um, as the rate of addition of metabolic acids to the fluids was higher than the rate of neutralization by dissolved shell. Crenshaw and Neff (9) calculated that at the measured rates of calcium dissolution a 100-g animal (shell weight) would lose about 2 mg of shell per hour. We used animals with shell weights of 40 to 80 g and internal shell surface areas of 44 to 64 cm^2. Assuming the dissolution rate to be uniform over the entire internal surface, one can calculate the thickness of shell that would be removed for every hour the shell is closed

$$\frac{\text{shell loss per hour}}{\text{unit weight}} \times \frac{\text{total weight}}{\text{surface area}} \times \frac{1}{\text{density}} = \text{thickness lost per hour}$$

For example, one of our specimens with valves weighing 64 g and an internal surface area of 56 cm^2 would lose 7.8×10^{-2} μm/hour (using a density of 2.93 g/cm^3 for aragonite). Our experimental *M. mercenaria* kept their valves closed for 2.5 to 12 hours (Fig. 3), and at the calculated rate of shell dissolution the thickness removed would be 0.2 to 0.94 μm. These values are sufficiently close to the measured widths (0.45 to 0.9 μm) of subdaily lines to suggest a causative relationship between the two.

To account for subdaily striations, then, it is necessary only to envision continuous and simultaneous secretion of organic matrix and calcium carbonate during the aerobic shell-building part of the animal's growth cycle. In the anerobic period, increasing acid in the extrapallial fluid dissolves a portion of newly deposited shell. Some of the associated matrix may also dissolve, but at least part of it is sufficiently insoluble to resist attack by metabolic acids and remains behind as a residue, to be covered by a new layer of calcified material during the next cycle of aerobic deposition. Because the matrix at this point is hardened by polymerization of the protein, it maintains its structural integrity during and after decalcification. As a result, the width of residual matrix provides a record of the length of time that the shell was exposed to metabolic acids. This hypothesis, supporting that of Lutz and Rhoads (7), does not require alternate secretion of crystals and proteins, calcification inhibitors (6), or the existence of preformed matrix layers or compartments (14).

We recognize that this model of growth-line formation is at variance with current theory in the following respects. First, arrays of subdaily as well as tidal or diurnal markings are also found in the shell ultrastructure of intertidal mollusks. If, as is commonly accepted, these animals actively pump and deposit shell continuously during periods of inundation, then dissolution would not occur. Although we cannot safely assume that behavior in the laboratory is the same as that in the field, subdaily frequencies of shell opening have been reported elsewhere for experimental "nontidal" clams (4). Second, our hypothesis does not account for the thickness of presumed diurnal or tidal markings (5), which is as much as 3 μm in our experience and corresponds to 35 to 40 hours of shell dissolution according to our calculations (Figs. 3 and 4). Third, in certain areas of our sections, the accumulated thickness of subdaily markings found between two daily or tidal-diurnal lines is equivalent to more dissoluton than we would calculate for 24 hours of valve closure. This implies that one or more daily lines are missing from the depositional cycle. Evidence for missing growth lines in mollusks has been reported by others (2, 15); however, Pannella (5), while admitting the possibility of gaps in the growth record, considers this exceptional.

Despite these questions, the correspondence between our calculated and observed subdaily line widths strongly suggests a connection between the appearance of these striations and rhythms of valve movement in *M. mercenaria*. The model of growth-line formation and shell dissolution (7) is thus quantitatively supported, at least for subdaily lines.

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8. Because we did not use calibration buffers of suitable ionic strength, we actually measured electrode potential rather than hydrogen ion concentration. Our graphs were converted to *p*H units for convenience.
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16. Supported by NSF grant BMS75-04842. Contribution No. 119 of the College of Marine Studies, University of Delaware.

24 March 1978; revised 11 July 1978

Radio Tracking of a Fin Whale (*Balaenoptera physalus*)

Abstract. *A tagged whale of the genus* Balaenoptera *was intermittently tracked by radio for 27.8 hours over a distance of about 145 kilometers. Data on breathing and movement show that during that time the whale took 58 breaths in 130 minutes and traveled 20 kilometers at more than 9 kilometers per hour. Precise measurements of such parameters and of other features of the life history of great whales, which travel long distances over the high seas, often in groups, are now possible through radio tagging.*

For many years scientists have recognized the need to mark whales in order to acquire basic biological data on such subjects as population identity, home range, migration, and behavior. The *Discovery* mark has been used for more than four decades, but its usefulness for these purposes is limited (1). An alternative is a visually detectable "streamer mark," which has the advantage that living whales may be followed, but this technique can be used only in the daytime in fair weather and requires the observer to be near the whale (2). Radio tags do not have these limitations.

We report here the remote implantation of a radio tag in a fin whale and subsequent tracking of the whale for 27 hours and 45 minutes. Our approach evolved from two earlier efforts. Schevill and Watkins (3) developed an implantable tag for right whales, *Eubalaena glacialis*, and Martin *et al.* (4) improved the response time of an automatic direction finder (ADF) for use in tracking porpoises. Subsequently, others have tracked whales by first capturing them and then attaching transmitters (5).

Whales on the high seas are among the most difficult animals to study. We chose

0036-8075/78/1103-0521$00.50/0

the fin whale because it has been one of the most important targets of commercial whaling (6). We chose the Gulf of Saint Lawrence because it is a small area of sea, where the chance of losing a tagged animal is reduced and local logistics are good. Blue, fin, and Minke whales patrol and feed close to shore there throughout the midsummer to autumn months (7). Currently, these whales are not hunted, and the identity of this fin whale population is in question (8).

Our implantable beacon transmitter (IBT) was fired from a modified 12-gauge shotgun (9). The IBT weighed 517 g and was 70 cm long, including a 46-cm antenna. Each IBT had a characteristic frequency and a characteristic pulse repetition rate, so that if more than one whale were tagged, the whales could be separately identified. The implanted transmitter generated two 100-msec pulses per second at 30.130 MHz (10). Ballistics tests indicated a muzzle velocity for the IBT of about 70 m/sec and a trajectory drop of about 1.5 m at a distance of 40 m (11). A light nylon line, attached to the pushrod of the IBT and to the firing platform, provided stability in flight, and could be used to retrieve the IBT in case of a miss or to remove the pushrod to expose the antenna after an implantation. The tag was also provided with a stop to prevent penetration deeper than 22 cm into the whale. As the IBT's angle of incidence to the whale is rarely perpendicular, the tag will usually not penetrate the total blubber thickness; for a fin whale the maximum blubber thickness is about 15 cm, near the dorsal fin.

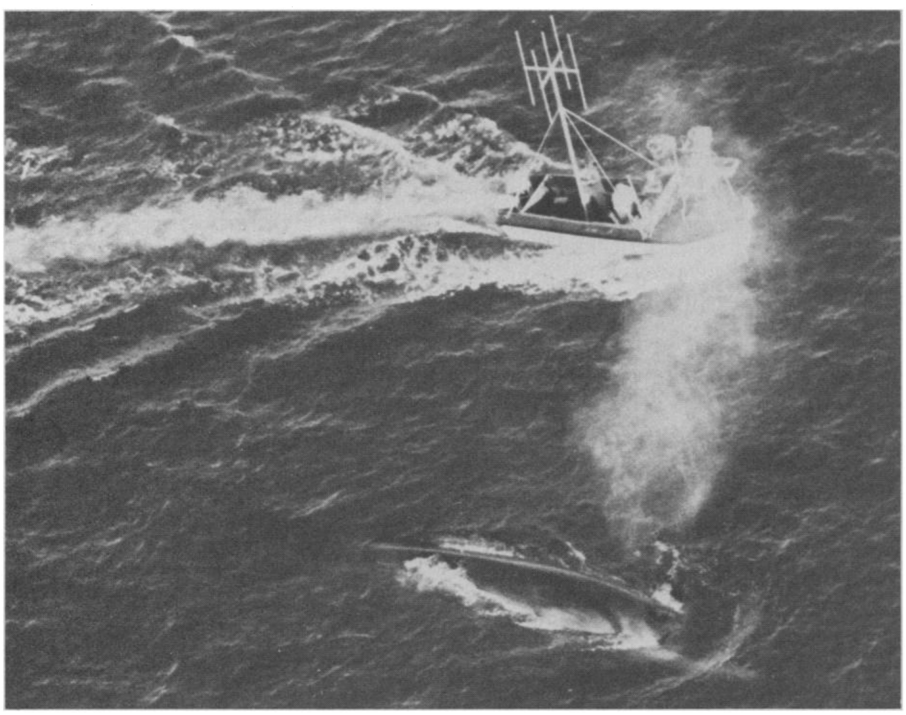

Fig. 1. Successful tagging of a fin whale. The breath of the whale partially obscures the tagger standing in the boat's bow pulpit. The pair of Adcock antennas are amidships.

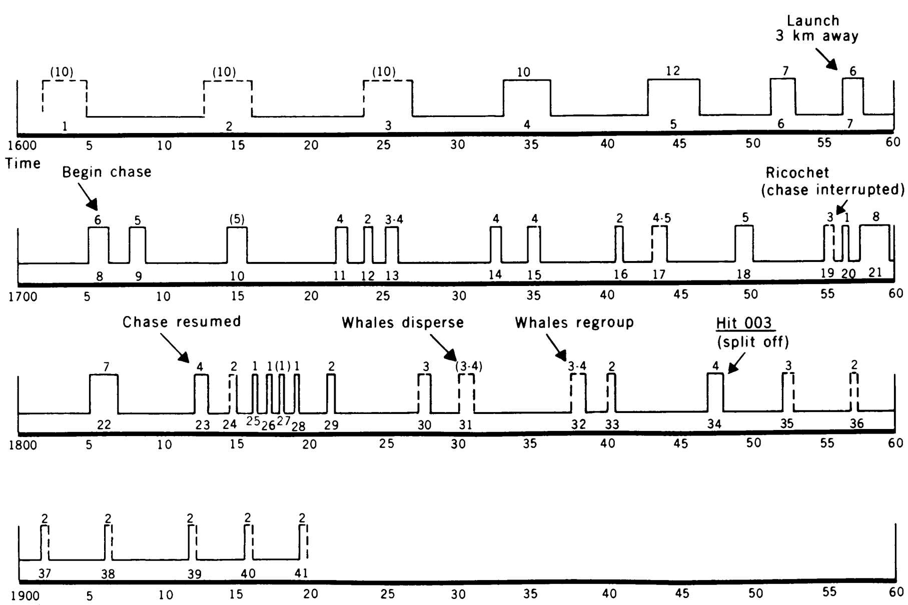

Fig. 2. Breathing record based on visual observations of a pod of three fin whales before and during pursuit (see text for explanation). After tagging, the record is of whale 003 and is based on signals received on the ADF. The number of breaths is given above the breathing curve; numbers in parentheses are estimated. Sequence numbers are given below the breathing curve. The bottom rows of numbers show the time.

We used a 7-m boat for tagging and tracking and a Cessna 170 aircraft for spotting and tracking. The boat carried two pairs of Adcock antennas at right angles to each other, and the aircraft carried a crossed ferrite core antenna in a 31 by 47 cm housing strapped to the belly aft of the wheels. Tagging was a cooperative effort involving boat and aircraft. Observers in the aircraft spotted the whales and directed the boat by radio toward the animals. The aircraft usually remained higher than 300 m to avoid disturbing the whales. We attempted to maneuver the boat to be able to place the tag near the midline in front of the dorsal fin, where the blubber is thickest. This is the part of the whale that rises farthest out of the water (12). All IBT's were coated with Furoxone antibiotic to reduce the possibility of infection (13).

On 17 August 1976 we pursued a pod of three whales, one of which we tagged after 55 minutes of pursuit (Fig. 1). Fin whales take evasive tactics when closely pursued, altering direction underwater, occasionally parting company, and breathing at irregular intervals. We recorded breathing patterns from the aircraft before, during, and after close pursuit of the pod. The data obtained before tagging are subject to error because of the difficulty of identifying individual whales surfacing and blowing in a pod. This difficulty leads to overestimation of the number of breaths per surface sequence and the duration of the surface sequence, and underestimation of the duration of "down time"—the time spent below the surface between surface sequences. The error in this case was small, however, since the whales tended to surface, breathe, and dive in synchrony. This error can be eliminated if the data are obtained from a tagged whale. The whales significantly altered all three measured parameters of their breathing behavior during the chase (Table 1). Figure 2 shows that before pursuit, from 1602 to 1657:30 hours (surface sequences 1 to 7), the whales breathed in unison about 65 times, averaging one breath every 51 seconds. From 1705 to 1756 hours (sequences 8 to 19) each whale breathed about 48 times, or once every 64 seconds. We tried to tag one whale at 1756 hours but the tag ricocheted (*14*). The whales were pursued again from 1812:30 to 1848 hours (sequences 23 to 34), during which time each breathed about 28 times, or once every 76 seconds.

At 1848 hours we tagged a whale, about 18 m long, which we called 003 from the identification number of the tag. The shot was from a distance of 20 to 25 m, broadside to the whale's left. The tag hit somewhat posterior to the shoulder, well below the highest point on the back. After 003 was tagged it did not rejoin its companions. It swam downriver, surfacing to take two to three breaths in 0.6 minute on the average. Darkness and the need to refuel caused us to cease operations at 1919 hours. We attempted to relocate the whale during the night from the boat, without success.

The next morning, searching by aircraft, we succeeded in finding 003 125 km downriver (Fig. 3). It had averaged 6.7 km/hour since the last contact, which is a minimum speed since the calculation was for travel in a straight line. We first detected 003 by means of the ADF from a distance of about 26 km, which we judged to be the maximum range of the ADF because the signals were weak and the directionality was barely detectable. Low placement of the IBT on the whale, the almost horizontal position of the antenna, and possible battery leakage may have contributed to this low range.

We followed 003 for 2 hours and 10 minutes, during which it traveled about 20 km. In spite of its speed of more than 9 km/hour, we were able to locate it by the ADF almost immediately after each surfacing. Hence, we have a complete record of surfacings (Fig. 4). The behavior of 003 indicates that it had returned to a breathing pattern similar to that observed before pursuit (Table 1). The whale's movements appeared leisurely. Although it took only two to four breaths during each surface sequence, the intervals between sequences averaged 6.5 minutes through the first nine sequences. During the remaining time, the intervals averaged 8.3 minutes.

During each surfacing of the whale to take a single breath, both on the day of tagging and the next morning, we received one to four radio pulses on the

Table 1. Breathing records of fin whales. Some of the data in row 1 are estimates (see Fig. 2); the data in rows 1 and 2 are biased, as discussed in the text. Values were statistically compared by use of the t-test. Differences between values with a common superscript are not significant. All other differences are significant at $P < .01$. The number of observations is given in parentheses.

Period	Breaths per surface sequence	Surface sequence duration (min)	Down time (min)
Before chase, 17 August, sequences 1 to 7	9.00 ± 2.08 (7)	2.43 ± 0.73 (7)	6.33 ± 1.63^{c} (6)
During chase, 17 August, sequences 8 to 19, and 23 to 34	3.10 ± 1.48^{a} (21)	0.87 ± 0.48^{b} (23)	3.46 ± 2.45 (23)
Tagged 003, 18 August, sequences 3 to 18	3.44 ± 1.03^{a} (16)	0.81 ± 0.34^{b} (10)	7.06 ± 1.66^{c} (13)

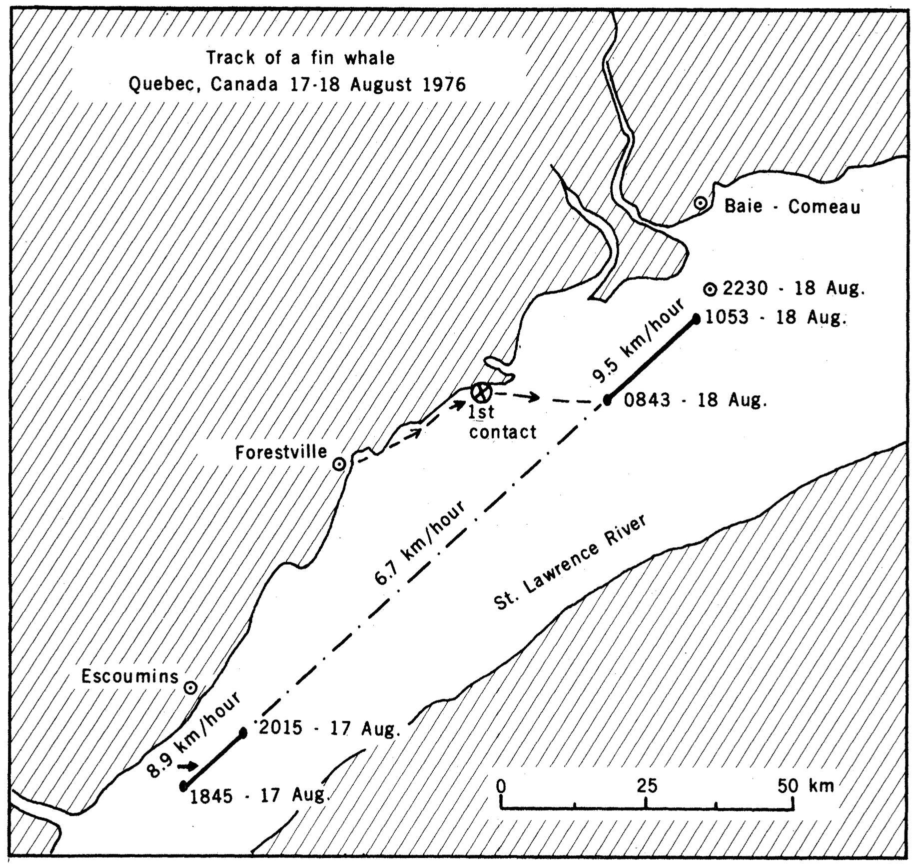

Fig. 3. Track of the tagged fin whale 003.

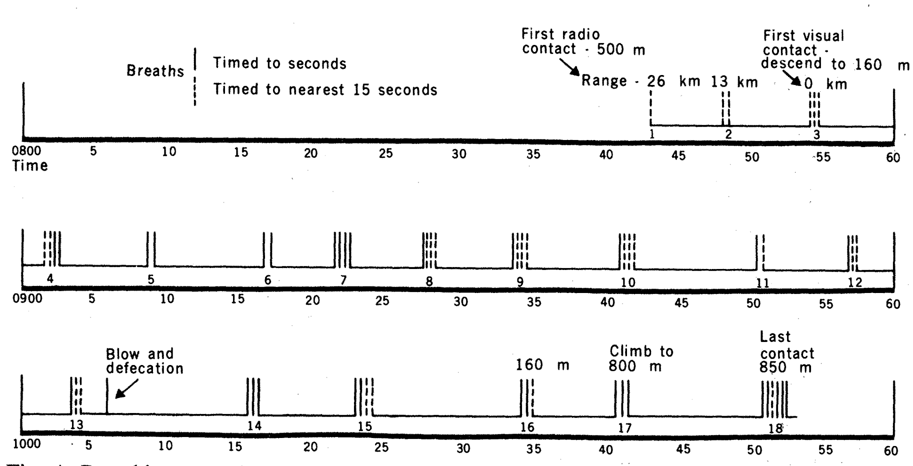

Fig. 4. Breathing record of the tagged fin whale 003. The complete record is derived from signals received on the ADF. See Fig. 2 legend for explanation.

ADF. As the tag pulse rate was two per second, 003 exposed the tagged part of its body for about 1 to 2 seconds. A tag placed on the dorsal surface might have been exposed for up to perhaps 3 seconds, or for a total of six pulses at the pulse rate we used (*15*). On the basis of 58 breaths in 130 minutes (Fig. 4) and a tag exposure time of 2 seconds per breath, our tag was exposed only about 1.5 percent of the time. Placement very high on the body could result in exposure for slightly more than 2 percent of the time. This suggests that the transmitter, which can operate for 200 hours continuously, might function for about 14 months on a fin whale.

On the evening of 18 August, we again received radio signals from 003 (Fig. 4). No tracking was possible as we soon lost the signal. On subsequent days, we unsuccessfully searched the Gulf of Saint Lawrence from the Saguenay River to Anticosti Island. Our failure to reestablish contact could be attributed to one of four causes: (i) the whale left the searched area, (ii) the transmitter was shed (*16*), (iii) the transmitter failed because of battery leakage or other malfunction, or (iv) the antenna did not emerge because of the low implant position and choppy seas. We do not know whether any of the last three occurred. However, we calculated that the probability of missing the whale within the searched area, if the transmitter was still functioning, was only .09 (*17*). Therefore, we believe that the transmitter failed about $1^1/_2$ days after implantation, probably because of battery leakage since this was subsequently found to be a problem with the IBT version we used (*9*).

Concurrently with our tagging of a fin whale, personnel of the National Marine Fisheries Service, Seattle, tagged humpback whales, *Megaptera novaeangliae*, in southeast Alaska (*18*), using the same equipment and experiencing some of the same problems. That we have followed living great whales at sea speaks of the potential of this radio tracking system, but we emphasize that the system has yet to be proved fully operational. Both technological and biological problems remain. The potential transmission range of about 60 km, even if it is realized in practice, is short for tracking on the open reaches of the high seas without a heavy logistics commitment. Also, we do not know how long the blubber will tolerate the tag (*19*). *Discovery* tags are retained in whales for up to 30 years (*1*), but the available data shed little light on the retention of a tag by blubber. Further, the radio tag is not completely implanted; the antenna remains exposed, and there is a hydrodynamic drag on it when it is submerged. Finally, it is difficult to estimate the distance and angle of incidence when shooting the tag into a whale at sea. Nevertheless, the results obtained to date indicate the potential of this technology for gathering life history data, hitherto practically unattainable, on the great whales at sea.

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References and Notes

1. The *Discovery* mark has been used since 1932. Thousands of whales have been marked with these metal projectiles, which are designed to be retained in the animal's deep musculature for retrieval at the factory, during processing. *Discovery* marking depends on the whaling industry and can give only two points in the life of the animal—that of marking and that of death. "Dispersal" and "track" are the principal data acquired [S. G. Brown, *Discovery Rep.* **26**, 355 (1954)]. Migration patterns, age, growth, reproductive rate, mortality, and population size are not easily determined because only large animals of unknown age can be safely marked and the recovery rate for tags in carcasses aboard factory ships is only 50 to 75 percent [J. T. Ruud and P. Øynes, *Nor. Hvalfangst Tid. (Norw. Whaling Gaz.)* **43**, 383 (1954); R. G. Chittleborough and K. Godfrey, *ibid.* **46**, 238 (1957)]. However, *Discovery* marks did indicate a hunting mortality of 4.9 percent for blue whales during the 1930's [G. W. Rayner, *Discovery Rep.* **19**, 245 (1940)], and the data were of major significance in recommendations to the International Whaling Commission that the catch be reduced [J. T. Ruud, *Nor. Hvalfangst Tid.* **41**, 649 (1952)].
2. Ruud *et al.* (*2a*) first developed the streamer mark from the technology of the *Discovery* mark. E. Mitchell and V. M. Kozicki [*Int. Comm. Whaling Rep. 24* (1974), p. 142] included a vital dye to mark growth layers in earplugs.
2a. J. T. Ruud, R. Clarke, A. Jonsgard, *Nor. Hvalfangst Tid.* **42**, 429 (1953).
3. W. E. Schevill and W. A. Watkins, *Woods Hole Oceanogr. Inst. Ref. No. 66-17* (1966).
4. H. Martin, W. E. Evans, and C. A. Bowers [in *IEEE '71 Engineering in the Ocean Environment Conference* (IEEE, New York, 1971), p. 44] report on an ADF system in which the direction of the transmitter relative to the tracking platform can be unambiguously determined on the basis of a signal as short as 10 msec. Display is visual on a cathode-ray oscilloscope. The brief time cetaceans spend on the surface precludes the use of antennas that must be rotated to give direction indication. W. E. Evans [*Ann. N.Y. Acad. Sci.* **188**, 142 (1971); in *The Whale Problem*, W. E. Schevill, Ed. (Harvard Univ. Press, Cambridge, Mass., 1974), p. 385] gives samples of the data acquired. The ADF we used was an improved version of that system.
5. K. S. Norris, W. E. Evans, G. C. Ray, in *The Whale Problem*, W. E. Schevill, Ed. (Harvard Univ. Press, Cambridge, Mass., 1974), p. 395; W. E. Evans, *U.S. Natl. Mar. Fish. Serv. Mar. Fish. Rev.* **36**, 52 (1974); K. S. Norris and R. L. Gentry, *ibid.*, p. 58. An earlier trial implantation on a gray whale gave a 13-hour track [J. Schultz, report to the director, Bureau of Commercial Fishery (1968)].
6. The fin whale was agreed on as the first target species at a meeting at La Jolla, Calif., December 1974, chaired by W. E. Schevill.
7. E. D. Mitchell, *Nat. Can. (Ottawa)* **2**, 9 (1973).
8. ———, in *The Whale Problem*, W. E. Schevill, Ed. (Harvard Univ. Press, Cambridge, Mass., 1974), p. 108.
9. Our IBT was an earlier version of the basic system described by W. A. Watkins and W. E. Schevill [*Woods Hole Oceanogr. Inst. Ref. No. 77-58* (1977)], who discuss the modifications made.
10. Radio output involves compromises between power, repetition rate, and length of life. In our design, power was provided by three 2.8-V organic lithium cells, which gave an IBT life-span of 200 hours of continuous operation. A seawater switch turned the transmitter off when the antenna was submerged. Range tests gave a maximum of 60 km from the transmitter at water level to an aircraft at an altitude of 160 m.
11. G. C. Ray and D. Wartzok, report to the National Marine Fisheries Service, Washington, D.C. (1975).
12. See figure 2 in Ruud *et al.* (*2a*).
13. There is debate about the effectiveness of surface antibiotics, since any systemic bacterial infection caused as a consequence of tag penetration could not be combated by the small amount of antibiotic on the tag. Nevertheless, users of the *Discovery* tag have often taken this precaution, and so did we.
14. We fired six times at whales during 9 days of tagging. One shot at a blue whale was a miss. Two at blues and one at a fin were hits, but ricocheted. All four of these tags were lost. Ricocheting was probably due to flexure between the tag and the pushrod during flight because nylon retaining screws were broken on firing and to the use of less than optimum point design (*9*).
15. A motorized 35-mm camera taking 2.7 frames per second, operated by R. Kinne, covered an entire surfacing in about 16 frames or 5.9 seconds. Movies taken by C. Ray at 24, 48, and 64 frames per second showed surfacing for 4.0 to 7.0 seconds ($N = 9$), averaging 5.4 seconds. Any one part of a whale's body, however, is exposed for only about half this time, as the whale rolls as it breathes and does not expose the entire dorsum at one time.
16. An aerial photograph taken on the morning of 18 August showed a glint of metal in the left shoulder region, which would not have been visible if the tag were fully implanted. This indicates that the tag was not fully implanted on impact or that it was being rejected by the whale's blubber.
17. The probability of receiving a signal is dependent on the proportion of time the animal is at the surface, P_u, and the proportion of time the receiver is within range of the transmitter. The probability of receiving a signal is

$$P = P_u + (1 - P_u)\left(\frac{2r}{st_c}\right)\left(\frac{\pi}{4}\right)$$

for $0 \leq 2r/st_c \leq 1$ and

$$P = P_u + (1 - P_u)\,\frac{\sin\theta' \cos\theta' + (\pi/2) - \theta'}{2\cos\theta'}$$

for $\cos^{-1}(st_c/2r) = \theta'$ and $1 \leq (2r/st_c)$, where r is the transmitter range, s is the speed of the tracking platform, and t_c is the length of one dive cycle. On the search for 003, we flew at 330 m and we assume a range of signal reception of only 26 km. The aircraft's speed was 3.2 km/min. Using the data given in the last row of Table 1 and 1.5 seconds of tag exposure per blow, we obtained $P = .91$. The probability of missing the whale is therefore .09.
18. M. F. Tillman and J. H. Johnson, reports to the National Marine Fisheries Service, Seattle (1976 and 1978).
19. "Spaghetti" tags (visual plastic streamers) are not rejected by dolphins provided the securing dart and all portions of the tag that penetrate below the skin are made of surgical grade stainless steel and provided no part of the tag penetrates below the blubber-muscle interface (W. E. Evans, personal communication).
20. We thank W. E. Schevill and W. A. Watkins for reviewing this report. We also thank R. Kinne for piloting the plane and taking aerial photographs, and G. Horonowitsch for assistance in all phases of fieldwork. Supported by NASA contract NAS2-9300 and ONR contract N00014-75-C-0701. Support for field operations was also provided by Environment Canada (Fisheries and Marine Science).

26 April 1978; revised 17 July 1978