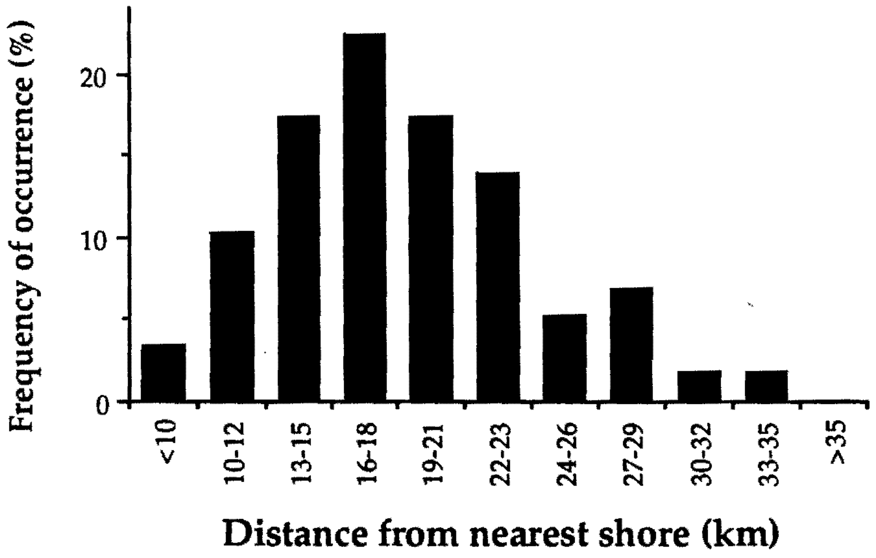


Figure 19. Average monthly sea surface temperatures at Puerto Peñasco, Sonora, Mexico. Data were provided by R. Boyer, Intercultural Center for the Study of Deserts and Oceans, Puerto Peñasco, Sonora.

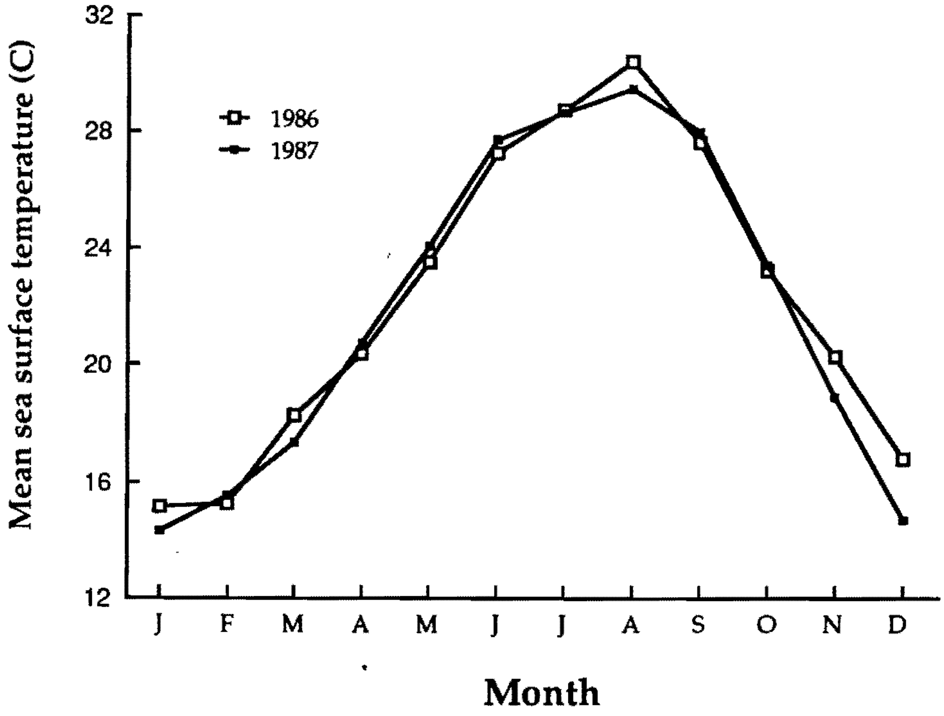


Figure 20. Power spectrum of a *Phocoena sinus* click.

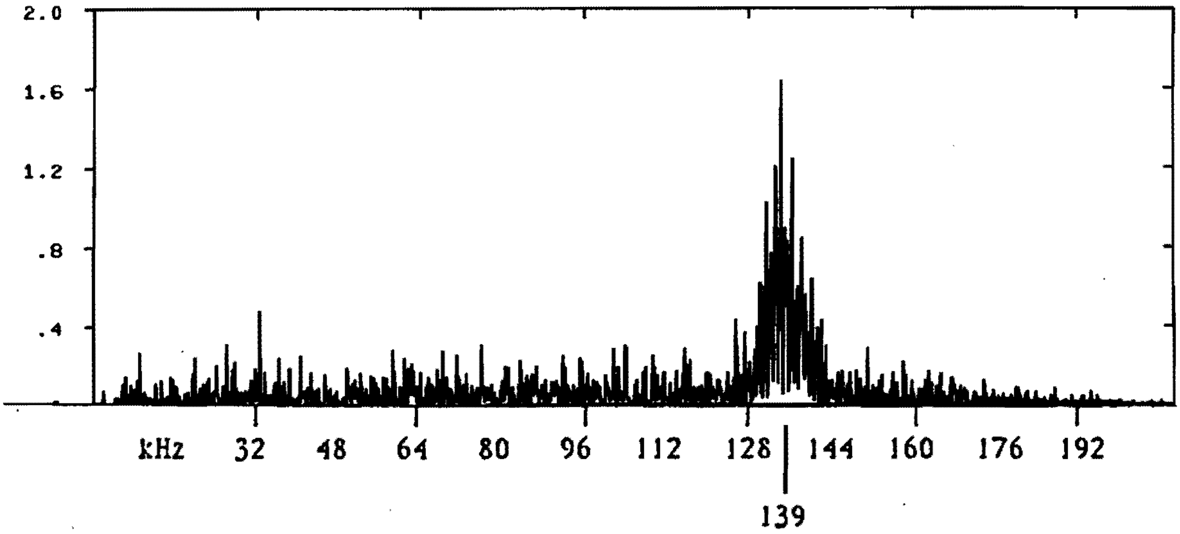


Figure 21. Waveform of a *Phocoena sinus* click.

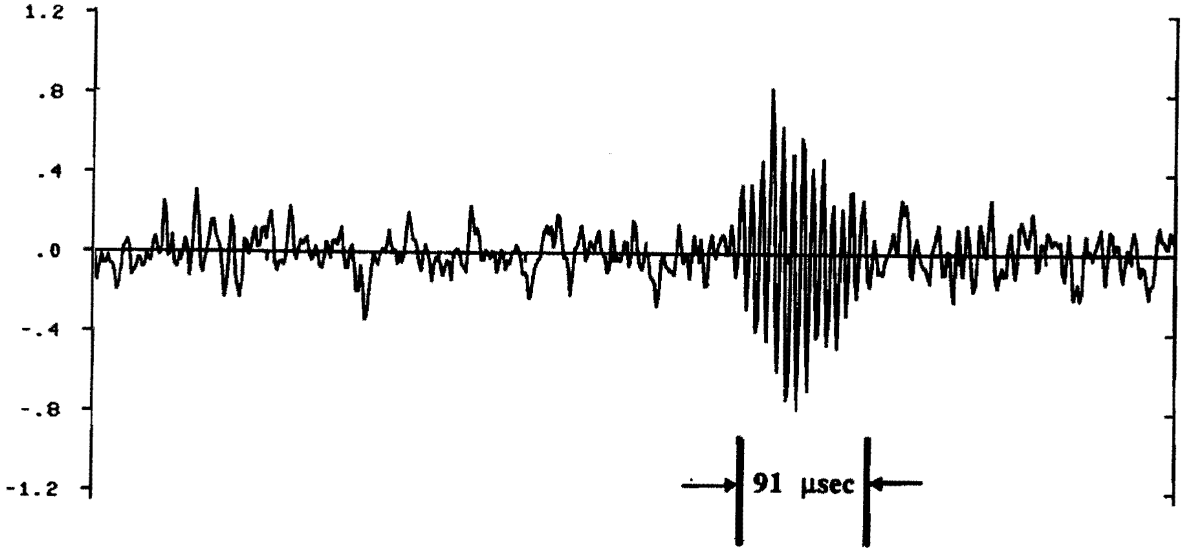


Figure 22. Distributions of living phocoenids (from Barnes 1985).

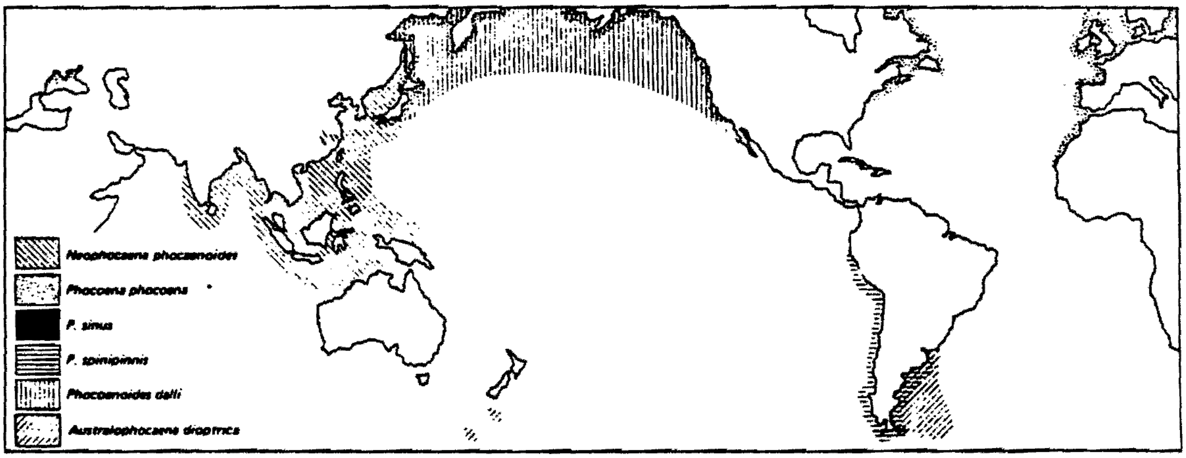


Figure 23. Locations where *Phocoena sinus* specimens or osteological material have been recovered.

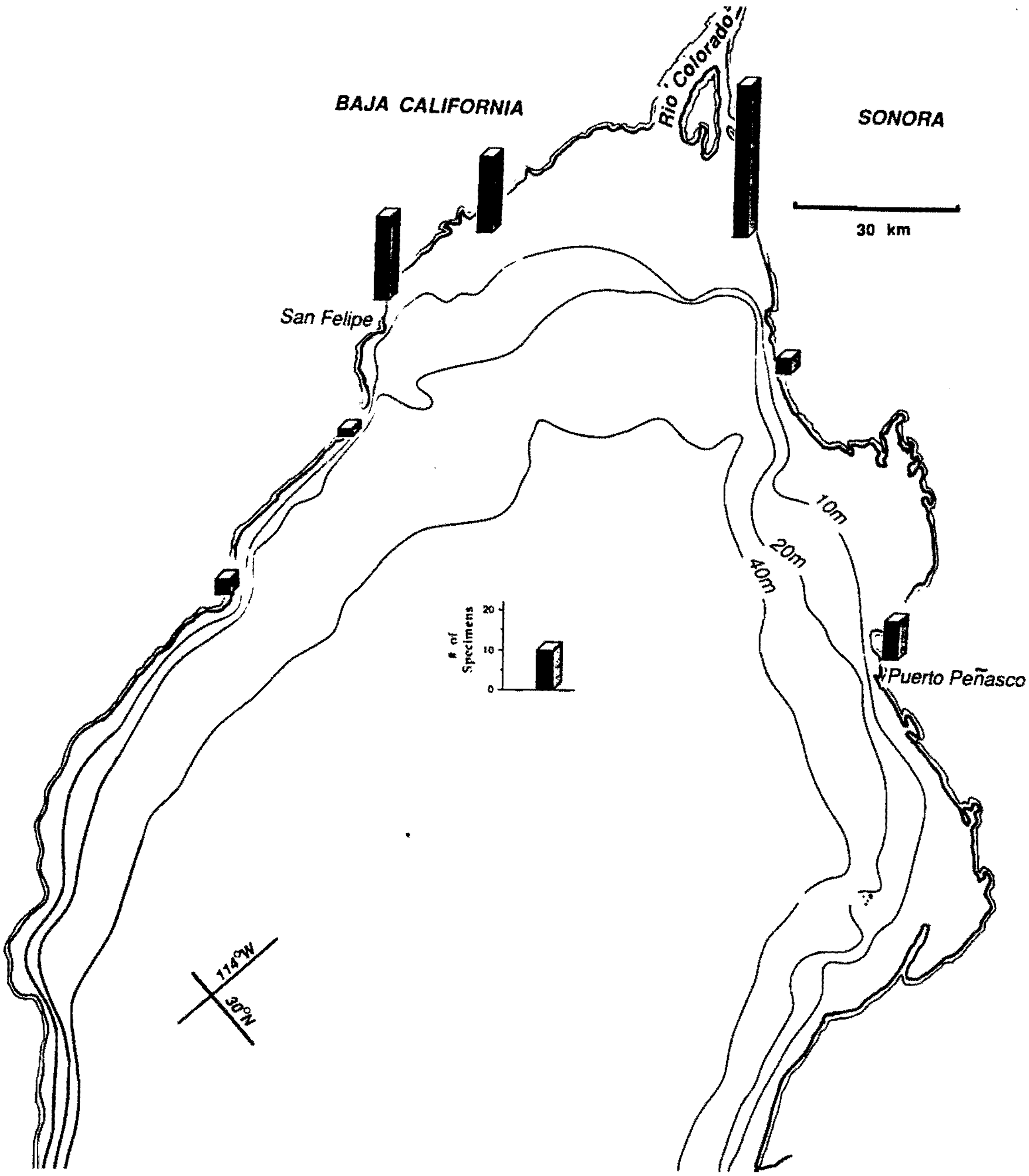


Figure 24. Bathymetric map of the northwestern Gulf of California (from Thompson 1969).

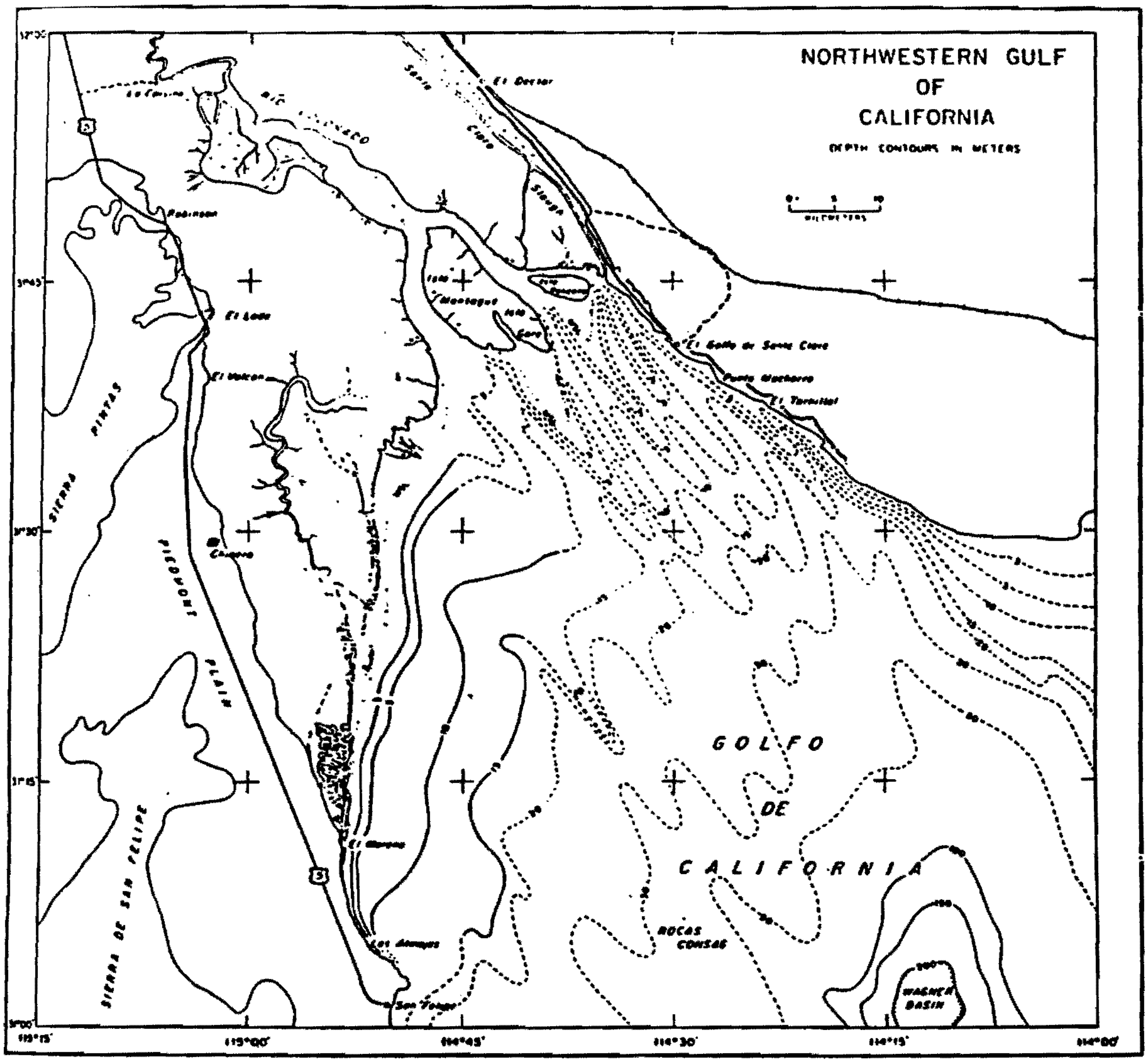


Table 1. Distance to shore, water depth, clarity, and temperature of cetacean sighting locations in the northern Gulf of California.

Species		Distance to Shore (km)	Water Depth (m)	Water Temperature (C)	Water Clarity (m)
Tursiops truncatus	N	140	140	38	23
	$\bar{X}$	5.4	12.4	19.0	2.6
	SD	5.79	9.60	2.08	1.90
	Range	0.125-34	2.5-46	15 - 21	0.5 - 6.5
Delphinus delphis	N	56	56	19	16
	$\bar{X}$	19.7	41.0	19.4	6.5
	SD	10.98	24.39	2.00	2.10
	Range	1.6 - 63.6	5 - 105	15 - 23	3.0 - 10.5
Phocoena sinus	N	58	58	32	32
	$\bar{X}$	18.4	26.6	21.5	5.1
	SD	5.84	7.67	2.23	3.12
	Range	2.4 - 24	13.5 - 37.0	17 - 26	0.9 - 12.0
Balaenoptera physalus	N	38	38	7	7
	$\bar{X}$	17.9	44.7	19.7	6.4
	SD	11.30	22.92	3.25	3.34
	Range	1.6 - 35.4	33 - 82	16 - 23	2.5 - 10.0
Balaenoptera edeni	N	6	6	2	
	$\bar{X}$	30.0	54.3	18.8	
	SD	11.05	33.16		
	Range	11 - 40	26 - 105	18.5 - 19.0	
Orcinus orca	N	2	2		
	$\bar{X}$	35.5	57.5		
	SD	2.12	7.78		
	Range	34 - 37	52 - 63		
Eschrichtius robustus	N	2	2		
	$\bar{X}$	16.5	45.5		
	SD	2.00	13.44		
	Range	15 - 18	36 - 55		

Table 2. Group size and sighting rate of cetaceans in the northern Gulf of California.

Species		Group Size	Sighting Rate (#/100 km)	Individuals (#/100 km)
Tursiops truncatus	N	140	4.3	43.8
	$\bar{X}$	10.1		
	SD	11.04		
	Range	1 - 60		
	Total individuals	1,416		
Delphinus delphis	N	56	1.7	440.0
	$\bar{X}$	254.3		
	SD	309.37		
	Range	4 - 1100		
	Total individuals	14,239		
Phocoena sinus	N	58	1.8	3.4
	$\bar{X}$	1.9		
	SD	1.20		
	Range	1 - 7		
	Total individuals	110		
Balaenoptera physalus	N	38	1.2	6.6
	$\bar{X}$	5.7		
	SD	10.48		
	Range	1 - 50		
	Total individuals	215		
Balaenoptera edeni	N	6	0.2	0.2
	$\bar{X}$	1.2		
	SD	0.41		
	Range	1 - 2		
	Total individuals	7		
Orcinus orca	N	2	0.1	0.5
	$\bar{X}$	8.5		
	SD	9.19		
	Range	2 - 15		
	Total individuals	17		
Eschrichtius robustus	N	2	0.1	0.1
	$\bar{X}$	1.5		
	SD	0.71		
	Range	1 - 2		
	Total individuals	3		

Table 3. Summary of vaquita sightings by water depth, distance to nearest shore, water temperature, and water clarity. Also indicated are the total number of sightings, and estimated total number of individuals. Group sizes are represented by mean, one standard deviation, and range.

Year	Dates		Number Seen	Distance to Shore (km)	Depth (m)	Water Temp. (C)	Water Clarity (m)
1986	2 Feb. - 27 Mar.	N	16	16	16	12	12
		$\bar{X}$	1.7	14.3	21.0	21.5	2.4
		SD	0.87	4.50	5.00	1.83	0.81
		Range	1-4	2-20	14-25	17-23	1-4
		# individuals	27				
1987	8 Apr. - 7 May	N	22	22	22	12	13
		$\bar{X}$	2.1	19.3	27.5	22.9	8.2
		SD	1.57	5.71	4.73	2.09	2.46
		Range	1-7	15-32	20-37	21-26	5-12
		# individuals	46				
1988	21 Mar. - 5 May	N	13	13	13	8	7
		$\bar{X}$	1.8	20.7	29.5	19.2	4.1
		SD	1.01	6.58	5.87	0.46	1.07
		Range	1-4	7-29	22-40	19-20	3-6
		# individuals	23				
1989	2 - 5 Sept.	N	7	7	7		
		$\bar{X}$	2	33.4	19.4		
		SD	0.82	12.63	3.46		
		Range	1-3	20-56	14-24		
		# individuals	14				
ALL YEARS		N	58	58	58	32	32
		$\bar{X}$	1.9	18.4	26.6	21.5	5
		SD	1.2	5.84	7.67	2.23	3.10
		Range	1-7	2-32	14-56	17-26	1-12
		# individuals	110				

Table 4. Summary of interviews with fishermen in La Paz, Baja California Sur and San Felipe, Baja California Norte.

Location		SAN FELIPE	LA PAZ
Number fishermen interviewed		7	17
Distance from home port (km)	$\bar{X}$	37.4	37.8
	SD	39.48	22.32
	Range	1-100	5-112
Number of years engaged in fishing	$\bar{X}$	17.8	23.4
	SD	12.5	15.51
	Range	6-35	5-51
Type of fishing		gillnet, longline, hook and line	longline, gillnet, trawl, diving
Target species		shrimp (N=6) totoaba (N=3) shark (N=2) marlin (N=1) dorado (N=1) yellowtail jack (N=1)	Spanish mackerel (N=14) shark (N=9) Pacific manta (N=1) snapper (N=1) striped mullet (N=1)
Fishing effort		12mo/yr (N=4) 3 mos/yr (N=3)	12mo/yr (N=11) 10 mo/yr (N=1) 3-6 mo/yr (N=3)
Recognition of photos of *P. sinus*		Yes (N=7)	Yes (N=1); No (N=16)
Estimated total porpoises killed		3-4	0
Common names used		cochito, cochonito, and vaquita = *P. sinus*	vaquita=*Kogia spp.* or *Phocoena spp.* duende = *Lagenorhynchus* cochonito = *Delphinus* cochito = *Globicephala*

Table 5. Bandwidth, duration, and frequency ranges of *Phocoena sinus* clicks.

	Dominant frequency (kHz)	Bandwidth (kHz)	Duration (µsec)
mean	132.9	17.1	136
sd	3.86	5.38	41.09
range	128.0-135.8	10.6-28.4	79-193

overall frequency range 122.2 - 160.0

Table 6. Reported characteristics of sound emissions by phocoenids and Cephalorhynchus spp.

Species	Click duration	Dominant frequency	Bandwidth	# Clicks per train	Repetition rate	Reference
P. phocoena	1.2-3.0 msec	2.0 kHz	1-6 kHz		200 Hz	Busnel et al. 1963
P. phocoena		2.0 kHz				Busnel and Dziedzic 1966
P. phocoena	0.5-5.0 msec	2.0 kHz	12 kHz		< 1000 Hz	Schevill et al 1969
P. phocoena	~200 µsec	>100 kHz				Dubrovskii et al. 1971
P. phocoena	100 µsec	128 kHz				Møhl & Andersen 1973
P. phocoena	115 µsec	120 kHz	70 kHz			Kamminga & Wiersma 1981
P. phocoena	140 µsec	138 kHz				Kamminga et al. 1986
P. phocoena	~140 µsec	140 kHz	40 kHz			Kamminga 1988
N.phocaenoides			4 kHz		80-800 Hz	Mizue et al. 1968
N.phocaenoides	40-80 µsec	128 kHz	15-25 kHz	15-300+	40-120 Hz	Kamminga et al. 1986
N.phocaenoides		128 kHz	55 kHz			Kamminga 1988
P. dalli	0.5-1.5 msec		12 kHz			Dierks et al. 1971
P. dalli	50 µsec-1.0 msec	130 kHz	63 kHz			Awbry et al. 1986
P. dalli	~75 µsec	135 kHz	35 kHz			Evans & Awbry 1988
P. dalli	50 µsec-1.0 msec	130 kHz	53 kHz			Kamminga 1988
P. sinus	79-193 µsec	132 kHz	17 kHz	3-57	10-50 Hz	This study
C. heavisidii	0.3-0.5 sec	800 Hz	<5 kHz		50-70 Hz	Watkins et al. 1977
C. commersonii	~57 µsec	125 kHz	50 kHz			Kamminga & Wiersma 1981
C. commersonii	~52 µsec	125 kHz	~90 kHz		< 600 Hz	Kamminga & Wiersma 1982
C. commersonii	~123 kHz	125 kHz				Kamminga et al. 1986
C. commersonii	~100 µsec	120-130 kHz	10-20 kHz			Evans & Awbry 1988
C. commersonii	238 µsec	116 kHz	31 kHz	5-10		Dziedzic & De Buffrenil 1989

Table 7. Extant species in the family Phocoenidae (from Barnes 1985).

Superfamily Delphinoidea (Grey 1821) Flower 1864

Family Phocoenidae (Grey 1821) Bravard 1885

Subfamily Phocoeninae (Grey 1825) Barnes 1985

Phocoena phocoena	(Linneaus, 1758)	harbor porpoise
Phocoena sinus	(Norris and McFarland, 1958)	vaquita
Phocoena spinipinnis	(Burmeister, 1865)	Burmeister's porpoise
Neophocaena phocaenoides	(Cuvier, 1829)	finless porpoise

Subfamily Phocoenoidinae Barnes 1984

Australophocoena dioptrica	(Lahille 1912)	spectacled porpoise
Phocoenoides dalli	(True, 1885)	Dall's porpoise

Appendix A.

Questionare for Fishermen

Fishing

Type of fishing:

Long line, trawl, gillnet, other? ______________________________

What type of fish do you catch? ______________________________

Season:

What months of the year do you fish? ______________________________

Does the type of fishing change with season? ______________________

Fishing Effort:

Average number of days/year OR days/month? ____________________

How many years have you been fishing? ____________

Location:

Area; water depth, distance from shore? ________________________

Boat:

Boat size? ___________________________

Marine Mammals

"Vaquita", Gulf of California harbor porpoise.

Have you seen this animal? (show photograph) ______

If so, about how big was it? ______________

Where was it seen? ____________________________________

How many porpoises in a group? __________________

Is the porpoise seen certain times of the year? _________________

What other kinds of dolphins or whales do you see when fishing? ___________

____

General Comments and Other Information