FEEDING BEHAVIOR OF THE HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, IN THE WESTERN NORTH ATLANTIC

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ABSTRACT

Observations on the feeding behavior of the humpback whale, *Megaptera novaeangliae*, were made from aerial and surface platforms from 1977 to 1980 in the continental shelf waters of the northeastern United States. The resulting catalog of behaviors includes two principal categories: Swimming/lunging behaviors and bubbling behaviors. A behavior from a given category may be used independently or in association with others, and by individual or groups of humpbacks.

The first category includes surface lunging, circular swimming/thrashing, and the "inside loop" behavior. In the second category, a wide variety of feeding-associated bubbling behaviors are described, some for the first time. The structures formed by underwater exhalations are of two major types: 1) bubble cloud—a single, relatively large (4-7 m diameter), dome-shaped cloud formed of small, uniformly sized bubbles; and 2) bubble column—a smaller (1-1.5 m diameter) structure composed of larger, randomly sized bubbles, used in series or multiples. Both basic structures are employed in a variety of ways.

Many of these behaviors are believed to be utilized to maintain naturally occurring concentrations of prey, which have been identified as the American sand lance, *Ammodytes americanus*, and occasionally as herring, *Clupea harengus*.

This paper reports on the feeding behavior of the humpback whale, *Megaptera novaeangliae*, in the continental shelf waters of the northeastern United States. We describe several feeding behaviors reported for the first time, as well as a number of behaviors known from other areas but not previously reported for these waters. Our collective observations provide the beginning of a more complete catalog than has previously been available.

Early observations of humpback feeding behavior were made by Ingebrigtsen (1929) from the Norwegian Sea near Bear Island:

> "It [the humpback] employed two methods of capturing 'krill' when the latter was on the surface of the water. One was to lie on its side on the surface and swim round in a circle at great speed, while it lashed the sea into a foam with flukes and tail and so formed a ring of foam. The frightened 'krill' gathered together in the circle. This done the humpback dived under the foam-ring and a moment later came up in the center to fill its open mouth with 'krill' and water, after which it lay on its side, closed its mouth, and the catch was completed.
>
> "The other method was to go a short distance below the surface of the water, swimming in a ring while at the same time it blew off. The air rose to the surface like a thick wall of air bubbles and these formed the 'net'. The 'krill' saw this well of air bubbles, were frightened into the centre, and then the manoeuvre of the first method was repeated."

Some 45 yr later, "bubblenetting" was reported from Alaskan humpbacks by Jurasz and Jurasz (1978), and later described in detail (Jurasz and Jurasz 1979). With the exception of the work of Watkins and Schevill (1979), accounts of feeding behavior of this species in the waters of the western North Atlantic are few and largely anecdotal.

MATERIALS AND METHODS

Observations were made from dedicated aircraft (a Cessna 337 Skymaster and a Beechcraft AT-11[4]), from dedicated surface vessels (the 27.5 m *Dolphin III* and the 21.3 m *Tioga*), from platforms-of-opportunity, and from shore stations.

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[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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All data were collected by experienced observers. Photographs taken in both 35 mm and 70 mm format documented most observations, and were supplemented by written and occasionally tape-recorded field notes. From the aircraft, observers estimated the critical dimensions of feeding-associated structures with respect to references such as the whale's body or flipper length. From shipboard, more precise measurements were obtained through reference to known dimensions on the vessel, or to a 25 cm diameter fiberboard disk which had been deployed in the immediate vicinity of the whale.

RESULTS

Feeding behaviors were observed on more than 150 occasions in the period April 1977 to May 1980. Observations were made in the area of West Quoddy Head, Mt. Desert Rock, Stellwagen Bank, the waters east and southeast of Cape Cod, and southeast of Block Island (Fig. 1). Feeding, or apparent feeding, was reported for individuals and for groups of up to 20 whales.

Behaviors

Circular Swimming/Thrashing

On 2 December 1978, a single humpback whale was observed and photographed swimming in a broad (23 m) circle, roiling the surface as it swam. Tail slashing (a rapid sideways sweeping of the flukes) may have accompanied this behavior. Dense flocks of birds were present over the whale, and dolphins were present by the head and body. The presence of both of these feeding-associated elements, as well as the resemblance to observations by Ingebrigtsen (1929), suggested that feeding was taking place.

This initial observation was substantiated in May 1980 when a number of shipboard observations confirmed the behavior as feeding associated. An initial thrust of the flukes was followed by the whale's swimming in a broad circle, roiling the surface with flippers and flukes. This was followed in many, but not all, cases by a feeding rush through the circle. This behavior was repeated many times by a single animal over a period of several hours.

The circular swimming/thrashing behavior, observed on two occasions, each time involving a single whale, is considered relatively uncommon.

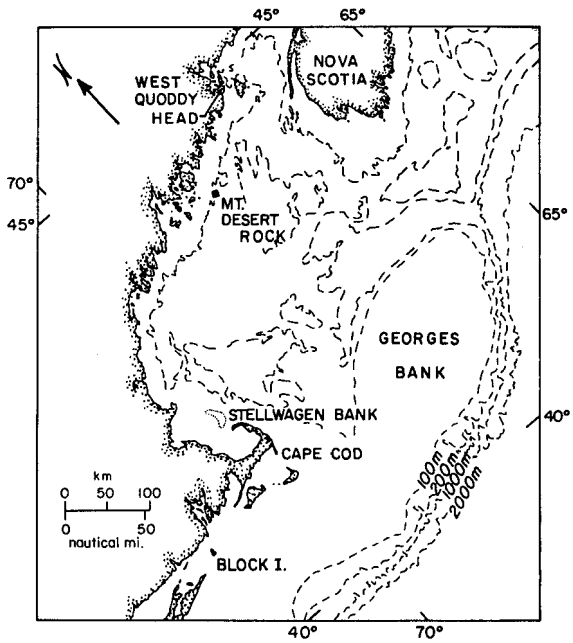

FIGURE 1.—Study area where observations of feeding behaviors were made. Place names on chart are those referred to in text.

Lunge Feeding

Lunge feeding is defined as an upward rush at the water surface with the longitudinal axis of the body intersecting the plane of the surface at an angle of 30°-90°. As the whale breaks the surface, the mouth is agape, and quite often a greatly distended throat region is seen. Up to one-third of the body length clears the surface before the whale falls or settles back into the water. Observations and photographs of prey at the surface, in the mouths of the whales, and picked up by closely associated birds leave no doubt that this is a capture mode of feeding behavior. This common behavior has been recorded in 21% of our feeding observations, from single animals as well as from groups. When several animals fed together, the lunges often were simultaneous and in close proximity (3 m). In several cases, two or more animals came in contact, bumping each other as they lunged. Bouts of lunge feeding may contain on the order of 20 lunges (3 animals in one case) in 25 min.

The speed at which the lunge takes place is highly variable. At times, the whale bursts through the surface in a vigorous upward rush. At other times, the rise to the surface and the subsequent extension of the rostrum and dis-

tended lower jaw above the surface are quite gradual. In several instances, humpbacks were observed feeding in this manner (the slow, gradual rise) in formation. Five or six whales arranged side by side and slightly staggered of one another acted in unison. This behavior has been similarly described from Alaskan waters and termed "echeloned" lunge feeding (Jurasz and Jurasz 1979).

Inside Loop Behavior

On 23 May 1980, a single humpback was observed feeding for over 1 h. The whale repeatedly displayed a behavior we have termed an "inside loop." As the whale begins a shallow dive, it sharply strikes the water's surface with its flukes. This action creates an area of turbulence in the water estimated to have an average diameter of 9 m. This area of foam and bubbles is seen clearly as the whale swims away at a shallow dive angle with the pectoral fins held horizontally. The whale, swimming rapidly, then rolls 180°, so that the white ventral surface of the flukes can be seen just below the surface. An inside loop (a sharp U-turn in the vertical plane) follows immediately, so that the whale is now swimming toward the area of turbulence. Finally, the whale is seen rising vertically in a slow lunge, with mouth widely agape, through the center of the turbulence created by the fluke slap. The horizontal distance covered by this "out-and-back" motion was on the order of 1½-2 body lengths of the whale. The behavioral sequence is illustrated diagrammatically in Figure 2.

Several variations on the basic behavior were observed. The humpback did not feed through the area of turbulence in every instance. Occasionally, the whale would surface to the side of the disturbance, not always feeding. On other occasions, a second whale would enter the general area and subsequently be seen lunge feeding through the disturbance created by the flukes of the first whale, either alone or in unison with the original whale.

The inside loop behavior, observed on a single occasion, involving a single whale later joined by a second, is at present considered relatively uncommon.

Bubbling Behaviors

Underwater exhalations or bubbling behaviors were seen in association with feeding, or apparent feeding, in 52% of our feeding observations. These exhalations appear to be of two major types, forming what we have termed "bubble columns" and "bubble clouds." In general, bubble columns and bubble clouds have been observed with about equal frequency.

BUBBLE COLUMNS.—Bubble columns are formed by the underwater exhalations of a whale swimming from 3 to 5 m (estimated) below the surface. As the bubble bursts are released, they rise vertically to the surface in the form of a somewhat ragged column. The columns are 1-2 m in diameter and are composed of random-sized bubbles estimated to be generally >2 cm. Series of from 4 to 15 bubble columns are used to form rows, semicircles, and complete circles or bubble nets (Figs. 3, 4).

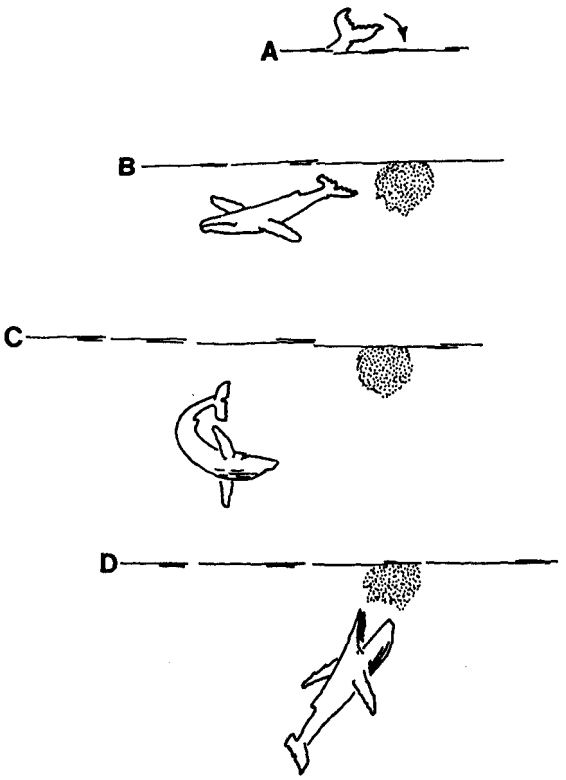

FIGURE 2.—"Inside loop" type of feeding behavior. A. Upon making a shallow dive, humpback whale strikes the surface sharply with flukes. B. Fluke slap creates an area of turbulence (foam/bubbles) as whale swims away in a shallow dive, flippers held horizontally. C. Whale executes a 180° roll and now does a sharp inside loop, or U-turn in the vertical plane. D. Whale lunge feeds through the area of disturbance created by original fluke slap.

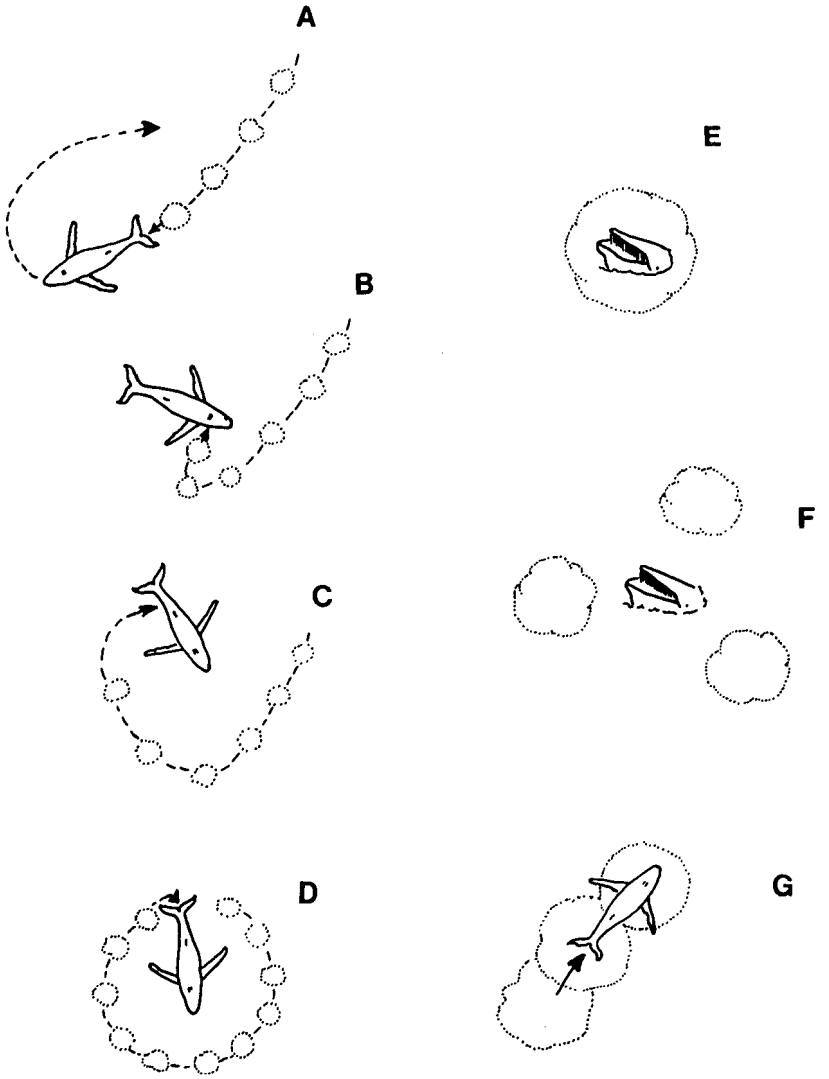

FIGURE 3.—The seven types of bubbling behaviors associated with feeding in humpbacks. A through D are structures using bubble columns, which are 1-1½ m in diameter and composed of nonuniform-sized bubbles (estimated at >2 cm). E through G are bubble cloud structures, 4-7 m in diameter, and composed of uniform-sized bubbles (estimated at <2 cm). A. Bubble row. B. Bubble row with "crook," whale feeding location shown. C. V or semicircle shaped bubble curtain. Whale feeds in and through open side of the semicircle. D. Complete circular formation, or bubble net. E. Single bubble cloud. In this example, one of several variations, whale lunge feeds through center. F. Triangular formation of multiple bubble clouds. G. Linear formation of multiple bubble clouds.

In the simplest configuration, bubble rows, the whale creates a line of columns (generally 4-6). When this has been completed, the whale turns sharply and feeds, open-mouthed, either at or below the surface, at an acute angle to the screen formed by the row of bubble columns. In some cases, the whale continues to release bubble bursts during its turn, so that the line of bubble columns has a "crook" in the end where the whale feeds. The behavior associated with a semicircle of bubble columns is similar, in that once a semicircle (or "V") has been constructed, the whale appears and feeds toward the concave portion of the screen.

Complete circles of bubble columns, termed bubble nets (Jurasz and Jurasz 1979), have been

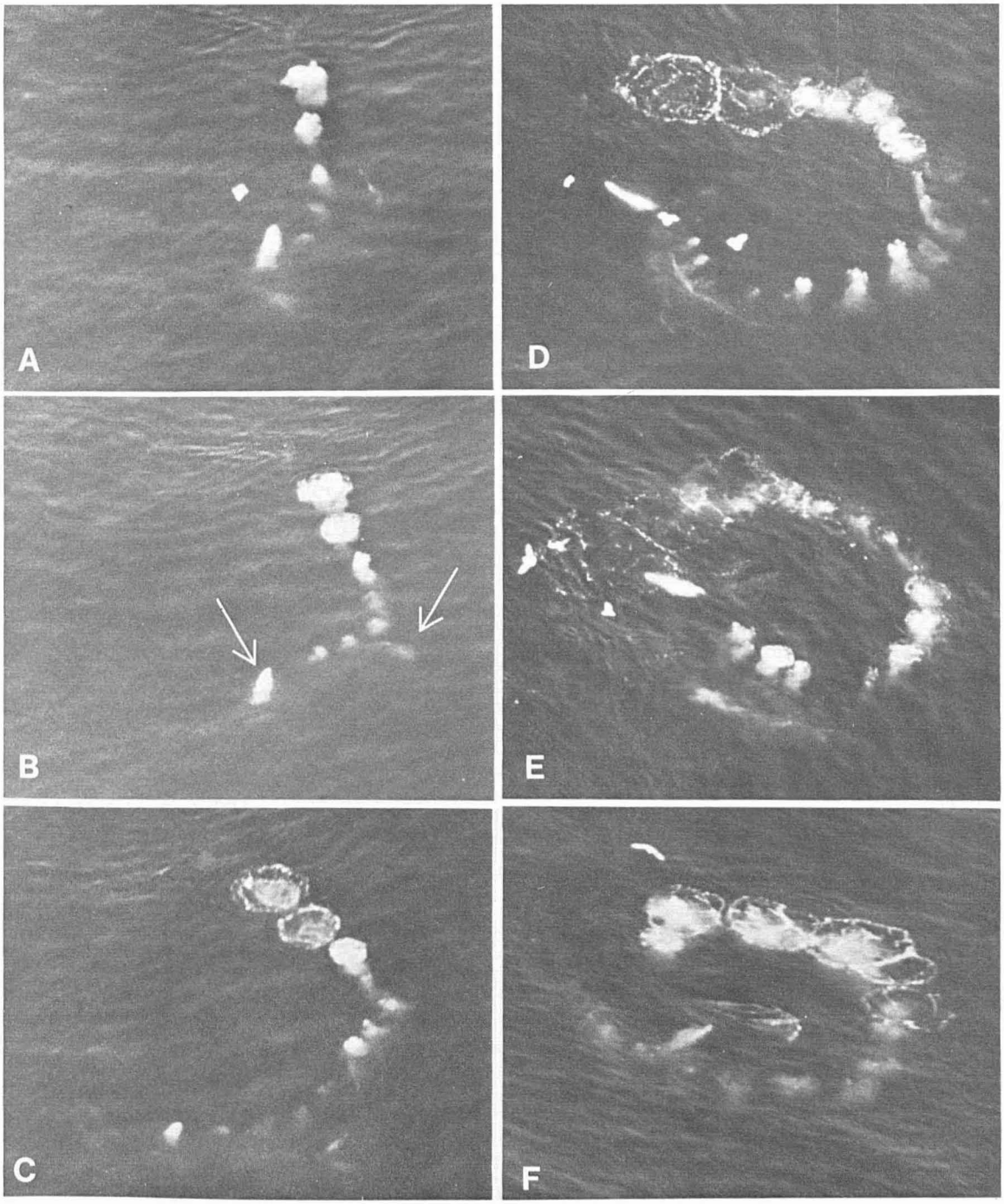

FIGURE 4.—Aerial views of bubble net construction by a humpback whale. A through E are 5 frames from a 29-frame sequence; F is from a sequence immediately following. Underwater exhalations are used to form a bubble net approximately 15 m in diameter, composed of some 15 individual bubble columns. Arrows in B indicate undersides of left pectoral fin and flukes. In A through C, whale is rotated on its longitudinal axis so that the blowhole and dorsal surface are toward the center of the circle. In D, whale turns sharply about on the right pectoral fin and prepares to pass through the center of the net. A stream of turbulence is seen trailing from the dorsal fin area, which is being sharply thrust to the whale's left. In E, the whale is seen in feeding posture, mouth agape, underwater in the center of the net. In F, the whale surfaces and blows weakly before exiting the area of the net. Photographs by S. Kraus.

seen on a relatively few occasions, approximately 8% of our observations. Our clearest observations have been from aircraft, particularly on 23 April 1979 when several sequences of bubble net formation were photographed (Fig. 4). The whale, maintaining its longitudinal body axis on a nearly horizontal plane, swims some 3-5 m (estimated) below the surface in a circular pattern. The dorsal surface (and blowhole) of the whale is rotated toward the center of the circle so that the flippers are oriented nearly in the vertical plane. As the whale swims in this manner, approximately 15 bubble bursts are released, which rise to the surface as columns and appear to form an effective corral. As the circle or net nears completion, the whale appears to pivot on the axis of the flippers. The flukes are thrust to the outside, and a stream of underwater turbulence is seen trailing from the region of the dorsal fin. The whale then banks to the inside and turns sharply into and through the center of the net—all below the surface of the water. The aerial photographs show apparent feeding, i.e., the mouth is agape and the lower jaw region is greatly distended. Only after this stage does the whale rise to the surface, pause, and blow one or more times before exiting the area of the bubble net. Measurements show the circle to be approximately equal in diameter to the whale's length—about 13-15 m. While bubble nets constructed in both the clockwise and counterclockwise directions have been observed, the clockwise direction appears to be more common.

There are several variations to the behavior described above. Shipboard observations in May 1980 showed that bubble nets are not restricted to 360° circles, but instead may include from 1¼-2 complete revolutions as the whale swims in a spiral of decreasing radius. Often, smaller bursts of smaller bubbles made up the greater portion of the outer ring, with the bursts and bubbles both increasing in size within the inner ring. Additionally, a line of bubbles 10-30 m in length would often directly precede the formation of the circular portion of the bubble net. This gave the overall structure the shape of a "6" or a "9." Finally, surface lunge feeding (gradual rise type), rather than underwater feeding, was reported from this series of shipboard observations.

BUBBLE CLOUDS.—Bubble clouds form the second major category of bubbling behaviors associated with feeding. There are several marked differences to the bubble columns described above. In this case, a single underwater exhalation forms a single, relatively large (4-7 m diameter), dome-shaped "cloud" made up of small (estimated to be <2 cm), uniformly sized individual bubbles (Fig. 5). In a few observations where we were able to see the early stages of bubble cloud formation, the cloud appeared quite narrow initially, about 2-3 m in diameter, but expanded as it rose toward the surface. In many observations, schools of American sand lance, *Ammodytes americanus*, were visible over wide areas in patches at the surface in the general area of feeding activity, but prior to the onset of any bubbling behavior in their immediate vicinity. In all observations, the whale dove out of sight to produce the bubble cloud which rose gradually toward the surface. The prey, appearing as a disturbance at the surface, would at times leap vigorously into the air when the bubble cloud surfaced into the school.

The subsequent appearance of the whale relative to the bubble cloud displayed a good deal of variation. Observations to date suggest five possible variations, as illustrated in Figure 6. When lunge feeding through the cloud's center was seen (Fig. 6A), the speed of the lunge was slower than lunge feeding observed in the absence of clouds. In the second type of behavioral sequence (Fig. 6B, the slow, horizontal appearance of the whale in the surfaced cloud), over 70 bubble cloud observations recorded from shipboard in 1978-79 suggest a repetitive, rigidly patterned activity composed of the following:

1) The whale sounds, usually with flukes in the air.

2) A cloud of bubbles appears beneath the sea surface up to 2½-3½ min after sounding.

3) The whale, not obviously swimming, rises slowly to the surface. Its back first appears in the center of the spent cloud of bubbles 5-9 s after the first bubbles in the cloud reach the surface.

4) Three to ten blows and slow, shallow diving precede the sounding dive which begins the next sequence.

In this common activity, the actual feeding probably takes place in the cloud and below the surface, with the whale's appearance marking the conclusion of the episode. Although no feeding is visible at the surface, the presence of a number of important elements (prey abundant in bubble clouds, similarity of structure to those in known

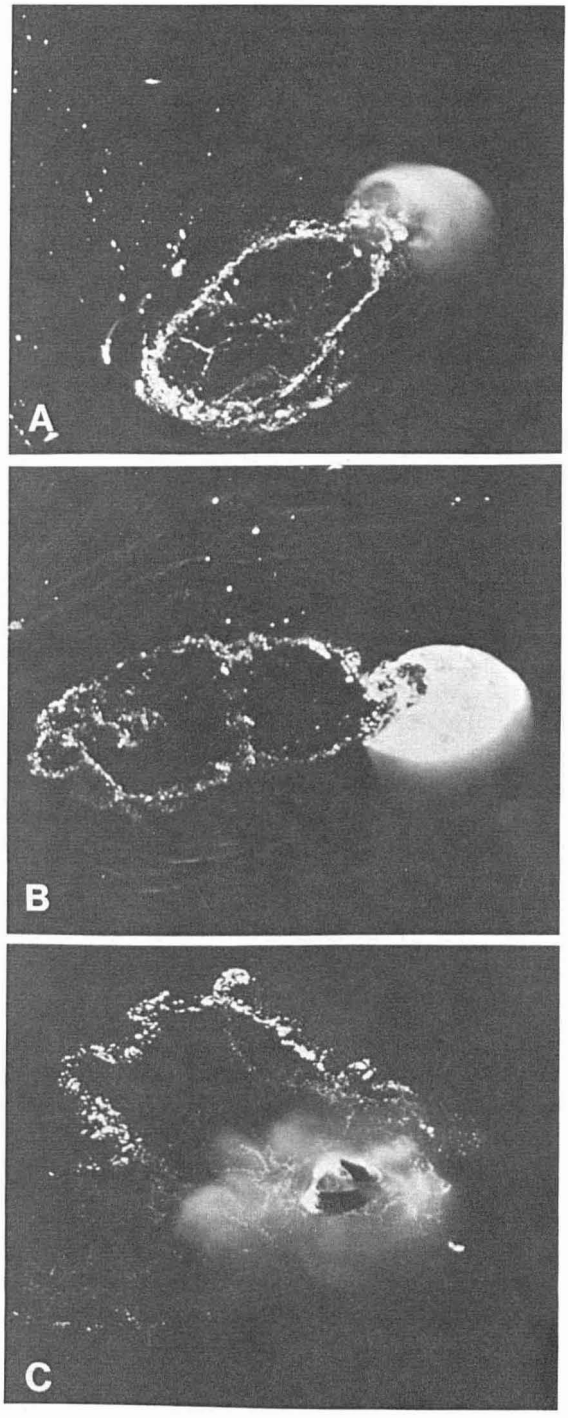

FIGURE 5.—Aerial views of bubble cloud formation and associated feeding. A. Dome-shaped bubble cloud, formed by underwater exhalation, seen rising toward surface. B. Bubble cloud after intercepting plane of surface—upper portion of structure is flattened. C. Lunge-feeding whale appears through center of bubble cloud. Photographs by A. Frothingham.

feeding events, repeated occurrence in known feeding areas, and the presence of feeding birds) is strongly suggestive of a feeding-associated behavior.

Bubble clouds were also observed being used in series or multiples. These clouds possess the characteristics described above but are used in groups, generally three, by one or more humpbacks. Two varieties have been seen (Fig. 3F, G): 1) individuals or groups of humpbacks blow clouds in either triangular or random patterns, and feed in the midst of the clouds or within a particular cloud—observed on a number of occasions and considered relatively common; and 2) an individual whale was seen to blow three linearly connected clouds, and then swim on the surface very slowly through the formation—observed on a single occasion and considered uncommon.

A final variation, which may or may not be directly associated with feeding, is poorly understood. At times, a lunge-feeding whale will exhale underwater, lunge feed to the surface, and be followed shortly by one to three bubble clouds appearing at the surface, closely adjacent to the whale but arriving at the surface after the whale instead of before, as described above.

Behavioral Strategies

It has been our experience that a given humpback whale will generally repeat a fairly rigid feeding pattern over a period of time. However, several individual humpbacks or groups of humpbacks feeding in the same area may or may not display the same feeding strategy. Several examples illustrate this observation.

In two instances on Stellwagen Bank in 1978, all humpback whales (five and seven individuals) within a 20 km^2 area displayed bubble cloud feeding (slow rise type) for an entire 1-h period of observation. Every whale in sight appeared to be using the same strategy.

During two of the three observation periods on one day in 1979, bubble clouds were formed by one individual in the vicinity of extensive schools of American sand lance, while three other whales were lunge feeding (no bubbling associated) several hundred meters away.

On a third occasion, a single humpback on the northern side of a school of American sand lance was observed forming bubble clouds (with apparent subsurface feeding), while three other animals, working the same school of American

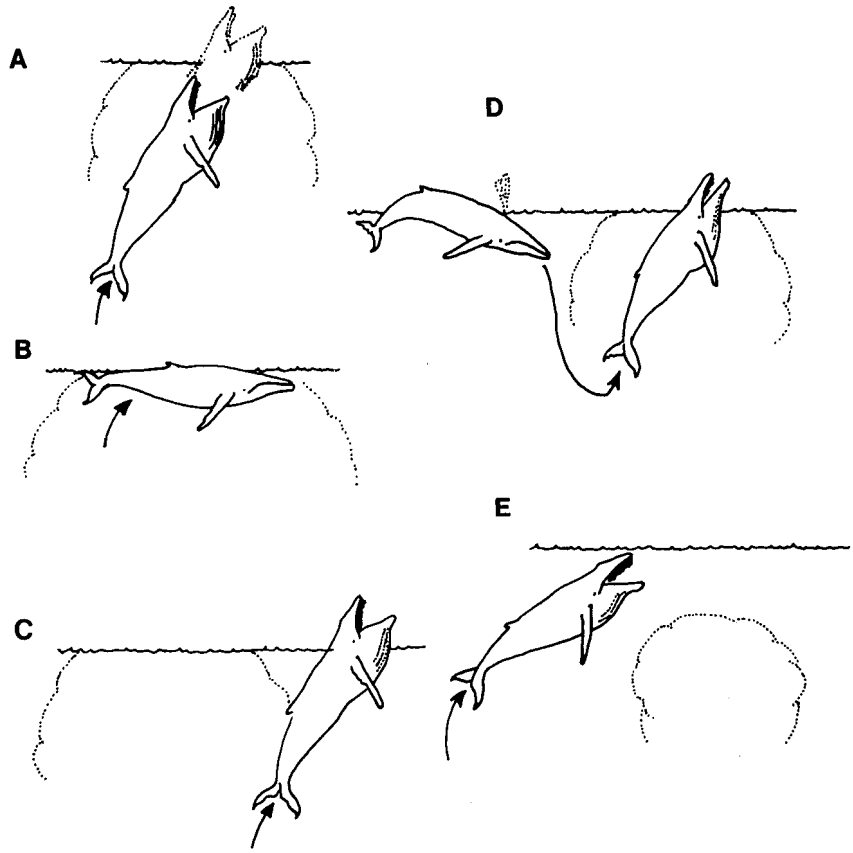

FIGURE 6.—The five feeding variations associated with bubble clouds. A. Whale lunge feeds vertically through the center of the cloud, as in Figure 5. B. Whale apparently feeds underwater and upon completion rises slowly through the center of the spent bubble cloud; the whale's body is on a horizontal plane and the mouth is not agape. C. Whale lunge feeds to one side of cloud. D. Whale surfaces alongside cloud, emits a weak blow, dives, and reappears lunge feeding through the center of the cloud. E. Whale swims vertically up alongside the rising cloud, and then passes horizontally, mouth agape, between the still-rising cloud and the water's surface.

sand lance, were generating bubbles in rows, as well as randomly, and lunge feeding.

Prey Species

Shipboard observations, primarily on Stellwagen Bank, provide direct visual and photographic evidence that concentrated schools of American sand lance are a frequent prey species in the area. American sand lance was identified in 50% of feeding events from the *Dolphin III* on Stellwagen Bank in 1978 and in 75% of observations in 1979. Photographs show American sand lance in the corners of the whale's mouth, being picked up by closely associated birds, and in concentrated surface schools in which the whale is feeding.

At least one other species is a target for humpback feeding. It appeared that humpbacks in the West Quoddy Head area took herring, *Clupea harengus*, close inshore and in coves, using the bubble cloud and lunge feeding techniques on a number of occasions.[5]

DISCUSSION

Humpback whales in the North Atlantic feed on a wide variety of prey species, with krill and schooling fishes the most important (Tomilin 1967). In Canadian waters, humpbacks feed heavily on capelin, with krill second in impor-

[5]S. K. Katona and P. V. Turnbull, College of the Atlantic, Bar Harbor, ME 04609, pers. commun. October 1980.

tance, although the data also suggest haddock, mackerel, whitefish, and sand lance (Mitchell 1973; Sergeant 1975[6]). The American sand lance has been suggested as a prey species in the Cape Cod area by Overholtz and Nicolas (1979). Our direct evidence confirms their observations and demonstrates the importance of this prey species in these waters. The sand lance is similar in size, summer habitat, and schooling behavior to the more northern capelin, *Mallotus villosus* (Overholtz and Nicolas 1979), and therefore may occupy a similar role in the diet of humpbacks in more temperate latitudes. Interestingly, Meyer et al. (1979) reported a significant increase in the relative abundance of sand lance since 1975 on Stellwagen Bank, a trend which was typical of the northwestern Atlantic from Cape Hatteras to the Gulf of Maine.

Indirect evidence suggests herring as a prey species in the northern Gulf of Maine. Watkins and Schevill (1979) also tentatively identified herring, along with pollock, *Pollachius virens*, from Cape Cod waters. These observations will require confirmation as additional knowledge on prey species in New England waters is gained.

With regard to the capture mode of feeding behavior, our observations on lunge feeding closely corroborate those of Watkins and Schevill (1979) and Jurasz and Jurasz (1979). The observations on underwater feeding by humpbacks were almost always in association with bubble structures, although Watkins and Schevill (1979) described several instances of underwater feeding in the absence of such structures.

"Apparent circling behavior" during feeding was reported by Watkins and Schevill (1979). Our description of what we term circular swimming/thrashing behavior expands somewhat on their observations. We speculate that the use of anatomical structures and swimming motion in the manner described bears some generic resemblance to the "flick feeding" reported from Alaskan waters by Jurasz and Jurasz (1979). This would seem to be particularly true for the inside loop behavior we have described. These behaviors may be placed together into a major subdivision of feeding behaviors, the various bubbling behaviors being the other major subdivision.

The effect of the whale's feeding behavior on the prey species, and the advantage conferred to the whale, remains a subject for conjecture, since few data are available. The bubbling behaviors are perhaps the most intriguing. Based on experiments with artificial bubble curtains, it is known that under certain circumstances, curtains of bubbles form an effective barrier to schooling fish (Brett and Alderdice 1958; Smith 1961; Bates and VanDerwalker 1964). Whatever the precise mechanism, it seems reasonable to conclude that humpback whale bubble nets can, and do, effectively corral schools of prey. Whether bubble nets concentrate the prey[7] or merely enclose and maintain naturally occurring concentrations of prey (as hypothesized here) can only be resolved by further study.

The humpback appears well suited to these behaviors; Edel and Winn (1978) have described in some detail the locomotion, maneuverability, and flipper movement required to execute the behaviors described here. It has been suggested (Howell 1970; Brodie 1977) that flashes from the long, white flippers are used to concentrate or herd the prey. This may play a role in the circling behavior, the bubble-netting, and perhaps other types of feeding. In the case of bubble-netting, in addition to their hydrodynamic function, the vertical orientation of the two extended flippers may act in unison with the bubble screen to help form the "curtain" which herds and/or entraps the prey.

While bubbling behavior appears to be commonly associated with feeding (52% of our feeding observations), some caution is in order. Underwater bubbling, even in the presence of feeding activity, may not always be directly related to feeding (see also Watkins and Schevill 1979). Underwater exhalations from humpbacks in nonfeeding situations have also been observed. On occasion, underwater exhalation by humpbacks when approached by ships has been recorded. From field observations and study of photographs, the possibility that some swimming and bubbling behavior may be "play" behavior, particularly when displayed in the presence of closely associated dolphins, is recognized. In the Pacific, Hubbs (1965) described underwater exhalations with no clearly apparent function, and Forestell and Herman[8] described the

[6]Sergeant, D. E. 1975. An additional food supply for humpback (*Megaptera novaeangliae*) and minke whales (*Balaenoptera acutorostrata*). Int. Counc. Explor. Sea, Mar. Mamm. Comm., C.M. 1975/No. 13:1-7.

[7]Earle, S. A. 1979. Quantitative sampling of krill (*Euphausia pacifica*) related to feeding strategies of humpback whales (*Megaptera novaeangliae*) in Glacier Bay, Alaska. Paper presented at The Third Biennial Conference of the Biology of Marine Mammals, 7-11 Oct. 1979, Seattle, Wash.

[8]Forestell, P. H., and L. M. Herman. 1979. Behavior of

apparent use of bubble screens as camouflage by an escort whale in order to protect a calf or mother-calf pair. It is likely that some functions of bubbling still remain to be discovered. At times, bubbling may be purely adventitious.

The humpback possesses a diverse repertoire of feeding behaviors. Whether environmental factors influence the choice of feeding method is presently unknown. Perhaps, as suggested by others (Jurasz and Jurasz 1979; Watkins and Schevill 1979), various prey species or densities elicit different feeding strategies and behaviors. For less mobile prey or high prey densities, relatively simple devices may be sufficient. For more mobile and evasive species, or for more efficient feeding in lower densities, more sophisticated methods may be advantageous.

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