

DIVING BEHAVIOR AND SWIMMING SPEED OF A  
FREE-RANGING HARBOR PORPOISE,  
*PHOCOENA PHOCOENA*

Our understanding of cetacean diving behavior has recently increased (Westgate *et al.* 1995, Heide-Jørgensen and Dietz 1995, Davis *et al.* 1996). However, there are few reports which measured swim speed of free-ranging cetaceans (Hanson and Baird 1998). Measurement of swim speed during diving helps to understand the dive function (Boyd *et al.* 1995, Crocker *et al.* 1997) and the swimming effort or energetics (Feldkamp 1987). We report here the first record of the diving behavior and swimming speed of a free-ranging harbor porpoise.

The set of instruments to measure the diving behavior consisted of a micro data logger, a time-scheduled releaser, a float, and an Argos transmitter (PTT). The micro data logger (UWE-200PDT, developed by National Institute of Polar Research and Little Leonardo Co., Tokyo; 20 mm in diameter, 90 mm long, 42 g in weight, 2 MB memory size) was set to record depth, number of rotations of the propeller, and water temperature at intervals of one second. The propeller was placed in front of the logger and rotated in response to water flow. Swim speed was calculated from the number of rotations of the propeller according to a linear relationship. The logger could detect speeds faster than 0.5 m sec<sup>-1</sup>. Depth and temperature sensors were placed on opposite sides of the logger. Absolute accuracy of the logger was 0.5 m in depth, 0.1°C in temperature, and 0.5 m sec<sup>-1</sup> in speed; resolution was 0.05 m, 0.01°C, and 0.04 m sec<sup>-1</sup>, respectively. The releaser was set to activate one day after the animal was released. The float had a mass of 195 g in air, and the dimensions were 170 X 90 X 40 mm. The PTT (T-2038, TOYOCOM Co., Ltd., Tokyo, 120 X 35 X 15 mm, 116 g) was implanted into the float except for its antenna. This was left exposed in order to facilitate transmission after the instruments were released from the porpoise. The total weight of the instruments was 486 g in air and -50 g in sea water. Details of instruments and attachment techniques were described in Otani *et al.* (1998).

The study was carried out at Usujiri (41°57'N140°58'E), Hokkaido, Japan, in July 1997. A female harbor porpoise was accidentally caught in a set-net off the coast of Usujiri (134 cm in body length and 37 kg in body mass).

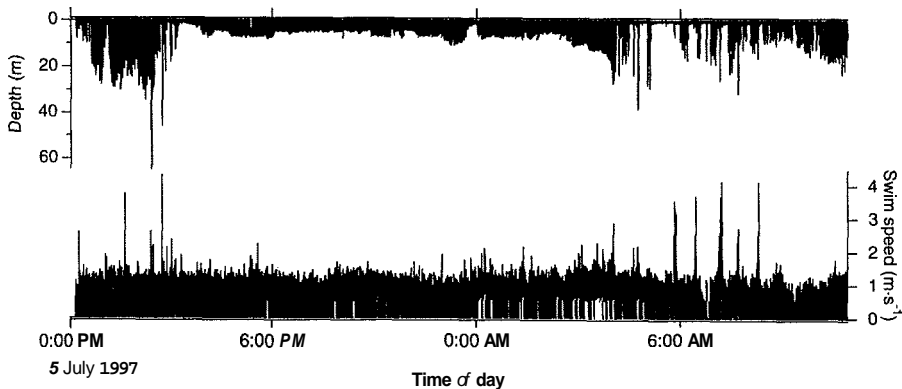


Figure 1. Total records of dive depth (upper) and swim speed ( $>0.5 \text{ m sec}^{-1}$ ) (bottom) for female harbor porpoise over period of 22.8 h.

After the instruments were attached to the porpoise, it was released about 2 km off the coast of Sawara ( $42^{\circ}09'N$ ,  $140^{\circ}41'E$ ), which is located about 30 km northwest of Usujiri. The release point was within Funka Bay; the depth was less than 100 m. After release the package was recovered using ARGOS-supplied PTT locations coupled with a board-based automatic direction-finding receiver (Gonio 400, Cubic-I Co., Ltd., Tokyo). The recorded data were downloaded from the logger to a personal computer. Horizontal speed was calculated from swim speed and depth change rate (vertical speed). Only dives deeper than 0.5 m were analyzed, because the absolute accuracy of the logger was 0.5 m.

We obtained 2,878 dives with speed data over the 22.8 h of continuous recording from the free-ranging harbor porpoise (Table 1, Fig. 1). The harbor porpoise dived continuously and repeatedly, as Otani *et al.* (1998) reported. More than 90% of the dives were shallower than 10 m and more than 80% were shorter than one minute in duration. The harbor porpoise swam at relatively slow speed. Its mean swim speed was  $0.9 \text{ m sec}^{-1}$  during the whole recorded period and more than 90% of records of swim speed were slower than  $1.5 \text{ m sec}^{-1}$ . The fastest speed recorded in this study was  $4.3 \text{ m sec}^{-1}$ .

Table 1. Summary statistics of diving records for female harbor porpoise.

	Mean $\pm$ SD	Max	Min.	Median
Dive depth (m)	$3.8 \pm 6.8$	64.7	0.6	1.1
Dive duration (sec)	$26.2 \pm 31.0$	193	2	10
Surface time (sec)	$3.9 \pm 7.2$	133	1	2
Descent speed ( $\text{m sec}^{-1}$ )	$0.8 \pm 0.3$	4.3	0.0	0.8
Ascent speed ( $\text{m sec}^{-1}$ )	$0.9 \pm 0.3$	4.1	0.0	0.9
Descent angle (deg.)	$31 \pm 20$	85	1	29
Ascent angle (deg.)	$17 \pm 10$	52	1	15

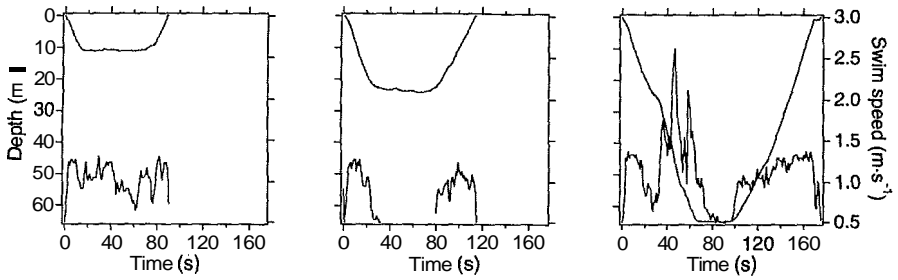


Figure 2. Example of dive depth (upper) and swim speed ( $>0.5 \text{ m sec}^{-1}$ ) (bottom) of dives with bottom time for harbor porpoise.

Leatherwood *et al.* (1988) reported that harbor porpoises can swim at about 12 kn. (about  $6.2 \text{ m sec}^{-1}$ ).

Horizontal speed was significantly faster than vertical speed (Wilcoxon signed rank test,  $P < 0.001$ ). Both horizontal and vertical distance increased during the 22.8 h of the recording period. Total horizontal distance (50.5 km) was about 2.9 times longer than the vertical distance (17.7 km). Distance traveled by the porpoise was estimated to be about 53 km per day. This value was within previous records (32–57 km per day) obtained using radio tracking (Westgate *et al.* 1995). In that case the horizontal distance was based on the distance calculated between two points where the radio signal was detected and was reasoned to underestimate total distance. Our value would also be an underestimate, because the logger does not detect speeds slower than  $0.5 \text{ m sec}^{-1}$ . Even so, this is the first measurement of the gross movement of cetaceans using such a method.

Descent speed (Spearman rank correlation test,  $r^2 = 0.57$ ,  $P < 0.001$ ,  $n = 2,451$ ), ascent speed ( $r^2 = 0.41$ ,  $P < 0.001$ ,  $n = 2,311$ ), descent angle ( $r^2 = 0.20$ ,  $P < 0.001$ ,  $n = 2,470$ ), and ascent angle ( $r^2 = 0.66$ ,  $P < 0.001$ ,  $n = 2,294$ ) were positively correlated with dive depth. Because the angle of shallow dives was smaller than that of deep dives, shallow dives had a relatively larger horizontal component.

Dives both with and without bottom time were observed in this study. Otani *et al.* (1998) assumed that porpoises foraged during the bottom phase of dives. For the dives with bottom time, swim speed at the bottom either decreased to less than the recording limit or it alternated between increase and decrease ( $0\text{--}2.0 \text{ m sec}^{-1}$ ) (Fig. 2).

Initial descent speed ( $r^2 = 0.27$ ,  $P < 0.001$ ,  $n = 2,451$ ) and initial descent angle ( $r^2 = 0.56$ ,  $P < 0.001$ ,  $n = 2,470$ ) were also positively correlated with dive depth. Otani *et al.* (1998) hypothesized that harbor porpoises anticipate the depth of their dives before initiating the dive process, because the initial descent rate increased as the dive depth increased. However, it was unclear whether the change of initial descent rate was caused by the change of descent speed or descent angle. In the present study we analyzed the swim speed data to determine whether porpoises changed the swim speed or dive angle when diving deeply. When the tagged porpoise dived deeply, it increased both its

dive speed and dive angle. It could therefore reach the bottom faster than on a slow dive or a dive with a less abrupt angle.

#### ACKNOWLEDGMENTS

The authors would like to thank Dr. H. Munehara, Mr. Y. Arashida, Mr. K. Nomura, Dr. K. Nakamura, and all the fishermen of Nomura Fishing Company and Usujiri Fisherman's Association in Usujiri, Hokkaido for their cooperation in collecting and keeping specimens, and Mr. R. Kawabe, Mr. S. Kaga, Mr. Y. Kaga, Mr. T. Kawamura, Mr. T. Matsui, and Mr. T. Fukuda for helping with the field work. We also thank three anonymous referees for valuable comments on the manuscript. This work was partly supported by a grant from the Sasakawa Scientific Research Grant from the Japan Science Society and a Grant-in-Aid for Scientific Research (No. 08660227) from the Japan Ministry of Education, Science and Culture.

#### LITERATURE CITED

- BOYD, I. L., K. REID AND R. M. BEVAN. 1995. Swimming speed and allocation of time during the dive cycle in Antarctic fur seals. *Animal Behavior* 50:769–784.
- CROCKER, D. E., B. J. LE BOEUF AND D. P. COSTA. 1997. Drift diving in female northern elephant seals: Implications for food processing. *Canadian Journal of Zoology* 75: 27–39.
- DAVIS, R. W., G. A. J. WORTHY, G. WÜRSIG, S. K. LYNN AND F. I. TOWNSEND. 1996. Diving behavior and at-sea movements of an Atlantic spotted dolphin in the Gulf of Mexico. *Marine Mammal Science* 12:569–581.
- FELDKAMP, S. D. 1987. Swimming in the California sea lion: Morphometrics, drag and energetics. *Journal of Experimental Biology* 131:117–135.
- HANSON, M. B., AND R. W. BAIRD. 1998. Dall's porpoise reactions to tagging attempts using a remotely-deployed suction-cup tag. *Marine Technology Society Journal* 32:18–23.
- HEIDE-JØRGENSEN, M. P., AND R. DIETZ. 1995. Some characteristics of narwhal, *Monodon monoceros*, diving behavior in Baffin Bay. *Canadian Journal of Zoology* 73:2120–2132.
- LEATHERWOOD, S., R. R. REEVES, W. F. PERRIN AND W. E. EVANS. 1988. Whales, dolphins, and porpoises of the Eastern North Pacific and adjacent arctic waters. A guide to their identification. Dover Publications, New York, NY.
- OTANI, S., Y. NAITO, A. KAWAMURA, M. KAWASAKI, S. NISHIWAKI AND A. KATO. 1998. Diving behavior and performance of harbor porpoise, *Pbocoena phocoena*, in Funka Bay, Hokkaido, Japan. *Marine Mammal Science* 14:209–220.
- WESTGATE, A. J., A. J. READ, P. GERGGREN, H. N. KOOPMAN AND D. E. GASKIN. 1995. Diving behaviour of harbour porpoises, *Pbocoena phocoena*. *Canadian Journal of Fisheries and Aquatic Sciences* 52:1064–1073.

SEIJI OTANI,<sup>1</sup> Department of Polar Science, The Graduate University for Advanced Studies, National Institute of Polar Research, Itabashi, Tokyo 173-8515, Japan; YASUHIKO NAITO and AKIKO KATO, National Institute of Polar Research, Itabashi, Tokyo 173-8515, Japan; AKITO KAWAMURA, Department of Bioresources, Faculty of Bioresources, Mie University, Tsu, Mie 514-8507, Japan.

<sup>1</sup> Current address: The Institute of Cetacean Research, Tokyo Suisan Building 4-18, Toyomicho, Chuo, Tokyo 104-0055, Japan; e-mail: ohtani@i-cetacean-r.or.jp. Received 11 May 1999. Accepted 8 February 2000.