Bones on the Beach: Marine Mammal Taphonomy of the Colorado Delta, Mexico

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How well does a death assemblage of marine mammal bones reflect the diversity, species composition, and proportion of bone types in the living fauna? Marine mammal remains were surveyed along the beaches of the Colorado River delta, Baja California, Mexico. Three carcasses and 470 bones were found among 112 localities along 4.0 km of shoreline. The location of each site was recorded and each bone was identified, photographed, and measured and its taphonomic condition was noted. The proportion of bone types found was compared to the proportions known in living marine mammals. The list of species found as bones was compared to the list of species known to live in the northern Gulf of California.

The maximum skeletal ratio of skull:vertebrae:ribs:phalanges:girdles/limbs in a typical Gulf of California marine mammal is 1:74:30:56:16. The 28 skulls and 442 post-cranial bones found provided a skeletal ratio of 1:12:3:1:1. Although vertebrae are the most common bones in the bone assemblage, only 316 were found, not the ~2,000 predicted by the 28 skulls, indicating that vertebrae are under-represented. Therefore, skulls provide the best estimate of the minimum number of individuals. Smaller bones appear to be more easily destroyed, buried, or transported away. Most vertebrae were in good condition, suggesting that most bones arrived on the beach recently.

Remains of 8 of the 18 species recorded in the northern Gulf were found: Zalophus californianus *(California Sea Lion, 8 skulls),* Delphinus delphis *(Common Dolphin, 7 skulls),* Tursiops truncatus *(Bottlenose Dolphin, 6 skulls),* Phocoena sinus *(Vaquita, four skulls),* Pseudorca crassidens *(False Killer Whale, one skull),* Kogia breviceps *(Pygmy Sperm Whale, one skull), and a possible* Mesoplodon *sp. (Beaked Whale, one skull). One* Physeter macrocephalus *(Sperm Whale) was identified by its large vertebrae.*

Differences in population size, habitat use, and behavior among species may affect species composition and abundance within the bone assemblage. Migrants and rare species are not as abundant as residents in the bone assemblage. Coastal species are more common than oceanic ones.

Marine mammal remains are common within the 3% of Colorado Delta shoreline surveyed, and provide a remarkably good sample of the living fauna. Surveys of mammal remains may be a valuable and cost-effective supplement to aerial and nautical surveys of the live fauna.

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INTRODUCTION

Despite their popularity with the general public and their fascinating evolutionary history (e.g., Gingerich et al., 2001, Thewissen et al., 2001), little is known about how marine mammals become fossils and how well their fossil remains reflect the composition and abundance of the living fauna. This is not surprising because most marine mammals spend most, if not all, of their lives at sea. Consequently, they most likely die at sea and direct examination of their subsequent decay and disarticulation can be accomplished only in rare circumstances. For example, Allison et al., (1991) used observations and collections made by deep-sea submersible to describe the post-mortem fate of a whale's soft-tissues and skeletal remains in a 1240-m deep site in the Santa Catalina Basin off California. Such study requires both advanced technology for access to the remains, and considerable luck in their initial discovery.

Some marine mammal remains do occur in shallow water—such as those from the Miocene/Pliocene Pisco Formation of Peru, which appears to have accumulated in a shallow lagoon (Esperante et al., 1999, 2002). The most easily accessible Holocene remains result from deaths following strandings or the post-mortem transport and beaching of floating carcasses. Indeed, Wilhelm Schäfer, the father of actuopaleontology (the study of the remains and behaviors of organisms that might become fossils some day) undertook extensive research on the decaying remains of whales and seals along the coast of the North Sea. His descriptions and drawings (summarized in Schäfer, 1962, 1972) rival those of a skilled medical examiner in their rich detail and insight into both the causes of death and the processes of decay, dismemberment, and burial.

However, no one to our knowledge has yet compared the marine mammal species found alive in an area to those found as bones on an adjacent shoreline. Live-dead comparisons are common in the literature on the taphonomy of marine shelly assemblages (for an analytical review, see Kidwell, 2001), and Beherensmeyer and her colleagues have undertaken extensive comparisons of live and dead terrestrial mammals in East Africa (Behrensmeyer, 1978; Behrensmeyer and Decant Boaz, 1980; Behrensmeyer et al., 1979).

This paper reports results from a preliminary survey of marine mammal remains along the Colorado River delta, Mexico, on the western shore of the northern Gulf of California. The number of entire carcasses are reported as well as partly articulated remains and solitary bones, the proportion of the different bones found, and the composition and relative abundance of species in the bone assemblage. The bone proportions found were then compared to those expected, and the species composition of the dead remains to that of the marine mammals known to inhabit the northern Gulf of California. This live/dead study provides insights into the taphonomic processes that affect the fossil record of marine mammals.

Marine Mammals in the Northern Gulf of California

The northern Gulf of California is defined here as the section of the Gulf north of 29° N. latitude (i.e., above the Midriff Islands). Fourteen species of marine mammals are known from the northern Gulf of California, as either

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TABLE 1—Species of marine mammals known in the northern Gulf of California. Asterisks indicate species found as bones on the Colorado Delta. Numbers in parentheses are the number of skulls found (except for *Physeter macrocephalus,* which was identified by the vertebrae).

Species known in the northern Gulf of California
Resident species
**Zalophus californianus* (8)
**Delphinus delphis* (7)
**Tursiops truncates* (6)
**Phocoena sinus* (4)
Migrant species
Balaenoptera edeni
Balaenoptera musculus
Balaenoptera physalus
Eschrichtius robustus
Globicephala macrorhynchus
**Kogia breviceps* (1)
Orcinus orca
**Physeter macrocephalus* (1)
**Pseudorca crassidens* (1)
Ziphius cavirostris
Rare sightings
Balaenoptera acutorostrata
Grampus griseus
**Mesoplodon* sp. (1)
Steno bredanensis

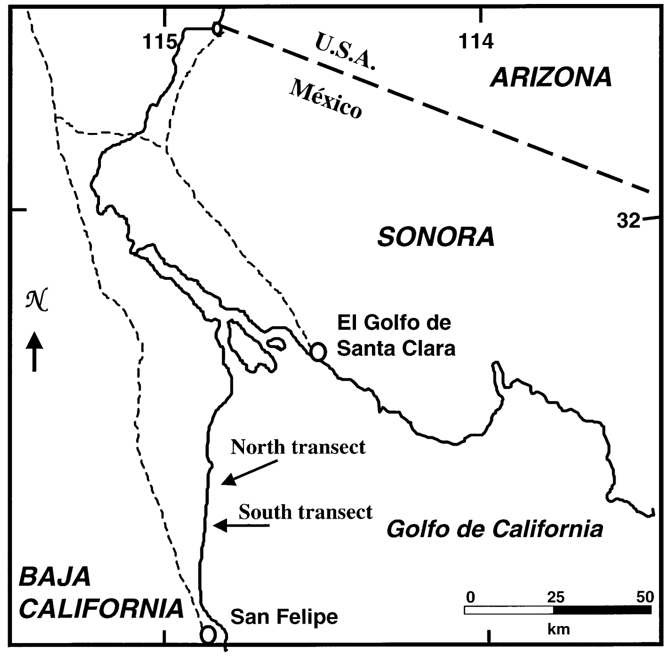

FIGURE 1—Study area. Colorado River delta and northern Gulf of California.

year-round residents or migrants. Table 1 lists the four resident species and the ten migrants known from the area, as based on the surveys and reviews of Wells et al., (1981), Leatherwood et al., (1988), and Vidal et al., (1993). The rare sightings of *Balaenoptera acutorostrata* (Minke Whale), *Steno bredanensis* (Rough-toothed Dolphin), *Grampus griseus* (Risso's Dolphin), and *Mesoplodon* sp. (Beaked Whales) noted by Vidal et al., (1993) are also included.

The most abundant resident species is *Zalophus californianus* (California Sea Lion). Their population in the northern Gulf is estimated at approximately 17,000 individuals (Vidal et al., 1993). *Delphinus delphis* (Common Dolphin) is the next most abundant resident species in the northern Gulf, where pods of thousands of individuals have been observed (Vidal et al., 1993). *Tursiops truncatus* (Bottlenose Dolphin) is probably the third most abundant marine mammal in the area. A survey conducted in the Upper Gulf over a one month period recorded 477 individuals of *Tursiops truncatus* (Wells et al., 1981). *Phocoena sinus* (Vaquita or Gulf of California Harbor Porpoise) is the rarest resident. *Phocoena sinus* is an endangered species endemic to the Colorado River delta region. The current population, as estimated from an aerial survey, is 224 individuals (Barlow et al., 1997). The population is thought to be declining because of incidental capture in fishing nets (D'Agrosa et al., 2000) and perhaps because of environmental changes caused by the near-cessation of Colorado River flow to the Gulf of California following construction of upstream dams and diversions. No estimates of pre-dam populations exist because the species was first described in 1958 (Norris and McFarland, 1958)—after large-scale diversions already had taken place.

MATERIALS AND METHODS

Two shoreline-parallel transects along shelly beaches (cheniers) and adjacent mudflats of the Colorado River delta were examined on December 6–8, 2001 (Fig. 1). The south transect extended for 0.9 km, and the north transect was approximately 3.1 km in length (Fig. 2). Together, the transects sample approximately 3% of the delta's total shoreline. The survey mainly focused on remains found on the shelly beaches; only 18 of the 112 bone-bearing localities included in this study were located on adjacent mudflats.

An advance team of three people walked parallel to the beach and each person marked all marine mammal remains within a three-meter radius. Collectively, this produced a beach-parallel transect of 18 meters in width. A following team of three people made detailed observations of the marked remains. At each bone locality, the latitude and longitude was recorded with a GPS unit, along with the number, type, and taphonomic condition of each bone. The remains were photographed and the thickness, width, length, and diameters of each bone were measured.

A locality is defined here as an area containing one or more bones that are either articulated, within close proximity of each other (within one meter), or clearly derived from the same individual (for example, one locality contained several large vertebrae and ribs scattered over a linear distance of 214 m).

In addition to the specimens found along each transect, two skulls and one vertebra were found in the vicinity of our campsite on the shelly beach. These bones are not included in the analyses of bone proportions because a systematic search for other bones in the vicinity was not conducted. However, the skulls are included in the estimate of species composition.

Because vertebrae were the most common bones found,

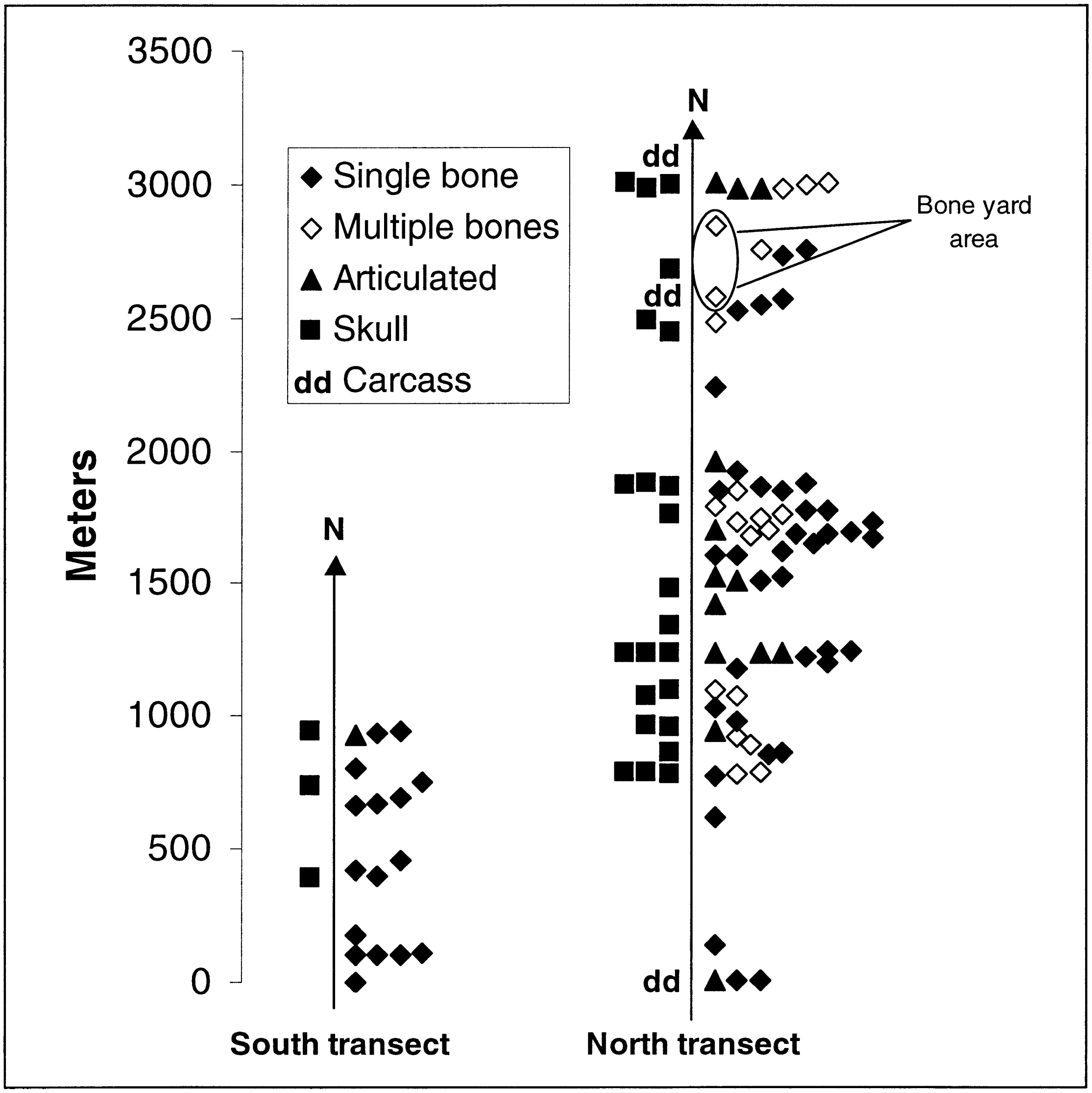

FIGURE 2—Locations of carcasses, skulls, articulated bones, multiple bones (bones found within a small area), and single bones found in this study; dd (carcass symbol) indicates location of dead dolphins. Position of bones along horizontal axis has no significance; skulls and carcasses shown to left of transect line, single and multiple bones to right of transect line.

their variation in taphonomic condition was analyzed. Only 315 of the 316 vertebrae found were included in the taphonomic analyses because notes and photographs were inadvertently not taken of one vertebra. Each vertebra was assigned into one of three taphonomic classes: (1) vertebrae in *good condition* were those that had smooth, hard surfaces and still-adhering flesh, complete processes, and no major cracks; (2) vertebrae in *fair condition* were those that showed slight wear and cracking, and partial erosion of the processes; and (3) vertebrae in *poor condition* were those that had either a spongy or splintered surface texture, and greatly reduced or absent processes.

Skulls were identified to the species level using both published descriptions of Gulf marine mammals (Tomilin, 1967; Odell, 1981; Caldwell and Caldwell, 1989; Heyning, 1989; Evans, 1994; Odell and McClune, 1999; Vidal et al., 1999; Wells and Scott, 1999) and comparison of photographs to reference specimens at the Natural History Museum of Los Angeles County. The proportions of bones found were compared to the known proportions of bones in a single individual as described in Tomilin (1967), Odell (1981), King (1983), Cummings (1985), and Vidal et al., (1999).

RESULTS

Four hundred sixty-seven bones were found among 109 localities, plus 3 carcasses in three additional localities (Fig. 2). In the 0.9 km of the south site, 39 bones were found among 20 localities, and 428 bones were found among 89 localities in the 3.1 km of the north site. Bones from the three carcasses were not included in bone counts. On average, 0.03 bone localities per meter were found, or one bone locality per 36 m. Figure 2 shows the locations of the carcasses, skulls, and other bones within each of the two transects.

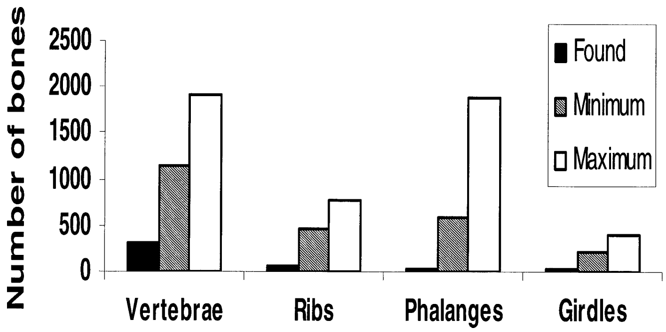

FIGURE 3—Number of bones found by type (solid), number of bone types expected based on 26 individuals and a minimum skeletal ratio (stippled), and number of bone types expected based on a maximum skeletal ratio (white).

Three carcasses were found, two of which were intact. The third was largely decayed and occurred in two mostly articulated, skin-encrusted clusters separated by 3 m. Twenty occurrences of articulated remains were found (19 groups of two or more vertebrae and one set of phalanges from a *Zalophus californianus* flipper) and 244 isolated bones.

Twenty-six skulls, 315 vertebrae, 65 ribs, 35 phalanges, 20 girdles or limb bones (pelvis, scapula, humerus, radius, ulna, femur, tibia, fibula), and six unidentifiable bones were found in the two transects (Fig. 3). Not counting the carcasses or the unidentifiable bones, the skeletal ratio of skull:vertebrae:ribs:phalanges:girdles/limbs is 1:12:3:1:1.

Among the species known from the northern Gulf, the maximum number of bones per skull is 74 vertebrae (*Delphinus delphis*), 30 ribs (*Balaenoptera musculus*, *Balaenoptera physalus*, and *Delphinus delphis*), 56 phalanges (*Zalophus californianus*), and 16 girdles/limb bones (*Zalophus californianus*), for a maximum skeletal ratio of 1:74: 30:56:16. The minimum per skull is 44 vertebrae (*Zalophus californianus*), 18 ribs (*Ziphius cavirostris*), 22 phalanges (*Eschrichtius robustus*), and 8 girdles/limb bones (all the toothed whales), for a minimum skeletal ratio of 1: 44:18:22:8. The maximum and minimum numbers of expected bones for 26 skulls are shown in Figure 3.

Most of the 315 vertebrae found were in good condition (62%), while only 24% were in fair condition and 14% were in poor condition (Fig. 4). It should be noted that of the 195 vertebrae that were in good taphonomic condition, only 15% were disarticulated, single vertebrae (i.e., most were still articulated with at least one other vertebra). Of the 76 vertebrae that were in fair condition, 43% were disarticulated, single vertebrae. All of the 44 vertebrae that were in poor condition were disarticulated, single vertebrae.

Very few teeth were found, either still within the jaw or as isolated elements. Still-rooted teeth were found more commonly in *Zalophus californianus* crania than in the crania of the cetaceans. Apart from those in the carcasses, only three mandibles were found.

The skulls of seven species were found and the presence of an eighth species (*Physeter macrocephalus*, Sperm Whale) was inferred based on the size and proportions of 22 vertebrae and 18 ribs scattered over a small area (Table 1). The most abundant species found in the bone assemblages was *Zalophus californianus* (California Sea Lion) (8 skulls). All of the whales found are odontocetes (toothed whales); no mysticetes (baleen whales) were found.

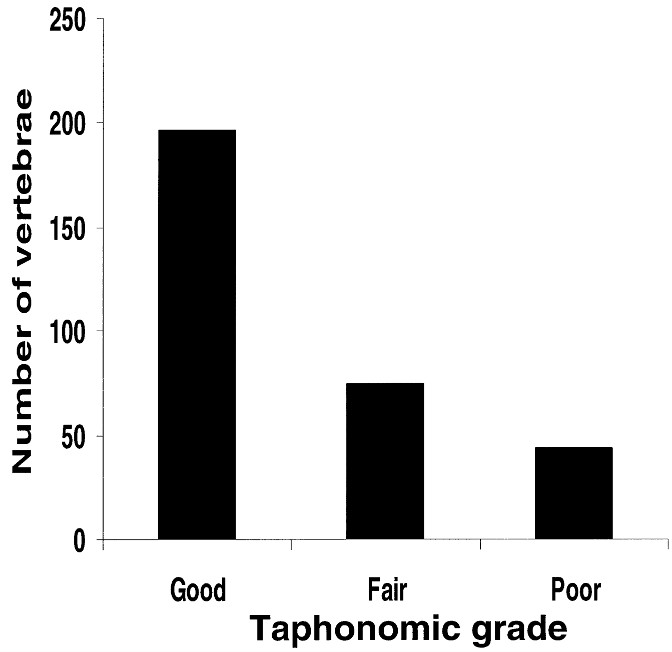

FIGURE 4—Variation in taphonomic condition among 315 vertebrae examined in this study. See text for explanation of taphonomic grades.

DISCUSSION

Time and Transport

The abundance of bones suggests either one or more episodes of mass mortality or the accumulation of the bones over some substantial period of time. Background mortality rates for marine mammals in the northern Gulf are not known. The bone assemblage on the delta's shelly beaches is most likely an attritional or time-averaged assemblage because of the great variation in degree of articulation (from whole carcasses to isolated bones) and taphonomic condition (from bones with still-adhering, dried skin to worn, nearly unrecognizable vertebrae). The abundance of bones (467 bones plus three carcasses within 4.0 km) may be a consequence of the Colorado Delta's isolation: it is still largely uninhabited, unexploited, and unvisited. Shorelines more easily accessible to fishermen, tourists, beachcombers, or scientists are likely to contain fewer remains simply because bones would be collected quickly in such settings.

The abundance of bones and their variation in taphonomic condition suggest a substantial amount of time for accumulation, but the amount of time is difficult to estimate. Most of the bones are suspected to survive for less than 50 years based on Behrensmeyer's (1978) analyses of bone weathering in the Amboseli Basin of Kenya and the overall good condition of bones found on the Delta. Behrensmeyer (pers. comm., 2002) found that most bones decompose beyond recognition in 10–15 years, although the skull of a rhinoceros killed in 1961 is still recognizable after 40 years. Because the Amboseli Basin is also hot and dry, the comparison may be useful.

It is worth stating the obvious here: most of the bones were transported to the beach and are no longer in their original habitat. The possible exception could be the bones of *Zalophus californianus*, the California Sea Lion, but even this seems unlikely. Although these animals are more amphibious than cetaceans and spend substantial amounts of time (sometimes two months during the breeding season according to Allen, 1974) out of the water, they typically congregate (when out of the water) in large colonies on rocky islands or promontories, not along low-lying, muddy coasts (Reidman, 1990) such as those studied here. Furthermore, concentrations of *Z. californianus* bones were not found that would have suggested a colony.

Some of the animals whose bones were found may have reached the beach under their own power rather than as floating carcasses or as solitary bones. Some cetaceans strand themselves (sometimes in groups) when disoriented or sick, or perhaps to assist a disoriented or sick member of the pod (Norris and Dohl, 1980).

Most of the bones were found scattered or partly disarticulated. This is in contrast to the skeletons found as fossils in the Miocene/Pliocene Pisco Formation where most are articulated to some degree (Esperante et al., 2002). The Pisco cetaceans occur in a diatomite that Esperante et al., (2002) interpret as having accumulated in a shallow bay. They attribute the whales' excellent preservation to their burial shortly after death.

The high concentration of bones in the northern part of the study area and the variable concentration of bones along the beach (Fig. 2) suggest that local variations in waves, currents, and bottom topography play some role in the accumulation of marine mammal remains. However, incipient bonebeds were not found.

It is difficult to say with certainty what proportion of bones arrives on the beach as part of a living animal, part of a decaying carcass, or as solitary bones. Many, if not most, likely arrive as part of a still-living animal or as part of a carcass in some stage of decomposition. Schäfer (1972) noted that whales with a high fat content float immediately after death, while those with a low fat content first sink, but float again after gases build up in the body cavity during decay—the so-called bloat and float means of post-mortem transport. Such carcasses could be transported easily to shore during the spring and summer, when prevailing winds are from the south, or during storms. Circulation in the northern Gulf of California is counter-clockwise, so the marine mammals could be derived from the eastern side of the northern Gulf, as well as from some unknown distance to the south. Schäfer (1972) suggested that carcasses can float for weeks in the North Sea and shed skeletal parts as they decompose. Disintegration is presumably more rapid in the much warmer waters of the Gulf of California, but estimates of likely transport distances cannot be made because quantitative estimates of current speeds and disintegration rates are lacking.

Some individual bones could arrive on the beach via bottom transport, but it is suspected that this is an unusual mode of transportation. A carcass shedding bones in the shallow subtidal zone may place some bones in reach of landward-directed wave transport, but waves are not strong along this coast because of the western Gulf's limited fetch and the Delta's very low slope. Although the shell-rich beaches (technically cheniers, see Thompson, 1968; Kowalewski et al., 1998) are evidence of landward transport of shells, only the smaller bones (some vertebrae, phalanges, some ribs, some limb bones) are likely to be moved easily by bottom currents. Transport during storms is possible, but major storms are infrequent in this area.

Bone Proportions

In marine mammals, as with all mammals, vertebrae are the most common bones. The maximum number of vertebrae found in one of the species found in the northern Gulf is 74 (*Delphinus delphis*). Although the most common bones found were vertebrae (316), this total is not near the ~1,900 maximum predicted from the 26 skulls found (26 x 74 = 1,924), nor is it near the minimum expected based on the 44 vertebrae in *Zalophus californianus* (26 x 44 = 1,144). This indicates that vertebrae are not as well represented as skulls. Vertebrae, however, are the best represented of the post-cranial elements, with the number found comprising 16% of the maximum expected number (28% of the minimum expected number). Ribs are represented at 8% of the maximum expected number (14% of the minimum expected number), girdles and limbs are represented at 5% of the maximum expected number (10% of the minimum expected number), and phalanges are represented at 2% of the expected maximum number (6% of the minimum expected number).

The sampling technique used may have caused us to overlook teeth, phalanges, many vertebrae, and the limb bones because of their small size. In addition, all bones commonly are similar in color to the white shells that make up the beach, making the detection of small bones even more difficult. Some of the smaller skeletal elements also may have been buried more quickly. In addition, the smaller skeletal elements may be destroyed more quickly by physical processes such as abrasion by wind-driven sand grains and/or flaking as a result of the desiccation and intense UV radiation in this sunny, hot, and arid region. Bones with a lower surface-area to volume ratio or a higher density may persist for longer periods, biasing the bone assemblage towards larger and denser bones.

Post-Mortem Processes

Mandibles and teeth are very rare in the bone assemblage observed. According to Schäfer (1972) mandibles were quickly lost from a floating dolphin carcass in Jade Bay (southern North Sea), and the lower jaws of a floating seal were only loosely attached 28 days after death and became detached by the 36th day. A stranded seal carcass lost its lower jaw 44 days after death (Schäfer, 1955). It may not be reasonable to extrapolate these observations to a desert coastline. Nevertheless, the early loss of mandibles may be a general phenomenon: Weigelt (1989) noted the early disarticulation of jaws in the decay of mammal corpses, going so far as to formulate a law of the lower jaws in the decay of carcasses. By way of further illustration, Weigelt (1989) commented on Lull's (1914) description of the partial disarticulation of the lower jaw in the skeleton of a fossil dolphin.

Schäfer (1972) noted the early loss of teeth in decaying, beached whale carcasses. He described how the drying, shriveling gums actually pull teeth out the jaw. The tooth-embedded tissues then separate from the bones of the upper and lower jaws. Isolated teeth, therefore, could have been present in the sediments adjacent to the skulls, but sampling methods used were not appropriate for detection of small objects.

Unlike the mammal remains on the beaches of the Colorado Delta, phalanges, limb bones, and teeth are relatively common in the accumulating bones in Amboseli Park, Kenya (Behrensmeyer and Dechant Boaz, 1980). These differences are mostly the consequence of the differences in skeletal construction between marine and terrestrial mammals. Phalanges and limb bones in terrestrial mammals are weight-bearing and thus often denser and larger than in marine mammals, making terrestrial bones more resistant to decay. Buffrénil et al., (1986) report that most of the thoracic limb bones and phalanges in *Delphinus delphis* (Common Dolphin) are less dense than those in the lion, *Panthera leo*.

Teeth in terrestrial mammals are generally larger and more deeply rooted than in toothed whales, which use their teeth for the capture, but not mastication of their food. Pinnipeds (such as *Zalophus californianus*), however, have robust, deeply-rooted teeth and many teeth were found still embedded in the upper jaws.

Although bacteria are important in the decay and scattering of both terrestrial and marine mammals, post-mortem disturbance by animals appears more important in Amboseli than on the Colorado Delta. The very hot and arid climate of the delta may retard infestation by insect larvae or adult carrion beetles; none were observed in the three carcasses. The location of most of the remains at or slightly above mean high water probably limits the effectiveness of scavenging crabs. Scavenging birds (vultures and various gulls) and coyotes (tracks have been observed) are the most likely consumers of the corpses. The two intact carcasses in the study already had de-gassed, apparently through the anus, as shown by the extruded intestines. Although their eyes had been removed (most likely by birds), neither carcass showed any bite marks or partial consumption, nor did any of the bones show signs of gnawing by coyotes. At the time the carcasses were observed, the skin was already very leathery and quite resistant to efforts to tear it with pliers or cut it with a small saw. Once beached, any post-mortem scattering of bones on the delta seems to take place through such physical means as storm surges, waves, and tides, not animals.

Live-Dead Comparison

Bones were found of all four resident species in the northern Gulf, and in rough approximation to their relative abundance in the living fauna. The discovery of four skulls (14% of the 28 skulls) of the now-endangered *Phocoena sinus* (Vaquita) is remarkable, given the species' very small population size today. The skull sample may include specimens from a time when the population was much larger or may reflect the high mortality rate of *P. sinus* today. Indeed, one partly articulated vertebral column was, judging from its size, likely from a specimen of *P. sinus*, although the skull was missing. The vertebral column was found entangled in a fishing net, suggesting death by drowning. Incidental capture in nets is a major source of mortality of the Vaquita (D'Agrosa et al., 2000).

Although the failure to find skulls of all species in the living marine mammal fauna is most likely due to the small areal extent of the survey, it is expected that differences in population size, habitat use, and behavior may also affect the composition and relative abundance of the fauna represented in the dead remains. For example, the abundance of *Zalophus californianus* in the sample is explained by the large population size and shallow-water habitat of this species. Migrant species may be underrepresented because individuals may spend only part of the year in the northern Gulf, thus decreasing their odds of death and subsequent stranding in this area. Among the species not found in the sample (see Table 1), *Balaenoptera musculus*, *Balaenoptera physalus*, *Balaenoptera edeni*, and *Eschrichtius robustus* are found more commonly in open water, thus decreasing their chances of becoming bones on the beach when compared to such coastal and estuarine species as *Zalophus californianus*, *Tursiops truncatus*, and *Phocoena sinus* (Nowak, 1999). In addition, those species known to strand themselves in groups are more likely to be found in the sample. At present, the relative importance of these biases is unknown.

The 28 skulls represent the minimum number of individuals in the sample. It is not surprising therefore, that only 44% of the species known from the area were found. In contrast, Behrensmeyer and Dechant Boaz (1980) found bones of 30 out of the 32 species (93.8%) greater than 15 kg known to live in Amboseli Park. They recorded a minimum of 381 individuals (skulls) in their much more extensive study.

Surveys of dead shelly invertebrates typically recover more species than surveys of the living shelly fauna (Kidwell, 2002). This is probably a consequence of both the large sample sizes of dead individuals (typically in the hundreds to thousands) and extensive time-averaging of shelly remains (Kidwell, 2002). Time-averaging increases species diversity because of the incorporation of transient or ephemeral species through time. Although much more work needs to be done on the comparative taphonomy of vertebrate and shelly remains, shelly remains may be more abundant because of shorter average generation times and shelly remains may be more time-averaged because calcareous shell may be more resistant to post-mortem destruction.

All four of the resident species, three of the ten migrants, and one of the four rare species of marine mammals known from the northern Gulf of California were found in the sample of 3% of the delta's shoreline. This is a remarkably high number for such a small sample and suggests that surveys of mammal remains may be a quick and cost-effective way of estimating the composition of the living fauna. Further study is needed to estimate the minimum sample size needed to recover bones of all the known species.

CONCLUSIONS

Bones of marine mammals are common on the beaches of the Colorado River delta. Their varying degrees of articulation and preservation suggest accumulation over some period of time (<50 years?) rather than a single episode of mass mortality.

The minimum number of individuals found as bones is best estimated by the number of skulls (28). Only 16% of the expected maximum number of vertebrae for 26 individuals were found, 8% of the expected number of ribs, 5% of girdles or limb bones, and 2% of the expected number of phalanges. Teeth and mandibles are very rare. Selective shedding of bones during transport and size-selective preservation, burial, and sampling once on the beach likely were important factors influencing the composition of the bone assemblage.

The good condition of most vertebrae suggests that most of the bones are relatively young. Most bones probably arrive on the beach in self-stranded individuals or as floating carcasses. Post-mortem decay of the tissues and bones likely occurs by bacterial processes, desiccation, UV radiation, waves, tides, and storms. In contrast to habitats where terrestrial mammal bone assemblages accumulate, scavenging animals are rare or ineffectual on the Colorado Delta beaches.

Discovery of all four resident species, three of the ten known migrant species, and one of the four rare species in the small sample (29 individuals and 3% of the shoreline) suggests that surveys of marine mammal remains may prove to be a reliable and cost-effective means of estimating the composition of the live fauna.

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