

A COMPARISON OF GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, FEEDING IN THE BERING SEA AND BAJA CALIFORNIA

JOHN S. OLIVER, PETER N. SLATTERY, MARK A. SILBERSTEIN, AND EDMUND F. O'CONNOR¹

ABSTRACT

Our observations indicate that gray whale feeding on benthic invertebrates is rare in the calving lagoons of Baja California and along the open coast near the Scammon's Lagoon complex. The biomass of benthic invertebrate prey is 20 times greater in the northern feeding grounds of the Bering Sea (482 vs. 24 g/m²). Although the abundance of infaunal invertebrates is only 1.5 times greater in the Bering Sea, most infauna in the calving lagoons are very small polychaetes, bivalves, and crustaceans inhabiting dynamic, coarse sands. The low infaunal abundance and biomass are not caused by gray whale activities in the calving lagoons, as adjacent southern lagoons which are rarely utilized by gray whales have the same infaunal patterns. San Quintin has a unique bottom community which is strikingly different from the more southerly lagoons in Baja California, as well as the northern lagoons in California. Surprisingly, San Quintin shares a number of faunal similarities with gray whale feeding areas in the Bering Sea. No fecal material or bottom excavations made by feeding whales were found in the lagoons of Baja California, including San Quintin. However, the possible expansion of the gray whale population may lead to dramatic changes in the rich bottom communities of San Quintin, and perhaps in shallow water benthic assemblages along the migration route, and in the Gulf of California, which also may harbor potential infaunal prey of gray whales.

Gray whales, *Eschrichtius robustus*, are the only baleen whales that feed primarily on benthic invertebrates (Pike 1962; Rice and Wolman 1971). They consume large numbers of benthic infauna, especially amphipod crustaceans (Zimushko and Ivashin 1980), apparently by ingesting sediment and filtering the infauna on the baleen while expelling sediment and other particles that pass through the baleen fringes (Ray and Schevill 1974). The major feeding grounds are the northern Bering Sea, particularly the central and western regions, and the Chukchi Sea (Bogoslovskaya et al. 1981). Here, the water depths are generally 30 to 40 m and the extensive and shallow continental shelf, the Beringian Platform, supports the largest numbers of bottom-feeding marine mammals in the world. In addition to gray whales, walrus, bearded seals, and sea otters feed primarily on benthic invertebrates in the Bering and Chukchi Seas (Lowry and Frost 1981; Frost and Lowry 1981).

Most gray whales leave the northern feeding grounds in the fall and migrate over 10,000 km to Baja California, where calving occurs in several large, shallow, protected lagoons (Scammon 1874). The whales return to the Bering Sea as the sea ice degenerates in the late spring (Rice and Wolman 1971). Very little feeding is believed to occur outside

the northern feeding grounds, as gray whale stomachs are generally empty along the migration route (Scammon 1874; Andrews 1914; Pike 1962; Rice and Wolman 1971), and in the southern lagoons (Scammon 1874). However, feeding has been suggested (Gilmore 1961; Pike 1962; Sund 1974) or documented (Howell and Huey 1930; Mizue 1951; Rice and Wolman 1971) outside the northern feeding grounds on several occasions.

There is additional evidence that gray whale feeding may be relatively common in and near the calving lagoons (Norris et al. in press). In the Bering Sea, many naturalists have observed distinct sediment plumes behind whales that apparently were filtering benthic invertebrates from ingested bottom sediments (Wilke and Fiscus 1961; Pike 1962; Harrison 1979; pers. obs. by authors). Similar sediment plumes or trails have been observed in the calving lagoons (Walker 1975; Norris et al. 1977; Sprague et al. 1978; Norris et al. in press), as well as sediment-laden water passing through the baleen (Norris et al. in press). This behavior suggests benthic feeding similar to that observed in the Bering Sea.

The bottom fauna has not been sampled from any of the lagoons of Baja California, except San Quintin (Barnard 1970). If bottom communities in the calving lagoons are similar to San Quintin, gray whale feeding should be common in Baja California. Laguna San Quintin is located 300 km north of the first calving lagoon, Guerrero Negro, and contains large numbers

¹Moss Landing Marine Laboratories, Moss Landing, CA 95039.

of amphipod crustaceans and polychaete worms (Barnard 1970). In fact, the most abundant crustacean, *Ampelisca agassizi* (*A. compressa* in Barnard 1970), is closely related to *A. macrocephala*, a major prey of gray whales in the Bering Sea (Rice and Wolman 1971). The total abundance of infaunal invertebrates in Laguna San Quintin is as high as 66,700 individuals/m² of bottom (Barnard 1970). Although there are no benthic biomass data from San Quintin, the species composition and abundance patterns suggest a significant quantity of potential gray whale prey. San Quintin may have been an important gray whale habitat in the past, and in the last several years has been visited by a few gray whales each season (Sprague et al. 1978).

The recent behavioral observations in the breeding lagoons and the quantity of potential prey in Laguna San Quintin suggest that gray whale feeding on benthic invertebrates may be relatively common in Baja California. If this hypothesis is accurate, perhaps gray whales migrate to the southern lagoons because of the availability of benthic prey, as well as for the warm temperature and protection for calves. Many whales occur at the entrances and outside the calving lagoons where apparent feeding behavior also has been observed (Norris et al. in press). Although we were primarily concerned with bottom communities within the lagoons, lagoon entrances and offshore habitats were explored as well.

Because stomach contents of gray whales are unavailable from recent years, we were unable to examine diets directly. Instead, we compared populations of benthic prey in the Bering Sea with the abundance and biomass of potential benthic prey in San Quintin and five other lagoons of Baja California (three calving and two noncalving lagoons). In addition, we searched the calving and noncalving lagoons for two important signs of gray whale feeding: Benthic feeding excavations and fecal material.

METHODS

Benthic invertebrate communities were surveyed in six coastal lagoons of Baja California during January 1981 (Fig. 1). Laguna San Quintin is the most northerly lagoon and is visited only infrequently by gray whales. There is little or no gray whale activity in Laguna Manuela and Estero Coyote, which are small southern lagoons with shallow entrances and channels. Laguna Guerrero Negro, Ojo de Liebre (Scammon's Lagoon), and San Ignacio are large lagoons and major calving areas for gray whales. The other important calving area, the complex of lagoons around

Bahia Magdalena, was not surveyed in the present study (Fig. 1).

The six lagoons were surveyed by divers with and without scuba. Because even the deeper lagoon channels are relatively shallow (often <10 m), bottom communities were surveyed by skin divers without scuba. Scuba was used to collect quantitative samples and to make more detailed observations of areas of special interest. About 40% of the dive areas shown in Figure 1 involved scuba. Each lagoon was surveyed by two sets of divers from two small boats.

Quantitative bottom samples were taken with diver-held corers (0.018 or 0.0075 m²), washed over a 0.5 mm screen, and preserved in a solution of 4% formaldehyde. Samples were taken in three major habitats: The central channel, eelgrass beds on the channel edges, and unvegetated sandflats above the eelgrass. Most benthic invertebrates were identified to the lowest possible taxon, and wet weight of the total fauna from each core sample was recorded. The

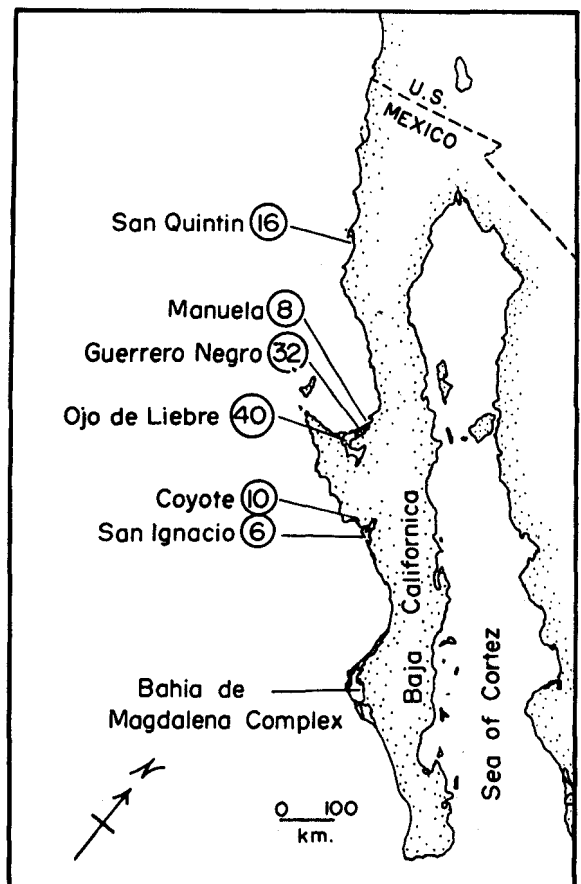


FIGURE 1.—Study sites along the Pacific coast of Baja California. Number of survey dives indicated for each site.

total length of several abundant crustaceans and polychaete worms was measured under a compound microscope with an ocular micrometer. Divers also made numerous visual observations in the relatively clear waters (visibility = 1 to 6 m) and collected qualitative samples of plants and animals.

Benthic invertebrate communities also were surveyed in the central portion of the northern Bering Sea and near St. Lawrence Island from 29 June to 10 July 1980 (Nerini in press) and the northeastern Bering Sea from May to June 1981 (Fig. 2). Water depths varied from 9 to 40 m and bottom-water visibility was generally low, ranging from 0.5 to 3 m. Bottom samples were taken by divers using scuba. The same techniques used to procure and process infaunal and sediment samples in Baja California were employed in the Bering Sea.

RESULTS

Fecal Material

Several fecal slicks were observed floating on the surface waters during the two Bering Sea visits. One

large slick was sampled on 10 July 1980 on the southeastern side of St. Lawrence Island (Fig. 2). This region is a feeding ground for gray whales, and earlier bottom sampling documented extensive crustacean communities dominated by the amphipod, *Ampelisca macrocephala* (Stoker 1978, 1981). Although *A. macrocephala* was abundant in the fecal sample (Table 1) and in our bottom samples (see section on Infaunal Prey), a group of large prey, including 10 species of gammaroid and talitroid amphipods (Table 1), did not occur in any of the bottom cores taken in 1980 or 1981 (core number = 156). Gam-

TABLE 1.—Prey items in a gray whale fecal slick collected from the sea surface near St. Lawrence Island, Bering Sea. From triplicate 1,000 ml subsamples.

	Size (mm)	No./1,000 ml
Amphipods		
Gammaroids (6 species)	15-20	176
<i>Ampelisca macrocephala</i>	15-20	154
Talitroids (2 species)	15-20	4
Talitroids (2 species)	5-10	140
<i>Calliopius</i> sp.	5	219
<i>Ischyrocerus</i> sp.	4-8	4,305
Isopods		
Idotheids	10-50	72

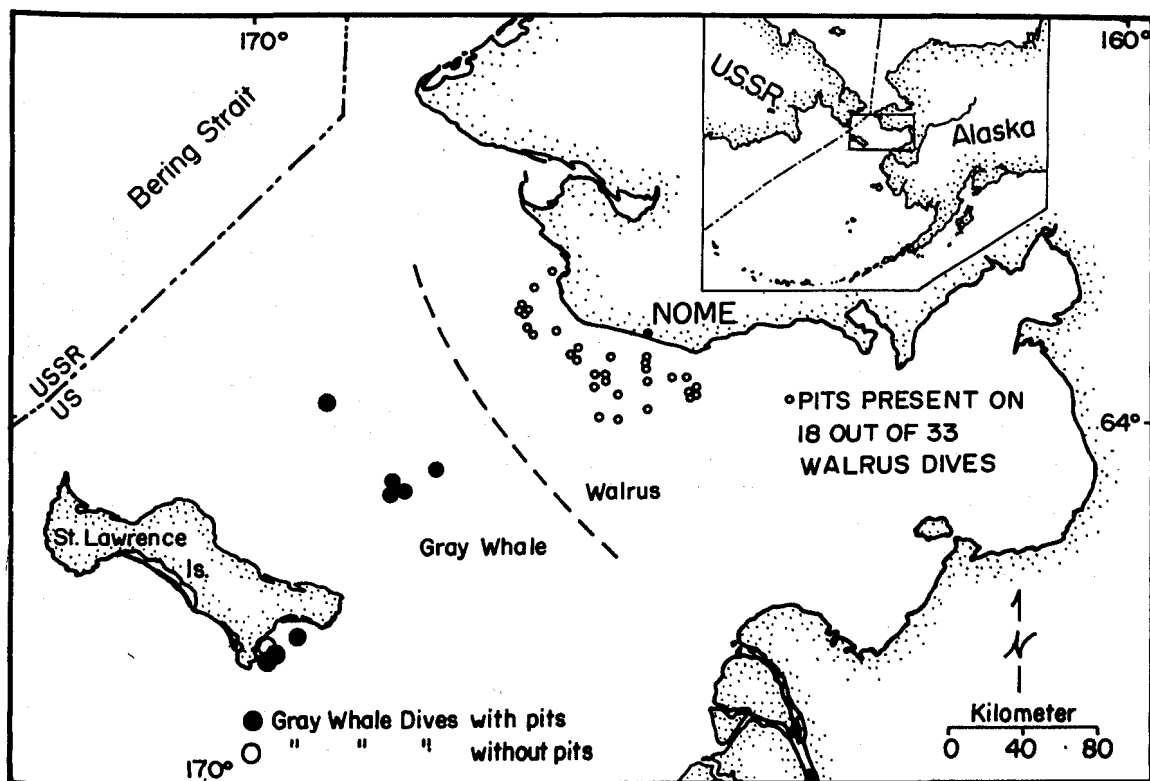


FIGURE 2.—Diving survey stations in the northern Bering Sea. No walrus excavations occurred outside the walrus feeding ground and no gray whale excavations occurred within this area.

maroids and talitroids commonly occur in intertidal, estuarine, and freshwater habitats (Bousfield 1973), and may be nestled among macroalgae in shallow, rocky areas around St. Lawrence Island. These large species (>10 mm) were conspicuous and easily counted without a microscope. Inspection of subsamples of the fecal slick under a dissecting microscope revealed a large number of smaller crustaceans (<5 mm), which were undetected by even the keen observer with the naked eye. The most abundant smaller forms were calliopiid and ischyrocerid amphipods (Table 1), nestlers and tube builders, respectively (Barnard 1969).

We were unable to locate the fecal slicks in the southern lagoons or to find anyone who has seen prey remains in fecal material.

Feeding Excavations

A remarkable record of the feeding activities of gray whales was found in the bottom sediments of the Bering Sea (Fig. 2) (Nerini in press). Divers located many

large pits (more than 50) covering as much as 70% of a local bottom area near St. Lawrence Island. Figure 3 is a scale drawing of a less disturbed pitted site observed during another dive. Although we did not observe a whale making an excavation (bottom visibility was about 2 m), a feeding whale is included in Figure 3 for scale. Gray whales and the fecal slick described earlier (Table 1) occurred within 1 km of the site depicted in Figure 3. These large excavations were 1×2 m and 0.5 m deep. Most pits had a distinct, oblong, bowl shape. The bottom of many pits contained a deposit of broken bivalve shells (nonliving) that were concentrated from the large volume of ingested sediment. The undisturbed level bottom at the highly pitted site was present only on the ridges between the large excavations. However, a well-developed, dense tube mat of *A. macrocephala* was located on a second dive within 50 m of this highly excavated bottom. Large and small gray whale excavations were encountered on several dives in deeper water (Fig. 2). No gray whale excavations were located on many dives along the eastern shore,

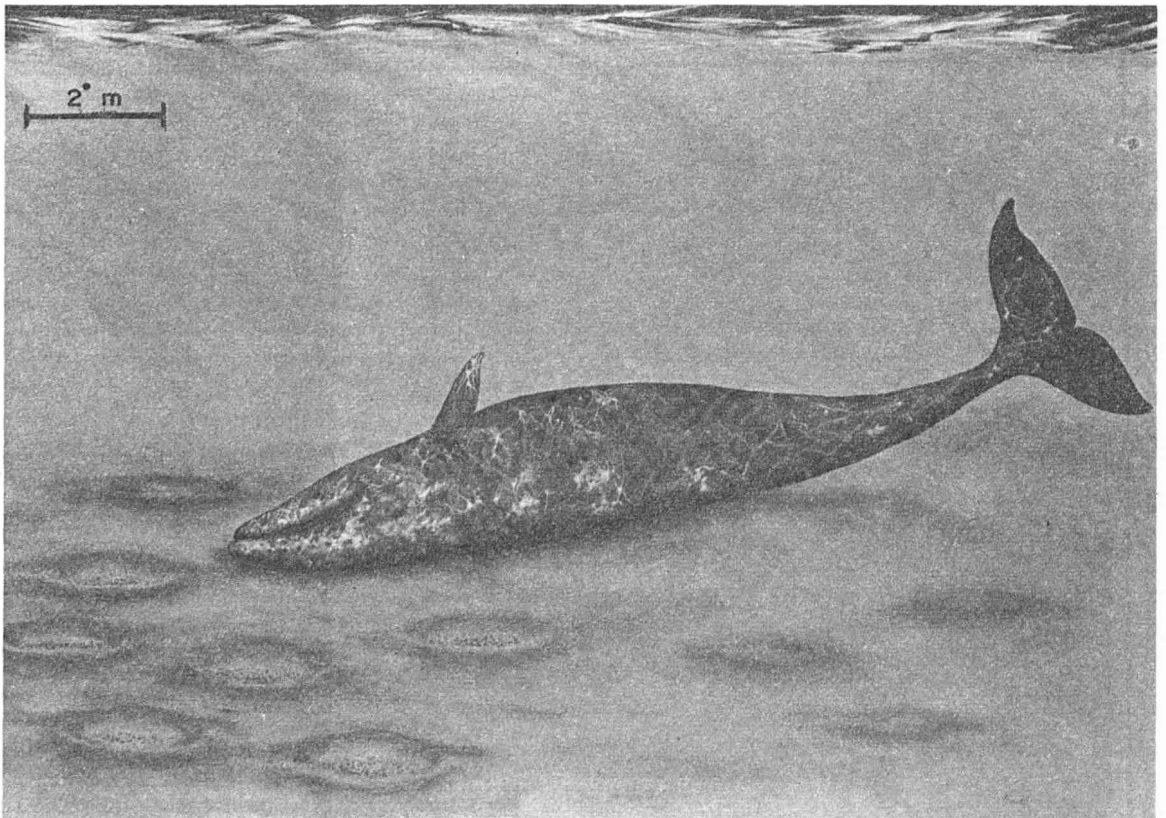


FIGURE 3.—A scale drawing of a heavily excavated bottom area observed by divers near St. Lawrence Island (21 m). No feeding whale was seen here, but a whale is included in the drawing for scale. (Drawn by Sandy Strause.)

where walrus feeding excavations were common (Fig. 2) (Oliver et al. 1983).

No gray whale feeding excavations were observed in Baja California, despite a large number of survey dives (Fig. 1) and better water clarity than the Bering Sea. Although the currents were relatively strong in many of the lagoons, other excavations and sediment structures were maintained in the surface sediments. For example, a large number of excavations produced by feeding rays was observed. These pits persisted in a number of lagoon habitats, but were usually found in the intertidal and shallow subtidal areas where gray whales did not occur. Rays were observed creating pits on several occasions. Qualitative bottom samples commonly revealed large bivalves, especially *Chione* spp., in areas where ray pits occurred. Dense infauna and other patches of potential gray whale prey did not occur in the ray feeding areas.

Infaunal Prey

The abundance of infaunal invertebrates in the gray whale feeding grounds of the Bering Sea was only 1.5 times greater than the total abundance of animals in the calving lagoons, which included Guerrero Negro, Ojo de Liebre, and San Ignacio (Fig. 4). However, ampeliscid amphipods were never abundant in the calving lagoons, while *A. macrocephala* dominated the Bering Sea fauna (also see Neiman 1963 and Stoker 1978). The abundance of infaunal crustaceans and *A. macrocephala* in the gray whale feeding grounds (Fig. 2) was as high as 67,746/m² and 21,448/m², respectively. Infaunal abundance was highest in San Quintin, the most northerly lagoon surveyed in Baja California (Fig. 4). Here we sampled from dense beds of *A. agassizi*, which accounted for 95% of the total individuals and occurred in abundances as high as 135,912/m².

In contrast to abundance, the biomass of the infauna was 20 times greater in the Bering Sea than in the calving lagoons (Fig. 5). Over 70% of the biomass in San Quintin was *A. agassizi*, and the total biomass was more than half of the Bering Sea value (Fig. 5). However, the Bering Sea data were averaged over a large group of stations sampled by Stoker (1978). The value shown for San Quintin was the densest *Ampelisca* bed we observed.

Most of the benthic invertebrates living in the southern lagoons were quite small. This was clearly reflected in the biomass data (Fig. 5). In addition to the rarity of large species and individuals, deposit feeders also were relatively rare among the polychaete worms, especially in the unvegetated

sedimentary habitats. For example, a suspension-feeding sabellid worm (probably *Fabricia*) was the only species that occasionally occurred in relatively high abundance (maximum of 250 in a 0.0075 m² core). This species was usually <5 to 6 mm long, and

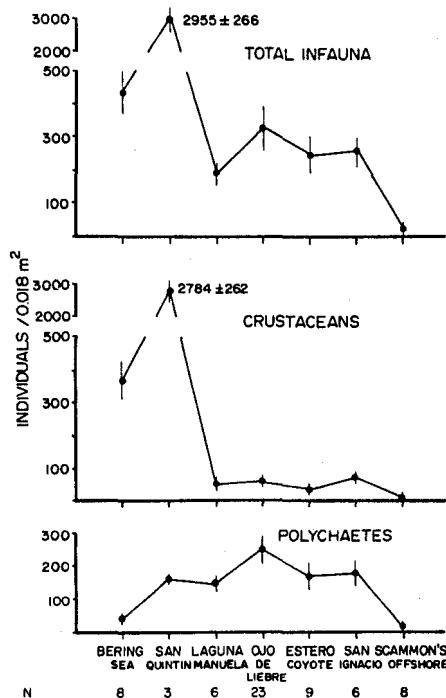


FIGURE 4.—Abundances of total infaunal invertebrates, crustaceans, and polychaete worms in the gray whale feeding grounds of the Bering Sea and in Baja California. Means and standard errors.

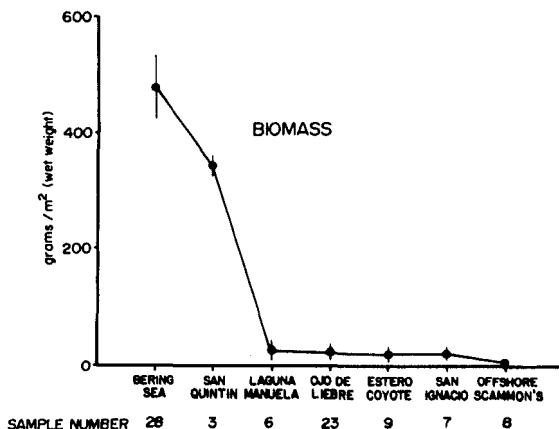


FIGURE 5.—Wet weight biomass of the total infauna from the gray whale feeding grounds in the Bering Sea (from Stoker 1978) and in Baja California. Means and standard errors.

accounted for the relatively high abundance of polychaetes in Ojo de Liebre (Fig. 4). The few infaunal crustaceans (Fig. 4) also were small species and individuals <6 mm in length vs. 20 mm for typical Bering Sea individuals). Although *A. agassizi* was a relatively large benthic crustacean for the lagoons of Baja California, this species was much smaller than *A. macrocephala* from the Bering Sea (Fig. 6).

Samples from the channel and eelgrass habitats in each lagoon were lumped for Figures 4 and 5, but infaunal abundance and biomass were highest in the eelgrass beds. When Laguna Manuela and Estero Coyote were considered together with the three calving lagoons (Fig. 1), the overall infaunal biomass was $24.3 \pm 0.9 \text{ g/m}^2$ ($\pm \text{SD}$; $n = 45$). Infaunal biomass in eelgrass habitats was $35.9 \pm 2.7 \text{ g/m}^2$ ($n = 21$) and was only $13.2 \pm 1.6 \text{ g/m}^2$ ($n = 24$) in the channels. This difference was highly significant ($P < 0.001$; Mann Whitney U test).

All the lagoon entrances were surveyed in the present study except San Ignacio. Qualitative sampling of the infaunal and epifaunal invertebrates revealed

very low numbers and biomass. Quantitative core samples taken at the entrance of Laguna Ojo de Liebre substantiated these observations (only 14 g/m^2).

The biomass of potential benthic prey was extremely low outside the lagoon entrances as well. Benthic invertebrate communities were surveyed outside the Scammon's Lagoon complex between Laguna Manuela and Guerrero Negro (Fig. 1). The infauna were sampled at two water depths (9 and 17 m) and in areas that were likely to harbor well-developed infaunal populations. The substrate was a coarse, mobile sand at each depth. When the depths were combined, the infaunal biomass was $2.7 \pm 3.3 \text{ g/m}^2$ (SD ; $n = 8$). This was considerably lower than the low biomass recorded from the lagoon channels ($P < 0.0001$; Mann Whitney U test). A dense concentration ($100\text{--}200/\text{m}^2$) of the heart urchin, *Lovenia cordiformis*, was not included in the biomass figures because this species is not a potential prey for gray whales. Our experiences along other wave-exposed coasts (Oliver et al. 1980) indicate that unobserved patches of dense infaunal prey probably do not occur in offshore habitats.

No large zooplankton, including euphausiids and galatheid crabs, were seen by divers in the offshore habitats, in the lagoons, or in the lagoon mouths (Norris et al. in press).

In addition to the plankton, conspicuous mobile epifauna were not abundant at the lagoon entrances or anywhere in the lagoons, either on reefs or over the soft sediments. Several groups of the mysid crustacean, *Mysidopsis californica*, were observed near eelgrass beds, but these patches were rare, covered a relatively small area (10 to 20 m^2), and did not contain a large number of individuals. Small groups of shrimp were even rarer.

The calving and adjacent noncalving lagoons in the southern part of Baja California had highly dynamic sedimentary environments. We observed tidal currents of 2 to 3 kn in several lagoons. Sediments were primarily coarse sand and gravel (see Phleger and Ewing 1962), and surface structures indicated highly mobile substrates. These structures included broken shell debris and ripple marks as large as 1 m in height. Surprisingly, these structures were not restricted to the lagoon mouth. For example, large lunate ripples (length about 10 m, height 30 cm) occurred in the channel of Estero Norte, an arm of the extreme back lagoon in Ojo de Liebre. These ripple marks were more than 10 m wide, were highly mobile, and changed direction with the tide. Unlike the more southerly lagoons, we encountered relatively fine sands and silts in San Quintin. Similar differences between the sedimentary habitats in San Quintin

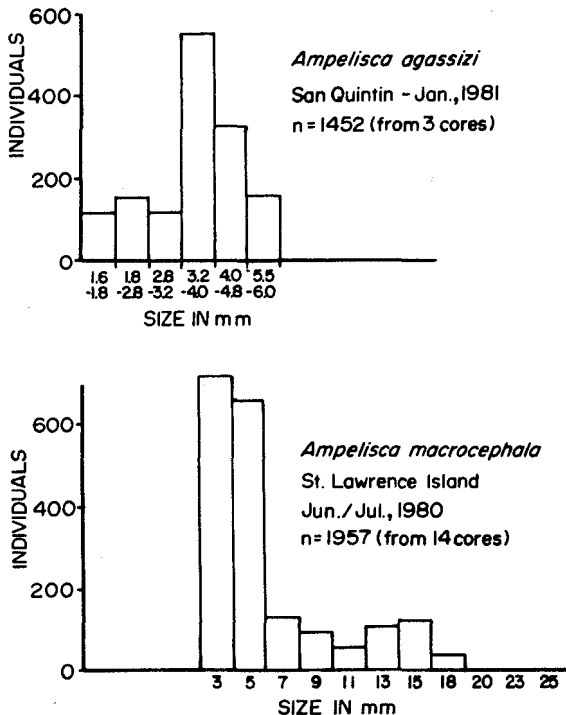


FIGURE 6.—Length-frequency histograms of *A. macrocephala* collected from a variety of stations in the Bering Sea and of *A. agassizi* from San Quintin. *Ampelisca macrocephala* populations were dominated by recently released young in summer samples (molt stages I and II). Most *A. agassizi* were preadult individuals from a midwinter population.

(Gorsline and Stewart 1962) and Ojo de Liebre (Phleger and Ewing 1962) were observed in earlier studies. The Bering Sea areas, like San Quintin, contained less mobile fine sands (Nelson 1982) harboring many relatively large infauna in tubes and burrows (Stoker 1978).

DISCUSSION

The absence of fecal material, benthic feeding excavations, and significant quantities of potential gray whale prey suggest that gray whale feeding on benthic invertebrates is not common in Baja California. No evidence of benthic feeding was encountered within the calving and noncalving lagoons, at lagoon entrances, and along the offshore sand bottoms. Gray whale stomachs collected in the southern lagoons also contained no benthic prey (Scammon 1874; Rice and Wolman 1971).

In contrast to Baja California, there is considerable evidence of gray whale feeding in the northern Bering Sea. Stomach contents are dominated by benthic infauna, especially a few species of large amphipod crustaceans (Table 2). Crustacean communities are well developed in the central and western portion of the area (Neiman 1963; Stoker 1978), the major gray whale feeding grounds. The Russian literature reports a benthic biomass of almost 1,000 g/m² in the feeding grounds (Neiman 1963; Alton 1974), and Stoker (1978) found a range from 149 to 991 g/m². Over 90% of the biomass was crustaceans, especially *A. macrocephala* in the central basin. Although we only located a few fecal slicks in the Bering Sea, benthic feeding excavations were common.

All the large benthic excavations observed in this study were undoubtedly created by feeding gray whales. Other likely explanations for their origin can be excluded. There are few bottom-feeding fish such

as rays or skates in the northern Bering Sea (Shmidt 1950; Wilimovsky 1974). These fish produce large pits in other habitats (Howard et al. 1977; Gregory et al. 1979; VanBlaricom 1982). The abundant bottom fish are in the cottid family (Wilimovsky 1974) and are relatively nondestructive bottom feeders (pers. obs.). One other bottom-feeding marine mammal, the walrus, occurs in the gray whale feeding grounds, but walrus produce entirely different bottom excavations than gray whales (Oliver et al.²). We know of no other likely biological explanation for the large pits.

Two physical processes produce large excavations on the sea floor, ice gouging and biogenic gas cratering. Although ice gouging produces deep excavations in the sea floor (Reimnitz et al. 1977), this scour does not produce regular, bowl-shaped depressions and usually causes much more extensive bottom disturbance (Reimnitz et al. 1977; Larsen et al. 1981; Thor and Nelson 1981; pers. obs. by authors). Release of biogenic gas from the sediment apparently produces large craters in Norton Sound, and several other areas with gas-producing strata, but not in the gray whale feeding grounds (Nelson et al. 1979).

Gray whale feeding excavations can be easily distinguished from the benthic feeding record of walrus (Oliver et al. 1983). Walrus excavations were common along the eastern shore, and gray whale excavations only occurred in the central study area (Fig. 2). Here, the gray whale prey (Stoker 1978) and feeding gray whales (Moore and Ljungblad in press) are much more abundant. Gray whales are infrequently encountered along the eastern shore, where bivalve

²Oliver, J. S., P. N. Slattery, M. A. Silbertstein, and E. F. O'Connor, 1983. Gray whale feeding on dense amphipod communities near Bamfield, British Columbia. Unpubl. manuscript. Moss Landing Marine Laboratories, Moss Landing, CA 95039.

TABLE 2.—Dominant prey species contained in gray whale stomachs. All are benthic and all but *Synidotea* sp. are amphipods. Stomachs usually contain one prey species which comprises 80 to 100% of total contents (Zimushko and Lenskaya 1970; Bogoslovskaya, et al. 1981).

Prey species	Number stomachs dominated by prey species					
<i>Ampelisca macrocephala</i>	12	11	1	1	(¹)	(¹)
<i>Pontoporeia femorata</i>	23	10				
<i>Atylus</i> spp.	7	1			(¹)	
<i>Anonyx nugax</i>	10					
<i>Byblis gaimardi</i>		4				
<i>Ampelisca eschrichti</i>	1					
<i>Synidotea</i> sp.	1					
Source	Zimushko and Ivashkin 1980	Bogoslovskaya et al. 1981	Coyle unpubl. manuscript. ²	Pike 1962	Zenko-vich 1957	Tomlin 1957

¹Dominant species where number of stomachs examined were unreported.

²Coyle, K. O. 1981. The oceanographic results of the cooperative Soviet-American cruise to the Chukchi and East Siberian Seas aboard the Soviet whale hunting ship Ryzashchil, Sept.-Oct. 1980. Unpubl. manuscript. University of Alaska, Institute of Marine Science, Fairbanks, AK 99701.

molluscs dominate the benthic biomass. The separation of the feeding grounds of gray whales and walrus can be documented by side-scan sonar, which clearly relates general changes in surface sedimentary structures to the large-scale feeding activities of gray whales and walrus.³ When properly calibrated with in situ observations, individual feeding excavations and multiple excavation patterns (footnote 2) may be accurately interpreted on side-scan sonographs (pers. obs. by authors).

Gray whales also produce benthic feeding excavations along Vancouver Island in British Columbia (footnotes 3, 4). Fecal material has been collected along this coast as well.⁴ We recently discovered dense beds of ampeliscid amphipods and an extensive benthic feeding record of gray whales near the Bamfield Marine Station (see footnote 2). Many whales apparently feed along Vancouver Island during the northward migration, and some individuals spend the entire summer here (Darling 1977).

In summary, despite considerable evidence of benthic feeding in northern habitats, there is no compelling evidence for benthic feeding in or near the lagoons of Baja California. The southern lagoons contain highly dynamic, coarse sediment harboring very small infauna and little prey biomass for gray whales. Most infauna are much smaller than the spaces between the gray whale baleen. The structure of benthic communities within the calving lagoons is not influenced by gray whale activities, because bottom communities in adjacent noncalving lagoons are similar to those in the calving lagoons.

Earlier studies of the gray whale diet imply highly selective feeding on large crustaceans (e.g., Pike 1962). While two species of large amphipods, *Pontoporeia femorata* and *A. macrocephala*, generally account for much of the prey biomass (Table 2), careful examination of the prey remains in a fecal slick revealed a surprisingly large number of smaller prey. Gray whales probably are relatively nonselective filter feeders, consuming most of the large and small infaunal forms. Despite the importance of benthic prey, gray whales are clearly opportunistic feeders, consuming both large and small benthic invertebrates, epifaunal invertebrates in kelp forests (Wellington and Andersen 1978) and along rocky

shores (see footnote 2), zooplankton (Rice and Wolman 1971; Norris et al. in press), and fish (Gilmore 1961; Sund 1975).

Although some observations of apparent feeding behavior in the breeding lagoons undoubtedly involve planktonic feeding (Norris et al. in press), and opportunistic consumption of some benthic animals, much of this behavior probably results in little or no food. A number of other explanations are likely. For example, a local fisherman and naturalist, Mario Rueda, directed us to a specific habitat near Piedras Island in Ojo de Liebre, where apparent feeding behavior was consistently observed. This area contained no concentrations of potential infaunal or epifaunal prey. However, the bottom relief was spectacular. Rocky outcrops formed a series of parallel ridges much like giant and stable ripple marks on the bottom. The vertical relief was 2 to 3 m. Between the rocky crests, there were deep basins where water currents were very low. The distance between crests was 5 to 10 m. The tidal currents above these ridges were extremely strong. Perhaps gray whales are attracted to this current regime where individuals can rapidly swim in and out of mild and strong currents over an undulating bottom.

Laguna San Quintin contains a unique bottom community, which is strikingly different from the lagoons of California and the five lagoons that were surveyed in central and southern Baja California. San Quintin harbors a large number of potential gray whale prey in a relatively small area. Future expansions of the gray whale population may bring more whales to San Quintin. If the whales arrive and do not avoid the lagoon because of human activities, we predict a dramatic change in the bottom communities of San Quintin. A small group of whales might spend much of the winter and spring feeding in San Quintin. Like the relatively small feeding areas along the coast of British Columbia, San Quintin could become a regular stopping place for certain individuals. There may be equally suitable areas for feeding around the Gulf of California, where gray whales were known to breed in the past (Gilmore et al. 1967). While these local patches of prey may be unimportant to the entire population, they may become important to certain individuals. Relatively few feeding gray whales could have considerable effects on local benthic habitats, and could produce long-term patterns of bottom population and community change.

ACKNOWLEDGMENTS

We are very grateful for the considerable support of Lloyd Lowry, Robert Nelson, and Kathy Frost (Alas-

³Hans Nelson and Kirk Johnson, U.S. Geological Survey, Menlo Park, CA 94025, pers. commun. August 1982.

⁴J. Hudnall showed underwater slides and a movie of feeding excavations and behavior at the 4th Biennial Conference on the Biology of Marine Mammals, San Francisco, Calif., December 14-18, 1981.

⁵J. Darling reported, at the 4th Biennial Conference on the Biology of Marine Mammals in San Francisco, Calif., December 14-18, 1981, that K. Norris and students collected this sample near the Bamfield Marine Station, British Columbia.

ka Department of Fish and Game). Luis Fleisher and his colleagues kindly helped provide access to the calving lagoons (Permiso No. 2 de Investigacion Cientifica, 1981). The field work in Baja California depended on our coworkers, James Oakden and Linda Martin. Paul Dayton, Glenn VanBlaricom, and Lloyd Lowry introduced us to the feeding ecology of gray whales and stimulated many ideas. Sheila and Alan Baldridge generously contributed to almost all aspects of our studies. Sandy Strause and Lynn McMasters drew the figures and Rosie Stelow typed the manuscript. The American Cetacean Society, World Wildlife Fund, and National Science Foundation (DPP 8121722) provided essential funds and encouragement. Collection of the 1980 Bering Sea data was funded by the Outer Continental Shelf Environmental Assessment Program, Juneau Project Office (principal investigators Mary Nerini, Howard Braham, and Linda Jones, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle, Wash). The manuscript was improved by comments from Glenn VanBlaricom, Bernd Wursig, and Kathy Frost.

LITERATURE CITED

- ALTON, M. S.
1974. Bering Sea benthos as a food resource for demersal fish populations. In D. W. Hood and E. J. Kelley (editors), *Oceanography of the Bering Sea*, p. 257-277. Inst. Mar. Sci., Univ. Alaska, Fairbanks, Occas. Publ. No. 2.
- ANDREWS, R. C.
1914. Monographs of the Pacific cetacea. I. The California gray whale (*Rhachianectes glaucus* Cope). Mem. Am. Mus. Nat. Hist. (New Ser.) 1:227-287.
- BARNARD, J. L.
1969. The families and genera of marine gammaridean amphipoda. U.S. Natl. Mus. Bull. 271:1-535.
1970. Benthic ecology of Bahia de San Quintin Baja California. Smithsonian. Contrib. Zool. 44:1-60.
- BOGOSLOVSKAYA, L. S., L. M. VOTOGROV, AND T. N. SEMENOVA.
1981. Feeding habits of the gray whale off Chukotka. Rep. Int. Whaling Comm. 31:507-510.
- BOUSFIELD, E. L.
1973. Shallow-water gammaridean Amphipoda of New England. Cornell Univ. Press, Ithaca, 312 p.
- DARLING, J.
1977. The Vancouver Island gray whales. J. Vancouver Aquarium 2:5-19.
- FROST, K. J., AND L. F. LOWRY.
1981. Foods and trophic relationships of cetaceans in the Bering Sea. In D. W. Hood and J. A. Calder (editors), *The eastern Bering Sea shelf: oceanography and resources*, Vol. 2, p. 825-836. Univ. Wash. Press, Seattle.
- GILMORE, R. M.
1961. The story of the gray whale. 2d ed. Privately publ., San Diego, 16 p.
- GILMORE, R. M., R. L. BROWNELL, JR., J. G. MILLS, AND A. HARRISON.
1967. Gray whales near Yavaros, southern Sonora, Golfo de California, Mexico. Trans. San Diego Soc. Nat. Hist. 14:197-204.
- GORSLINE, D. S., AND R. A. STEWART.
1962. Benthic marine exploration of Bahia de San Quintin, Baja California, 1960-61. Marine and quaternary geology. Pac. Nat. 3:282-319.
- GREGORY, M. R., P. F. BALLANCE, G. W. GIBSON, AND A. M. AYLING.
1979. On how some rays (Elasmobranchia) excavate feeding depressions by jetting water. J. Sediment. Petrol. 49:1125-1130.
- HARRISON, C. S.
1979. The association of marine birds and feeding gray whales. Condor 81:93-95.
- HOWARD, J. D., T. V. MAYOU, AND R. W. HEARD.
1977. Biogenic sedimentary structures formed by rays. J. Sediment. Petrol. 47:339-346.
- HOWELL, A. B., AND L. M. HUEY.
1930. Food of the gray and other whales. J. Mammal. 11:321-322.
- LARSEN, M. C., C. H. NELSON, AND D. R. THOR.
1981. Sedimentary processes and potential geological hazards on the sea floor of the northern Bering Sea. In D. W. Hood and J. A. Calder (editors), *The eastern Bering Sea shelf: oceanography and resources*, Vol. 1, p. 247-261. Univ. Wash. Press, Seattle.
- LOWRY, L. F., AND K. J. FROST.
1981. Feeding and trophic relationships of phocid seals and walruses in the eastern Bering Sea. In D. W. Hood and J. A. Calder (editors), *The eastern Bering Sea shelf: oceanography and resources*, Vol. 2, p. 813-824. Univ. Wash. Press, Seattle.
- MIZUE, K.
1951. Gray whales in the East sea area of Korea. Sci. Rep. Whales Res. Inst. (Tokyo) 5:71-79.
- MOORE, S. E., AND D. K. LJUNGBLAD.
In press. Gray whale (*Eschrichtius robustus*) in the Beaufort, Chukchi, and Northern Bering Seas: Distribution and sound production. In M. L. Jones, S. Swartz, and S. Leatherwood (editors), *The gray whale*. Academic Press, N.Y.
- NEIMAN, A. A.
1963. Quantitative distribution of benthos on the shelf and upper continental slope in the eastern part of the Bering Sea. In Soviet fisheries investigations in the northeast Pacific, Part I, p. 143-217. (Transl. from Russian by Israel Prog. Sci. Transl., 1968.)
- NELSON, C. H.
1982. Late Pleistocene-Holocene transgressive sedimentation in deltaic and non-deltaic areas of the northeastern Bering epicontinental shelf. Geol. Mijnbouw 61:5-18.
- NELSON, C. H., D. R. THOR, M. W. SANDSTROM, AND K. A. KVENVOLDEN.
1979. Modern biogenic gas-generated craters (sea-floor "pockmarks") on the Bering Shelf, Alaska. Geol. Soc. Am. Bull. 90:1144-1152.
- NERINI, M. K.
In press. A review of the gray whale feeding ecology. In M. L. Jones, S. Swartz, and S. Leatherwood (editors), *The gray whale*. Academic Press, N.Y.

- NORRIS, K. S., R. M. GOODMAN, B. VILLA-RAMIREZ, AND L. HOBBS.
1977. Behavior of California gray whale, *Eschrichtius robustus*, in southern Baja California, Mexico. *Fish. Bull., U.S.* 75:59-172.
- NORRIS, K. S., B. VILLA-RAMIREZ, G. NICHOLS, B. WURSIG, AND K. MILLER.
In press. Lagoon entrance and other aggregations of gray whales, *Eschrichtius robustus*. In R. Payne (editor), AAAS 1980 Symposium Proceedings on Whales. Westview Press, Boulder, Colo.
- OLIVER, J. S., P. N. SLATTERY, L. W. HULBERG, AND J. W. NYBAKKEN.
1980. Relationships between wave disturbance and zonation of benthic invertebrate communities along a subtidal high-energy beach in Monterey Bay, California. *Fish. Bull., U.S.* 78:437-454.
- OLIVER, J. S., P. N. SLATTERY, E. F. O'CONNOR, AND L. F. LOWRY.
1983. Walrus feeding in the Bering Sea: A benthic perspective. *Fish. Bull., U.S.* 81(3): 501-512.
- PHLEGER, F. B., AND G. C. EWING.
1962. Sedimentology and oceanography of coastal lagoons in Baja California, Mexico. *Geol. Soc. Am. Bull.* 73:145-181.
- PIKE, G. C.
1962. Migration and feeding of the gray whale (*Eschrichtius gibbosus*). *J. Fish. Res. Board Can.* 19:815-838.
- PIKE, G. C., AND I. B. MACASKIE.
1969. Marine mammals of British Columbia. *Fish. Res. Board Can., Bull.* 171, 54 p.
- RAY, G. C., AND W. E. SCHEVILL.
1974. Feeding of captive gray whale, *Eschrichtius robustus*. In W. E. Evans (editor), *The California gray whale*, p. 31-38. *Mar. Fish. Rev.* 36(4).
- REIMNITZ, E., P. W. BARNES, L. J. TOIMIL, AND J. MELCHOIR.
1977. Ice gouge recurrence and rates of sediment reworking, Beaufort Sea, Alaska. *Geology* 5:405-408.
- RICE, D. W., AND A. A. WOLMAN.
1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). *Am. Soc. Mammal., Spec. Publ.* 3, 142 p.
- SCAMMON, C. M.
1874. *The marine mammals of the north-western coast of North America*. John H. Carmany and Company, San Franc., 319 p.
- SHMIDT, P. YU.
1950. Fishes of the Sea of Okhotsk. *Acad. USSR Trans. Pac. Comm.*, Vol. 6, 370 p. (Transl. from Russian by Israel Prog. Sci. Transl., 1965, 392 p.)
- SPRAGUE, J. G., N. B. MILLER, AND J. L. SUMICH.
1978. Observations of gray whales in Laguna de San Quintin, northwestern Baja California, Mexico. *J. Mammal.* 59: 425-427.
- STOKER, S.
1978. Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi Seas. Ph.D. Thesis, Univ. Alaska, 259 p.
1981. Benthic invertebrate macrofauna of the eastern Bering/Chukchi continental shelf. In D. W. Hood and J. A. Calder (editors), *The eastern Bering Sea shelf: oceanography and resources*, Vol. 2, p. 1066-1091. Univ. Wash. Press, Seattle.
- SUND, P. N.
1975. Evidence of feeding during migration and of an early birth of the California gray whale (*Eschrichtius robustus*). *J. Mammal.* 56:265-266.
- THOR, D. R., AND C. H. NELSON.
1981. Ice gouging on the subarctic Bering shelf. In D. W. Hood and J. A. Calder (editors), *The eastern Bering Sea shelf: oceanography and resources*, Vol. 1, p. 279-291. Univ. Wash. Press, Seattle.
- TOMLIN, A. G.
1957. Cetacea. In V. G. Heptner (editor), *Mammals of the USSR and adjacent countries*, Vol. 9, 756 p. *Izd. Akad. Nauk-SSSR, Mosc.* (Transl. from Russian by Israel Prog. Sci. Transl., 1967.)
- VANBLARICOM, G. R.
1982. Experimental analyses of structural regulation in a marine sand community exposed to oceanic swell. *Ecol. Monogr.* 52:283-305.
- WALKER, T. J.
1975. *Whale primer*. Cabrillo Hist. Soc., San Diego, 65 p.
- WELLINGTON, G. M., AND S. ANDERSON.
1978. Surface feeding by a juvenile gray whale, *Eschrichtius robustus*. *Fish. Bull., U.S.* 76:290-293.
- WILIMOVSKY, N. J.
1974. Fishes of the Bering Sea: the state of existing knowledge and requirements for future effective effort. In D. W. Hood and E. J. Kelley (editors), *Oceanography of the Bering Sea*, p. 243-256. *Inst. Mar. Sci., Univ. Alaska, Fairbanks, Occas. Publ. No. 2.*
- WILKE, F., AND C. H. FISCUS.
1961. Gray whale observations. *J. Mammal.* 42:108-109.
- ZENKOVICH, B. A.
1934. Research data on cetacea of far eastern seas (the California gray whale, *Rhachianectes glacius* Cope). *Bull. Far East Branch Acad. Sci. USSR* 10, 9-25. (M.S. private transl. from Russian, 33 p.)
- ZIMUSHKO, V. V., AND S. A. LENSKAYA.
1970. Feeding of the gray whale (*Eschrichtius gibbosus* Erx.) at foraging grounds. *Ekologiya* 1(3):26-35. (Transl. from Russian by Consultants Bureau, Plenum Publ. Corp., 1971.)
- ZIMUSHKO, V. V., AND M. V. IVASHIN.
1980. Some results of Soviet investigations and whaling of gray whales (*Eschrichtius robustus*, Lilljeborg, 1961). *Rep. Int. Whaling Comm.* 30:237-246.