mammals when different methods are used. To complicate the picture further, Riggs (1960), using a buffered system at a pH of 7.4, observed that animals of varying size had identical P_{50}'s at that pH.

In order to make meaningful evaluations of the dissociation curves in marine mammals, the in vivo P_{CO_2} and pH need to be determined. Rieu and Hamar (1968) point out the difficulties of drawing a representative arterial blood sample although these arterial data have been collected from one species, *Tursiops truncatus*, by Ridgway (1968). In short, more work needs to be done.

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MFR PAPER 1053

Feeding of a Captive Gray Whale, *Eschrichtius robustus*

G. CARLETON RAY and WILLIAM E. SCHEVILL

ABSTRACT

The feeding of a captive yearling female Eschrichtius robustus *was observed while diving with her as well as from the surface. She sucked food off the bottom while swimming tipped over about 120° so that her cheek was nearly parallel to the bottom. An increase in mouth volume is apparently caused by action of the tongue, resulting in strong suction, during which the lower lip is opened and food enters the mouth. How food is separated from water and mud or detritus is not known. The observed behavior is probably natural and illuminates earlier records of stomach contents, external markings, and asymmetrical baleen. Clearly, much needs to be learned about the mechanism of feeding of baleen whales. This species' feeding habits may be unique among them.*

INTRODUCTION

Observations on the food of *Eschrichtius robustus* (Lilljeborg, 1861), the gray whale, have been summarized by Zimushko and Lenskaya (1970) and Rice and Wolman (1971), indicating that the diet consists predominantly of benthic animals, mostly amphipods and a few other crustaceans; incidental items include polychaete worm tubes, shells, gastropod opercula, feathers, kelp, bits of wood, sand, mud, and gravel. Tomilin (1957, p. 346-347) suggests that *Eschrichtius*

Figure 1.—*Eschrichtius robustus* calf, Gigi, in Sea World tank, tilted to her right, with water (and some squid near rear end) pouring into her mouth. One block of frozen squid is over the forward end of her mouth. Note open blowholes. Photograph by W. E. Schevill.

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is to some extent vegetarian (which would make it a most exceptional cetacean), supposing that seaweed found in the stomach is food and not merely incidentally swallowed. Howell and Huey (1930) found the planktonic *Euphausia pacifica* in the baleen of a gray whale taken off northern California on 21 July 1926. Gilmore (1961, p. 11) gives a winter observation of presumed feeding by gray whales, "criss-crossing thru a dense school of small fish, like anchovies, off San Diego," and Ken Balcomb (pers. comm.) informs us that a gray whale beached 15 miles north of Grays Harbor, Wash., in April, had a gullet packed with several gallons of *Osmerus mordax* (rainbow smelt). It would appear that *Eschrichtius* is not limited to eating small benthic crustaceans, but will also eat a variety of other food as opportunity offers.

Gray whales seem to do most of their feeding in the Bering and Chukchi Seas (Pike, 1962, p. 831-832). Rice and Wolman (1971, p. 24-25) conclude that all organisms found in the stomachs of gray whales killed on the Arctic summer grounds are "infaunal benthic species." They state that 95 percent of the food species found in one Bering Sea sample were gammaridean amphipods 6 to 25 mm long, and that the predominant species from this sample, *Ampelisca macrocephala*, "occurs mainly *on* sandy bottoms at depths of 5 to 300 meters" (italics ours). Zimushko and Lenskaya (1970) say that gray whales feed on nectobenthos, some 70 species in all, but that only six species of amphipods are of primary importance. We assume that though such active creatures as amphipods may be infaunal at times, their well-known tendency, when disturbed, to move just off the bottom, would make them readily available to a sweeping whale. One of us (Ray) observed this amphipod behavior from a submersible in the Bering Sea in 1972. Nemoto (1959) has discussed probable feeding behavior of whales in the light of mouth shape and baleen characteristics. During the last century many authors have alluded to gray whales surfacing with mud visible on the beak or other dorso-lateral parts. Pike (1962, p. 823) cites a particularly illuminating communication from Dr. F. H. Fay, who mentions a gray whale supposed to be feeding in 5 fathoms: "As this whale surfaced close to the vessel, mud was seen washing from its back." Although Tomilin (1957, p. 347) supposes that these whales may actually dig their mouths into the bottom, scooping and plowing, it seems to us (see below) that their behavior and anatomy are better adapted to sweeping the bottom than for digging; this accords well with the evidence of asymmetrical barnacle infestation and baleen wear reported by Kasuya and Rice (1970).

The gray whale calf, Gigi, which was captured in March 1971 and kept by Sea World, San Diego, was initially fed an artificial diet, but was soon taught to eat full-grown squid, *Loligo opalescens*. By the time of our observations (28 January-1 February and 11 March 1972), her daily diet was 900 kg of squid, dropped frozen into her tank in 9 kg blocks, and her weight gain was almost 40 kg a day. Our behavioral observations were made both from the water's surface and by scuba-diving with Gigi. We also used underwater motion pictures made by John Seeker of Sea World when Gigi was about 6 months old. To aid in our interpretation, we have consulted her trainers (Bud Donahoo and Susan Bailey), and we have solicited observations on Gigi and on other gray whales from several of our colleagues. To them, who are mentioned below, to the Naval Undersea Center, and to the management of Sea World, we are grateful.

BEHAVIORAL OBSERVATIONS

Before detailing our observations, we remind the reader that a gray whale's head is roughly triangular in cross section, the gular region being the base while the cheeks form the sides, sloping inwards at about 60° towards the narrow beak-like upper jaw. The curved mouth is at about the middle of the cheeks. The mouth has effectively only lower lips; the upper lips are represented by the rabbet-like recess above the gum line into which the lower lips fit snugly.

In the course of teaching Gigi to eat squid, trainers Donahoo and Bailey taught her to relax the edge of the left lower lip and turn it outward in response to light taps on the head. Food was placed by hand in the opening thus created, passing into the throat either through or under the baleen. This was in contrast to the feeding of the artificial liquid diet, when the jaws were opened while accepting the feeding tube; during the hand-feeding of squid, the jaws remained closed and the lip was opened, as was also the case later on when one of us thrust an arm down her pharynx. Training Gigi to move her lip voluntarily was critical, for normally the lip was held so tightly shut that a man could not forcibly pry it open. This training was done while she was grounded in the tank almost empty of water; it was not long before she would thus accept food while swimming. Soon thereafter she was feeding freely without the aid of her trainers. Gigi was always fed from the left side (Donahoo has mentioned having been

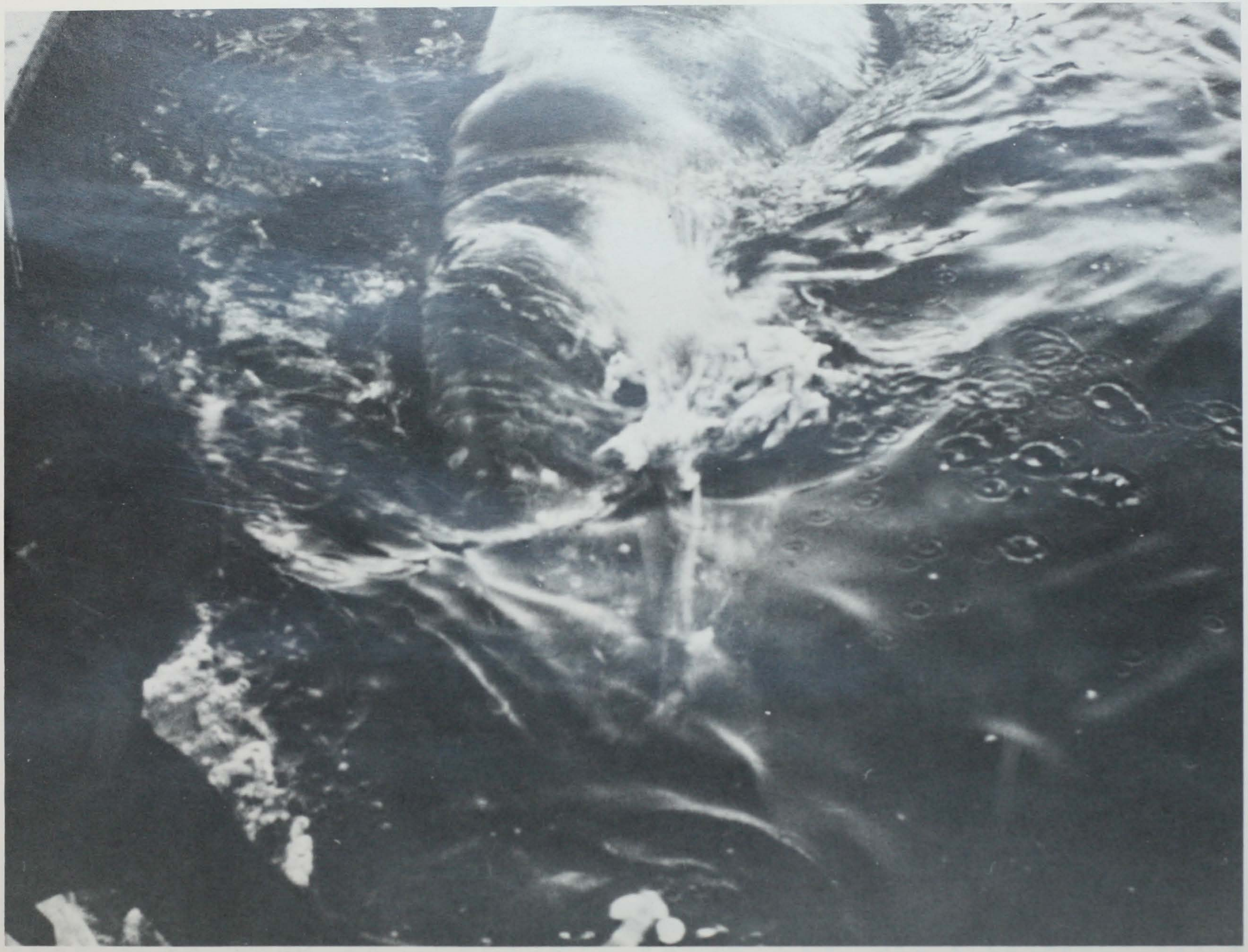

Figure 2.—Gigi, tilted to her right, jetting water upward as she makes noisy pulses while nibbling at a block of frozen squid (near end of mouth). Photograph by W. E. Schevill.

Figure 3.—*Eschrichtius robustus* calf, Gigi, in Sea World tank, tilted on her left side (top of head toward viewer), sweeping over bottom in general direction of arrow. Note open right lip and shut jaws. Photograph by G. C. Ray.

Figure 4.—Gigi, tilted on her left side (throat toward viewer), sweeping over the bottom of her tank in the direction of the arrow. Note expanded gular region indicated by the gular grooves. Photograph by G. C. Ray.

a horseman before becoming acquainted with whales), which may account for the left-sided sweeping behavior described below; Kasuya and Rice (1970) reported that of 34 gray whales that they investigated, 31 were right-sided.

We observed that the edges of the lips could be turned out and down through about 60°, either one or both sides at a time. Motion pictures further show a fluttering of the posterior part of this edge during hand-feeding, especially near the major flexure.

Voluntary feeding was as follows: The frozen blocks of squid floated at the surface and, as they thawed, the squid mostly sank slowly to the bottom. Gigi often "nibbled" at the thawing corners of the blocks, using the left side of her mouth and usually, but not always, holding the block at about the place where the fluttering had been noted. The nibbling was occasionally accompanied by a noisy pulsation called "earthquaking" by the trainers, and splashing or jetting of water and air for nearly half a meter (Figures 1 and 2). The jet was usually at this same place near the after end of the mouth, but it sometimes ran nearly the entire length of the baleen (not quite to the forward end of the mouth). Often the jetting was on both sides of the mouth. When Gigi's mouth was at the surface, air was involved in the jetting, but not always when her mouth was completely submerged, and not at all when she was on the bottom of the tank. We assume that this air was adventitiously taken in, as in eating soup.

After most of the squid had fallen to the bottom of the tank, Gigi's behavior altered markedly. As she approached them, she would roll over toward her back some 120°, so that her cheek was nearly parallel to the bottom and about 10-20 cm above it. As she swam over the squid, she left a clean swath 30-50 cm wide. It was apparent that the squid were being sucked up in a sort of pulsation, as some squid briefly reappeared after their first disappearance into her mouth. It is presumed that she could easily see the squid lying in her path. In the cylindrical tank she described a track slightly dorsad of straight ahead, so that she swept over the squid at about a 30° angle to the mouth (Figures 3 and 4). Then three separate actions were seen: (1) an opening of the edge of the mid to posterior part of the left lip so as to fold it away from the baleen, (2) a swelling of the gular region and expansion of the gular grooves (Figure 4), and (3) an opening of the right side of the mouth, during which squid were sometimes jetted out. The third item may merely mean that it is easier to open both sides of the mouth symmetrically, though Gigi had showed us that she could flex her lips one side at a time. Since we could not see all these parts of the whale at once, we can only infer the presumable sequence of these related events. Then Gigi righted herself and swam away; sometimes turbid jets could be seen pulsing from both sides of her mouth.

ANATOMICAL INTERPRETATION

Our understanding of the mechanisms involved is hampered by our ignorance of the myology and other soft anatomy of this species. We have been able to find only osteological anatomical descriptions and have had no carcass available for even rough dissection. W. C. Cummings and J. Sweeney made, on our account, some exploratory sections of the lower lips of dead neonates found on the beaches of Laguna Ojo de Liebre, Baja California, and found them to be well muscled. D. W. Rice reminds us that the tongue is also well muscled, much more so than in *Balaenoptera;* it is well figured and described by Andrews (1914, p. 254, pl. 21, fig. 4, and pl. 22, fig. 6).

All this, as well as observations of behavior, strongly indicates that the gray whale's oral anatomy is adapted for suction and that motion of the lips is voluntary. We had but limited opportunity to manipulate Gigi's mouth ourselves; one of us (Schevill) had his arm in her mouth several times while she was "earthquaking" and could feel no motion at all of the tongue and only a slight agitation near the larynx. But W. E. Evans (in litt.) states that "the tongue cannot be pulled back and forth very easily; however, it can be raised high, displacing a reasonably good percentage of the volume of the mouth cavity". Donahoo had his hand in Gigi's mouth repeatedly; both he and Evans have emphasized the tongue's strength and mobility. Donahoo asserts that it moves so as virtually to vacate the oral cavity and that this involves a shape change. He further asserts that the shape change travels rearward and that this movement of the "ball" of the tongue can be seen from outside, as the gular grooves expand. This posteriorly moving expansion of the gular region was also seen by one of us (Ray) underwater. Further, Donahoo said that as the tongue moves back, a strong inflow appears at the outfolded lip. He added that Gigi's feeding was not simply accepting, but quite selective. When presented a mixture of squid, "Pacific mackerel" (chub mackerel, *Scomber japonicus*), and "whitebait" (probably jacksmelt, *Atherinopsis californiensis*, or topsmelt, *Atherinops affinis*), all three were sucked from the bottom, but only squid were retained, the others being rejected.

CONCLUSIONS

Nothing benthic of the size of squid has been reported in the diet of *Eschrichtius*, so we should be cautious in interpreting this captive's feeding style as indicative of natural behavior of the species, bearing in mind that Gigi was completely isolated from her kind throughout captivity. Nevertheless, her bottom-sweeping habit we suppose may be natural, since it appears appropriate for catching the animals that comprise the recorded natural food of this species of whale. Our captive's habit of sweeping a few centimeters off the smooth tank bottom does not deny the probability that sweeping a soft or irregular bottom at sea could get mud on the sweeper's back (cf. Fay in Pike, 1962, p. 823), especially if the prey is actually benthic.

Cetological literature is full of poorly supported conjecture, and we hesitate to add more. Although we have learned a number of things from the captive Gigi, there is still much unknown. For one thing, her jetting water in pulses from a particular restricted part of her mouth seems to imply, perhaps, a special activity of the tongue. Furthermore, we do not understand the mechanics of the hydraulics that bring the food-bearing water into the mouth. This is no mystery in whales that swim along with the mouth wide open, but it is not so obvious in a whale which swims along rather slowly with only a narrow slit open, as did our *Eschrichtius*. Here it seems necessary to increase the volume of the mouth to cause useful inflow of water. We are handicapped by our imperfect understanding of the functions of the muscular tongue. W. E. Evans (pers. comm.) has told us that Gigi's tongue once pressed his hand painfully hard against her palate. Such pressure might serve to push the gular region downward, enlarging the mouth cavity, and this idea fits with the observations of Donahoo and Ray of the migrating tongue-bulge visible from beneath.

Thus we suppose, from the assorted evidence, the following concatenation of events in feeding: First the whale rolls over far enough so that the cheek is about parallel with the bottom, and the lip is opened as the tongue, pressing against the palate, pushes the gular region away so that it expands, producing an inflow which brings in the epibenthic food. Then the tongue relaxes and the gular musculature tightens, reducing the size of the mouth cavity and expelling water; the food is trapped in the baleen fringes. We do not know exactly what happens next; perhaps a slight renewed suction of water removes the food from the baleen fringes, and swallowing presumably follows.

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MFR PAPER 1054

Sounds Produced by the Gray Whale, *Eschrichtius robustus*

JAMES F. FISH, JAMES L. SUMICH, and GEORGE L. LINGLE

ABSTRACT

Underwater sounds produced by a young captive gray whale are described. A "metallic-sounding pulsed signal," consisting of 8 to 14 pulses in bursts lasting up to 2 sec was the most common vocalization. Other sounds included a low-frequency "growl" or "moan," similar to a sound recorded from gray whales at sea; a short, broadband, "gruntlike" sound; a low-pitched "blowhole rumble"; and a long "metallic-sounding pulse train" that merged into a low-frequency "groan." The sounds could not be correlated with specific behaviors. Also described are "clicks" recorded in the presence of the whale when she was returned to sea and similar "clicks" recorded from gray whales in Wickaninnish Bay, Vancouver Island, Canada.

This report describes a variety of sounds recorded from Gigi, a young gray whale, *Eschrichtius robustus*, while she was in captivity at Sea World, a marine park in San Diego, Calif., and sounds recorded in the vicinity of the whale when she was returned to the ocean nearly a year later. Also described are the sounds recorded in the presence of gray whales in Wickaninnish Bay, Vancouver Island, Canada.