

Observations of a Female North Atlantic Right Whale (*Eubalaena glacialis*) in Simultaneous Copulation with Two Males: Supporting Evidence for Sperm Competition

Bruce Mate,¹ Peter Duley,² Barbara Lagerquist,¹ Frederick Wenzel,³
Alison Stimpert,³ and Phil Clapham⁴

¹Fisheries and Wildlife, Coastal Oregon Marine Experiment Station,
Hatfield Marine Science Center, Oregon State University, Newport, OR 97365, USA

²P.O. Box 25, Sullivan, ME 04664, USA

³Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543, USA

⁴National Marine Mammal Laboratory, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115, USA

Abstract

Given the huge size of their testes (approximately 1,000 kg), it has been hypothesized that North Atlantic right whales (*Eubalaena glacialis*) have a mating system that is based upon sperm competition. Herein, we report an observation which provides support for this hypothesis. On 11 August 2000 in the Bay of Fundy in Canada, a mature female right whale was observed copulating simultaneously with two mature males. The female made no attempt to resist copulation. For anatomical reasons, double copulation would be difficult or impossible in most mammals; however, it is quite feasible in right whales, and the fact that it actually occurs provides strong support for the belief that females of this species promote sperm competition as a mating strategy.

Key Words: North Atlantic right whale, *Eubalaena glacialis*, mating system, mating strategies, sperm competition

Introduction

Relatively little is known regarding the mating systems of most baleen whales. Inferences have been drawn for a few species based largely upon observations of courtship-related behaviors and of both inter- and intra-sexual interactions. Among those species which have been subject to such study, it is clear that significant behavioral differences exist, reflecting a variety of mating systems.

For example, humpback whales (*Megaptera novaeangliae*) possess a polygynous system, with features that resemble those of a lek (Clapham, 1996; Mobley & Herman, 1985). Male humpbacks advertise by singing; also, they directly compete—often aggressively—with each other

for access to females. In addition, molecular genetic data have shown that successive calves of individually identified females are fathered by different males (Clapham & Palsbøll, 1997).

In contrast, right whales (*Eubalaena* spp.) rarely exhibit aggressive intrasexual interactions (Kraus & Hatch, 2001). Courtship groups consisting of a single female and sometimes many males are observed virtually year-round, however, with males jostling for position next to the female (Kraus & Hatch, 2001; Stone et al., 1988). Such assemblages are known as Surface Active Groups (SAGs) and have been recorded in all major right whale habitats. Copulation sometimes is observed in SAGs, with the female often lying upside-down at the surface during intromission.

Brownell & Ralls (1986) reviewed available data on testes size in male baleen whales and found considerable interspecific differences relative to body mass. Despite being the largest mysticetes, blue whales (*Balaenoptera musculus*) have small testes that represent only about 0.06% of maximum body mass; the mating system of this species (and of most other balaenopterids) is unknown. In marked contrast, right whales possess the largest testes in the animal kingdom. At a combined weight of approximately one metric ton, they represent 1.3% of the maximum body weight of the animal. Brownell & Ralls used these data to hypothesize that sperm competition (Parker, 1970) was a major feature of the mating system of right whales. Specifically, they proposed that male right whales should not exhibit direct intrasexual aggression but, rather, should compete primarily through the quantity and quality of sperm delivered to a female; this is in contrast to humpback whales, which have relatively small testes and (as predicted) frequently fight over access to females. They also noted that the penis is disproportionately

long in right whales (Brownell & Ralls, 1986), an adaptation which presumably facilitates delivery of semen as close as possible to the cervix.

A common feature of a mating system based upon sperm competition is that females mate with multiple males, sometimes in quick succession (Birkhead & Moller, 1998; Clutton-Brock, 1989; Parker, 1970). Multiple matings of a single female within a short period of time have been reported for North Atlantic right whales (*E. glacialis*) by Kraus & Hatch (2001) and Stone et al. (1988), and for southern right whales (*E. australis*) by Payne (1986). Herein, we report the first observation of a female right whale copulating simultaneously with two males.

Materials and Methods

The observations described here were made during a research cruise conducted in August 2000 in the Bay of Fundy, which is the principal known summer feeding and nursery area for North Atlantic right whales (Kraus et al., 1986a). The purpose of the cruise was to characterize the summer feeding habitats of this population by attaching satellite-monitored radio tags and time depth recorders to right whales, and to conduct related oceanographic sampling. The work was based from the 47-m research vessel *Delaware II*; tagging operations were conducted using two rigid-hulled inflatable boats (RHIBs). Observations were filmed using a Panasonic digital video recorder. Right whales were identified individually from the pattern of callosities on their heads, as well as from prominent scars (Kraus et al., 1986b).

Results

On 11 August 2000 at 1552 h (Eastern Daylight Time), one of the RHIBs encountered a SAG in position 44° 34.7' N, 66° 33.9' W (approximately 10 miles southeast of Grand Manan Island). The group consisted of three individual right whales and was characterized by typical SAG behaviors, including rolling and jostling at the surface. The two males were distinguished here by their field identity codes, JOS-E and JOS-B. At 15:52:54 h, the female in the group rolled over and presented her ventral side at the surface. A few seconds later, the first male (JOS-E) rolled on his left side to the left of the female; JOS-E's ventral aspect was presented to the female, and his penis clearly was extruded. He stroked her with his right pectoral fin, first near the genital region and then in a more anterior location on the body just behind her right flipper. Intromission was achieved at 15:53:20 h, with the tip of the penis clearly inside the female's

vagina. Copulation lasted until JOS-E disengaged to roll and breathe at 15:54:57 h. Several undulations of the penis were observed during the copulation, but it is not known whether these were associated with ejaculation.

The group continued with general SAG behaviors but with no further copulation until 16:11:02 h when the female once again rolled onto her back. As she rolled, a new male in the group (JOS-Y) surfaced on her right side. JOS-E also was positioned on her right side, and at 16:11:05 h moved across her peduncle to resume his previous position along the female's left side, again stroking her with his right flipper. Intromission was achieved by JOS-E at 16:11:30 h. At 16:11:29 h, a bubble cloud was observed from a third unidentified male, who then surfaced between the female and JOS-Y, taking the position along the female's right side. JOS-Y remained at the surface to the right of the female, oriented towards her midsection, but did not copulate with her. At 16:12:03 h, the third male's penis was observed to have entered the female's vagina. Simultaneous copulation (Figure 1) continued for 40 s until 16:12:43 h, when JOS-E broke contact to roll and breathe. It was not clear if the third male also disengaged at this time, but he appeared to break contact before the female rolled to breathe 15 s later. Identification of the third male could not be confirmed, but based on positioning, it appears this whale was JOS-B. No further copulation occurred thereafter, and the group dove and appeared to break up. We could not confirm whether either of the two males ejaculated during the copulation period.

Subsequent analysis of photographs revealed that the three principal individuals in this event were North Atlantic Right Whale Catalogue (NARWC) #1241, NARWC #2201, and NARWC #1152. NARWC #1241 is a known mature female born in 1982. She has had three calves, most recently in 2002, and was not seen with a calf in



Figure 1. Simultaneous copulation of two male right whales with a female in the Bay of Fundy, 11 August 2000

the season following this mating event. NARWC #2201 (JOS-E) is an 8-year-old male, and NARWC #1152 (JOS-B) is an adult male of unknown age, first seen in 1981. The fourth individual was identified as NARWC #1150 (JOS-Y), a known adult male first seen in 1979.

Discussion

The event described above provides strong support for the hypothesis by Brownell & Ralls (1986) that sperm competition is a principal feature of the right whale's mating system. Simultaneous intromission by both males clearly was observed; the female remained passively on her back throughout; and no male intrasexual aggression was evident at any time. The huge size of right whale testes have presumably evolved to facilitate production of large volumes of seminal fluid to compete with, and possibly "wash out," the sperm of other males in serial or simultaneous copulation events. Similar explanations have been put forward with regard to a wide variety of other taxa in which males are characterized by large testes (Birkhead & Moller, 1998).

It must be noted that right whale calves are born almost exclusively in midwinter following a one-year gestation (Best, 1994; Kraus et al., 1986a). Although delayed implantation is common in pinnipeds, there is no evidence for it in any cetacean (Boness et al., 2002). Consequently, sexual activity among right whales occurring during spring, summer, and autumn does not directly lead to reproductive success, and its function at these times remains unclear. This does not necessarily negate the validity of the present observation as evidence for sperm competition, but it does suggest that the function of sexual interactions (including copulation) in this species can be socially complex.

The role and strategy of the female right whale in the event described here is unclear, although it is probably significant that she made no efforts to resist the initiation of copulation by either male. For anatomical reasons, double copulation would be difficult or impossible in most mammals; however, it is quite feasible in right whales (and many other cetaceans), and the fact that it actually occurs provides some support for the belief that females actively promote sperm competition as a mating strategy. That double copulation was observed at the surface also may mean it is more common than previously thought if it is occurring more frequently than that under water, where the majority of right whale matings are believed to occur (Kraus & Hatch, 2001). It also is possible (though perhaps unlikely) that females are actually not enthusiastic participants in these events

and submit solely because it takes less energy than continued resistance and pursuit.

That females frequently lie at the surface upside-down in SAGs may confer an advantage upon larger males since the penis of a younger or smaller animal may not be sufficiently long enough to extend across a female's body to achieve intromission. Whether this represents an intentional strategy by females seeking to select larger, older mates is unknown, but this is an interesting possibility that merits further consideration.

Acknowledgments

We thank Richard Merrick, Koen Van Waerebeek, and an anonymous referee for their comments on the manuscript, and Marilyn Marx and the New England Aquarium for identifying the individual right whales involved. Thanks are also due to the scientific staff and crew of the NOAA ship *Delaware II* for their help in the field. This work was conducted under a research permit issued by the Canadian Department of Fisheries and Oceans.

Literature Cited

- Best, P. B. (1994). Seasonality of reproduction and the length of gestation in southern right whales, *Eubalaena australis*. *Journal of Zoology*, 232, 175-189.
- Birkhead, T. R., & Moller, A. P. (1998). *Sperm competition and sexual selection*. New York: Academic Press. 856 pp.
- Boness, D. J., Clapham, P. J., & Mesnick, S. L. (2002). Life history and reproductive strategies. In R. Hoelzel (Ed.), *Marine mammal biology: An evolutionary approach* (pp. 278-324). Oxford: Blackwell Science.
- Brownell, R. L., & Ralls, K. (1986). Potential for sperm competition in baleen whales. *Reports of the International Whaling Commission*, 8(Special Issue), 97-112.
- Clapham, P. J. (1996). The social and reproductive biology of humpback whales: An ecological perspective. *Mammal Review*, 26, 27-49.
- Clapham, P. J., & Palsbøll, P. J. (1997). Molecular analysis of paternity shows promiscuous mating in female humpback whales (*Megaptera novaeangliae*, Borowski). *Proceedings of the Royal Society of London Series B*, 264, 95-98.
- Clutton-Brock, T. H. (1989). Mammalian mating systems. *Proceedings of the Royal Society of London Series B*, 236, 339-372.
- Kraus, S. D., & Hatch, J. J. (2001). Mating strategies in the North Atlantic right whale. *Journal of Cetacean Research and Management*, 2(Special Issue), 237-244.
- Kraus, S. D., Prescott, J. H., Knowlton, A. R., & Stone, G. S. (1986a). Migration and calving of right whales (*Eubalaena glacialis*) in the western North Atlantic. *Reports of the International Whaling Commission*, 10 (Special Issue), 139-144.

- Kraus, S. D., Moore, K. E., Price, C. A., Crone, M. J., Watkins, W. A., Winn, H. E., & Prescott, J. H. (1986b). The use of photographs to identify individual North Atlantic right whales (*Eubalaena glacialis*). *Reports of the International Whaling Commission*, 10(Special Issue), 145-151.
- Mobley, J. R., & Herman, L. M. (1985). Transience of social affiliations among humpback whales (*Megaptera novaeangliae*) on the Hawaiian wintering grounds. *Canadian Journal of Zoology*, 63, 762-772.
- Parker, G. A. (1970). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews*, 45, 263-281.
- Payne, R. S. (1986). Long-term behavioral studies of the southern right whale (*Eubalaena australis*). *Reports of the International Whaling Commission*, 10(Special Issue), 161-167.
- Stone, G. S., Kraus, S. D., Prescott, J. H., & Hazard, K. W. (1988). Significant aggregations of the endangered right whale, *Eubalaena glacialis*, on the continental shelf of Nova Scotia. *Canadian Field Naturalist*, 102, 471-474.