MARINE MAMMAL SCIENCE, 10(1):87–92 (January 1994)

ANNUAL REPRODUCTION BY INDIVIDUALLY IDENTIFIED HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN ALASKAN WATERS

We report here on five North Pacific female humpback whales (*Megaptera novaeangliae*) which demonstrated successful annual reproduction. Two of these females were observed with a different calf in three consecutive summers, and three females were observed with a calf in two consecutive summers. Survival was confirmed through the first migration for 12 calves, with survival documented beyond weaning for two of these whales.

Early studies of humpback whales indicated that the most common breeding cycle was every two years. Matthews (1937) reported that humpbacks usually breed every two years but hypothesized that if a whale bred early in the season, two pregnancies could occur in three years. Chittleborough (1958) reported that a two-year cycle was typical, but that some percentage of females could conceive after a postpartum ovulation, and could produce two calves in two seasons. He also noted the possibility of an ovulation following the loss of a calf, which would appear to be an annual cycle but produce only one successful calf in two seasons.

More recent studies, on the sighting histories of naturally marked whales, have found a two- or three-year breeding cycle to be most common (Baker *et al.* 1987; Clapham and Mayo 1987*a*, 1990; Perry *et al.* 1990). These studies have shown there is considerable individual variability, ranging from one to five years, in the reproductive interval of female humpback whales.

A number of studies have documented the occurrence of annual reproduction on the breeding grounds; however, the frequency of this event is not known. A total of eight females with annual calving intervals was reported from the Hawaiian islands (Darling 1983; Glockner-Ferrari and Ferrari 1984, 1990; Baker *et al.* 1987) but, by comparing the study areas and sighting dates, there are possible overlaps among these data. Observations of annual calving on the breeding grounds do not distinguish between annual reproduction and postpartum pregnancy due to the death of a neonate. With Glockner-Ferrari and Ferrari's data it was impossible to demonstrate whether the annual cycle was due to a postpartum ovulation after the loss of the calf observed the previous year, or whether the calves had survived.

This question has been problematic because annual calving intervals have rarely been observed on the feeding grounds (three reported from Alaskan waters), and determining the continued survival of these offspring was impossible because there were no records of calf survival beyond the first year (Darling and McSweeney in Darling 1983; Baker *et al.* 1987; Clapham and Mayo 1987*a*, 1990; von Ziegesar and Matkin 1989). If a female humpback whale was

observed with a calf in consecutive seasons on the feeding grounds, after the mother and calf had successfully migrated, it could be safely assumed that the mother had undergone a postpartum ovulation while suckling a calf, and that the ovulation was not a result of losing a neonate on the breeding grounds. The presence of calves on the feeding grounds, born to the same female in successive years, demonstrates that some proportion of postpartum ovulations will result in successful consecutive pregnancies and calf survival.

Individually identified humpback whales (Katona *et al.* 1979) have been systematically studied in southeastern Alaska since 1981. Data were collected by the National Park Service (NPS), Glacier Bay National Park (GBNP) (NPS unpublished annual humpback whale monitoring reports available from GBNP, Gustavus, AK 99862, authors; 1985–1987 C. S. Baker, 1988 C. S. Baker and J. M. Straley, 1989–1990 J. M. Straley, 1991–1992 C. M. Gabriele), University of Hawaii, and independent researchers (Baker 1985; Baker *et al.* 1985, 1986, 1992; Perry *et al.* 1990; Straley 1990; Gabriele 1992). In some cases observations from earlier years were available to confirm minimum age of individuals, although not reproductive status (Jurasz *et al.* 1981, Jurasz and Jurasz 1981). Sighting histories were developed based on repeated boat-based observations and photographs of the ventral surface of the flukes of each individual whale. We determined that a mother/calf pair was an adult whale accompanied by a small calf (estimated length 4–8 m) which exhibited a close, consistent affiliation. Minimum ages of the females in this study were calculated by using 5 yr as the average age at sexual maturity (Chittleborough 1959, Nishiwaki 1959, Robins 1960, Clapham and Mayo 1987*b*, Clapham 1992), and assuming that females had reached this age just prior to the year each female was observed with her first calf.

Five females in the study area were observed with a calf in two or three consecutive summers (Table 1). Whales #581 and #193 were each seen with a different calf in three consecutive summers. Whales #235, #895, and #1121 were each seen with different calves in two consecutive summers. Three of these females have had long-term sighting histories in southeastern Alaska, as shown in Table 1.

A total of 12 calves were born to these five females during annual calving intervals. Ten calves were photoidentified and two have since been resighted. All three of #581's 1987–1989 calves were photographed. Her 1987 calf was resighted in 1990, 91, and 92. All three of #193's 1990–1992 calves were photographed. None have been resighted. One of #235's calves was photographed and has not been resighted. Whale #895's 1987 calf was photographed in its birth year and resighted in 1990. Both of #1121's calves were photographed and have yet to be resighted.

These data demonstrate that calves born during annual cycles can survive to the feeding grounds and that postpartum ovulation and conception occur in the absence of neonatal mortality. In addition, calves born at the start of an annual cycle (calves suckled while the mother was pregnant) can survive to later years, as seen with #581's first annual calf, and calves born later in the sequence

Table 1. Sighting histories of female humpback whales calving in consecutive years.

	Year															
ID#	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
235	A	*	A	A	M	*	*	M	*	A	M	M	A	A	M	A
193	*	*	A	*	A	M	A	A	A	M	A	A	A	M	M	M
581	*	*	*	*	A	A	A	M	A	A	M	M	M	A	M	A
895	*	*	*	*	*	*	M	*	*	M	M	*	*	*	A	*
1121	*	*	*	*	*	*	*	*	*	*	*	*	*	*	M	M

Note: A = adult without calf; * = no sighting; M = mother with calf.

(gestation occurred while the mother nursed an older sibling) can also survive to later years, as seen with #895's last calf.

Based on long-term sighting histories of three whales (#235, #193, and #581) annual reproduction occurred when they were a minimum of 9–14 yr old, and after the production of at least one calf (Table 1). This suggests that older females are better able to achieve annual reproduction. Corroborating studies from Massachusetts Bay (Clapham and Mayo 1990) and Prince William Sound (von Ziegesar and Matkin 1989) show annual calving occurred later in the sighting histories, after having one or two calves, for all females with one-year reproductive cycles. The estimated age at which postpartum ovulation occurred in eight western Australia females is between 10 and 36 yr and is evenly distributed across this age range (Chittleborough, personal communication).

We consider it likely that postpartum ovulation is a common event in female humpback whales, but that only a proportion of ovulating females can maintain annual pregnancies. The behavior of male 'escorts' on the breeding grounds actively pursuing females with newborn calves (Darling *et al.* 1983, Mobley and Herman 1985) has been interpreted as males searching for females in estrus. This further corroborates that ovulation occurs postpartum and, if fertilization is successful, that maintaining the pregnancy could be dependent on the physiological and metabolic condition of the mother (Gabriele 1992).

Larger body size with the increased ability to store fat may be an important component enabling older females to achieve annual reproduction. The ability to find prey may rely in part on experience, which would also increase with age. In baleen whales the energy demands of pregnancy and, especially, lactation are high (Lockyer 1984). Clapham and Mayo (1987*a*) suggest that the survival of calves born in successive years might be lower than those born to whales at two or more year intervals due to these energy demands. Although our observations are insufficient to provide conclusions on survival rates of whales born in different calving intervals, we have provided evidence that annual reproductive intervals can result in successful survival of these offspring, independent of their position in the annual cycle. It seems likely that to sustain annual reproduction, sufficient prey resources must be found for at least one feeding season preceding conception, through the first pregnancy, continuing during the year of simultaneous pregnancy and lactation, and through the lactation of the second calf. We conclude that yearly ovulation may not be atypical, with the potential of conception and carrying the foetus to term dependent on the female's body condition.

This research was supported by the National Park Service, Glacier Bay National Park, Alaska; J. Straley Investigations, Sitka, Alaska; and the Marine Mammal Commission (contract number MM3309822-5). These data were collected under National Marine Fisheries Service scientific research permit #600 issued to Glacier Bay National Park and permit #571 issued to J. Straley. The authors thank J. Jacobsen, D. Matkin, and A. Perry for assistance in data collection and G. Chittleborough for contributing historical data. We also thank G. Chittleborough, P. Clapham, S. Mizroch, A. Perry, and an anonymous reviewer for commenting on the draft manuscript.

Literature Cited

Baker, C. S. 1985. The population structure and social organization of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. Ph.D. dissertation, University of Hawaii. 306 pp.

Baker, C. S., L. M. Herman, A. Perry, W. S. Lawton, J. M. Straley and J. H. Straley. 1985. Population characteristics and migration of humpback whales in southeastern Alaska. Marine Mammal Science 1:304–323.

Baker, C. S., L. M. Herman, A. Perry, W. S. Lawton, J. M. Straley, A. A. Wolman, G. D. Kaufman, H. E. Winn, J. D. Hall, J. M. Reinke and J. Ostman. 1986. Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. Marine Ecology-Progress Series 31:105–119.

Baker, C. S., A. Perry and L. M. Herman. 1987. Reproductive histories of female humpback whales *Megaptera novaeangliae* in the North Pacific. Marine Ecology-Progress Series 41:103–114.

Baker, C. S., J. M. Straley and A. Perry. 1992. Population characteristics of individually identified humpback whales in southeastern Alaska: summer and fall 1986. Fishery Bulletin 90:429–437.

Chittleborough, R. G. 1958. The breeding cycle of the female humpback whale, *Megaptera nodosa*. Australian Journal of Marine and Freshwater Research 9:1–18.

Chittleborough, R. G. 1959. Determination of age in the humpback whale, *Megaptera nodosa* (Bonnaterre). Australian Journal of Marine and Freshwater Research 10:125–143.

Clapham, P. J. 1992. Age at attainment of sexual maturity in humpback whales, *Megaptera novaeangliae*. Canadian Journal of Zoology 70:1470–1472.

Clapham, P. J., and C. A. Mayo. 1987*a*. Reproduction and recruitment of humpback whales, *Megaptera novaeangliae* observed in the Massachusetts Bay, 1979–1985. Canadian Journal of Zoology 65:2853–2863.

Clapham, P. J., and C. A. Mayo. 1987*b*. The attainment of sexual maturity in two female humpback whales. Marine Mammal Science 3:279–283.

Clapham, P. J., and C. A. Mayo. 1990. Reproduction of humpback whales (*Megaptera novaeangliae*) observed in the Gulf of Maine. Reports of the International Whaling Commission (Special Issue 12):171–175.

Darling, J. D. 1983. Migrations, abundance and behavior of Hawaiian humpback whales, *Megaptera novaeangliae* (Borowski). Ph.D. dissertation, University of California Santa Cruz. 147 pp.

Darling, J. D., K. M. Gibson and G. K. Silber. 1983. Observations on the abundance and behavior of humpback whales (*Megaptera novaeangliae*) off West Maui, Hawaii, 1977–1979. Pages 201–222 *in* R. S. Payne, ed. Communication and behavior of whales, AAAS Selected Symposia Series. Westview Press, Boulder, CO.

Gabriele, C. M. 1992. The behavior and residence characteristics of reproductive classes of humpback whales (*Megaptera novaeangliae*) in the Hawaiian islands. Master's thesis, University of Hawaii. 99 pp.

Glockner-Ferrari, D. A., and M. J. Ferrari. 1984. Reproduction in humpback whales, *Megaptera novaeangliae*, in Hawaiian waters. Reports of the International Whaling Commission (Special Issue 6):237–242.

Glockner-Ferrari, D. A., and M. J. Ferrari. 1990. Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters, 1975–1988: the life history, reproductive rates and behavior of known individuals identified through surface and underwater photography. Reports of the International Whaling Commission (Special Issue 12):161–169.

Jurasz, C. M., and V. P. Jurasz. 1981. Censusing and establishing age composition of humpback whales (*Megaptera novaeangliae*) by employing photodocumentation

in Glacier Bay National Monument, Alaska. Unpublished report available from NPS, 2525 Gambell St., Anchorage, Alaska 99503. 44 pp.

JURASZ, C. M., V. P. JURASZ AND E. L. NOBLE. 1981. An examination of the distribution of humpback whales (*Megaptera novaeangliae*) in southeast Alaska. Unpublished report available from the State of Alaska, Department of Fish and Game, Division of FRED, Juneau, Alaska 99801. 87 pp.

KATONA, S., P. BAXTER, O. BRAZIER, S. KRAUS, J. PERKINS AND H. WHITEHEAD. 1979. Identification of humpback whales by fluke photographs. Pages 33–44 *in* H. E. Winn and B. L. Olla, eds. Behavior of marine mammals, Volume 3. Plenum Press, New York, NY.

LOCKYER, C. 1984. Review of baleen whale (Mysticeti) reproduction and implications for management. Reports of the International Whaling Commission (Special Issue 6):27–50.

MATTHEWS, L. H. 1937. The humpback whale, *Megaptera nodosa*. Discovery Reports 17:7–92.

MOBLEY, J. M., AND L. M. HERMAN. 1985. Transience of affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. Canadian Journal of Zoology 63:762–772.

NISHIWAKI, M. 1959. Humpback whales in Ryukyuan waters. Scientific Reports of the Whales Research Institute 14:49–87.

PERRY, A., C. S. BAKER AND L. M. HERMAN. 1990. Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. Reports of the International Whaling Commission (Special Issue 12):307–317.

ROBINS, J. P. 1960. Age studies on the female humpback whale, *Megaptera nodosa* (Bonnaterre), in east Australian waters. Australian Journal of Marine and Freshwater Research 11:1–13.

STRALEY, J. M. 1990. Fall and winter occurrence of humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. Reports of the International Whaling Commission (Special Issue 12):319–323.

VON ZIEGESAR, O., AND C. MATKIN. 1989. A catalogue of Prince William Sound humpback whales identified by fluke photographs between the years 1977 and 1988. Available from North Gulf Oceanic Society, P.O. Box 15244, Homer, Alaska 99603. 28 pp.

JANICE M. STRALEY, P.O. Box 273, Sitka, Alaska 99835; CHRISTINE M. GABRIELE, Glacier Bay National Park, Gustavus, Alaska 99826; C. SCOTT BAKER, Kewalo Marine Laboratory, PBRC, University of Hawaii, 41 Ahui Street, Honolulu, Hawaii 96813. Received 26 January 1992. Accepted 6 August 1993.