

TEMPERATURE-VISCOSITY RELATIONS OF BOWHEAD  
WHALE BLOOD: A POSSIBLE MECHANISM FOR  
MAINTAINING COLD BLOOD FLOW

ROBERT ELSNER

Institute of Marine Science,  
University of Alaska, Fairbanks, Alaska 99775, U.S.A.  
E-mail: ffre@ims.uaf.edu

HERBERT J. MEISELMAN

Department of Physiology and Biophysics,  
Keck School of Medicine,  
University of Southern California,  
Los Angeles, California 90033, U.S.A.

OGUZ K. BASKURT

Department of Physiology,  
Akdeniz University, Faculty of Medicine,  
Antalya, Turkey 07070

Cetacean temperature regulation depends in part on adjustments of peripheral circulation, notably in the tail flukes, to the needs for heat conservation or dissipation. The structural basis for such regulation is associated with two circulatory pathways: countercurrent heat conservation by thermal transfer from blood flowing in arteries to surrounding venous networks, and an alternate heat loss route *via* more superficial arteriovenous anastomoses (AVAs) (Scholander and Schevill 1955, Elsner *et al.* 1974).

The habitat of the bowhead whale, *Balaena mysticetus*, includes the Chukchi-Beaufort Seas north of Alaska during the ice-covered season (Burns *et al.* 1993) and results in several months exposure to freezing sea water, temperature  $-1.8^{\circ}\text{C}$ . The bowhead's defenses against this cold exposure include a massive subcutaneous blubber layer, up to 50 cm over the midbody. Additionally, the bowhead whale's surface to volume ratio, predictably the smallest of any cetacean due to its more globular shape, endows this species with superior heat retention geometry. Indeed, analysis by Hokkanen (1990) suggests that, because of these conditions, large whales may be threatened by overheating rather than cooling, even while immersed in ice water.

Somewhat at odds with the Hokkanen conclusion regarding the whale's thermal state in cold water are recent observations suggesting that the bowhead's thermal balance may be influenced by other features. Its deep body temperatures, determined by multiple deep thermocouple probes, remain constant for several

hours after death at 33°–34°C (J. C. George, D. Goering, M. Sturm, R. Elsner and E. Follman, unpublished data). These direct observations contrast with the Hokkanen (1990) assumption of a 37°C core, indicating a reduced likelihood of overheating and a greater dependence upon mechanisms for heat conservation. Temperatures within its tail in the regions where circulatory thermal exchange occurs are about 5°–10°C. Further, AVAs isolated from the tail flukes respond more vigorously to sympathetic vasoconstrictor activation than do arteries of the countercurrent complex (R. Elsner, J. C. George and T. O'Hara, unpublished data), demonstrating the existence of effective mechanisms in support of heat conservation when required.

Blood flow in a given vascular bed is determined in part by the network geometry and the fluidity of blood (Schmid-Schönbein 1988). In turn, blood fluidity is determined by properties of blood cells and plasma, and by shear rate, which is roughly comparable to flow rate (Chien 1975). Blood viscosity increases as temperature is lowered, as demonstrated in samples of human (Rand *et al.* 1964) and bird (Clarke and Nicol 1993) blood. Such temperature dependent decreases of blood fluidity significantly increase flow resistance, thereby limiting the function of thermoregulatory mechanisms.

The question that we wished to explore was whether the temperature dependence of whale blood flow behavior might show adaptation for maintaining peripheral blood flow in these animals, such an adaptation being beneficial for the animal's temperature regulation. Accordingly, we investigated the apparent viscosity versus shear rate properties of bowhead whale blood over a range of temperatures known to be present in their tail thermal exchange circulation. The study was conducted at the Barrow Arctic Science Consortium facility, Barrow, Alaska, during the spring subsistence whaling season. Bowhead whales were harvested in sea ice leads by Inupiat Eskimo hunters and towed to the ice edge where they were hauled out for processing. The whale hunt is carried out in accordance with agreements established between the Native community and the International Whaling Commission.

Blood samples were obtained from two adult female whales, 11.7 m and 15.4 m long and of normal appearance, shortly after beaching on the ice and approximately four and seven hours, respectively, after death. Heparinized (15 IU/ml) blood samples were drawn from superficial veins in the roof of the mouth of the whales, a region exposed to cold sea water from death until blood drawing. The samples were placed in insulated containers to prevent freezing and were transported within one hour to the laboratory. Whole blood and red blood cell (RBC) suspension hematocrits were determined by the microhematocrit method, centrifuged at  $12,000 \times g$  for 4 min. Whale RBC, mean corpuscular volume (MCV), and mean corpuscular hemoglobin concentration (MCHC) were determined by an electronic hematology analyzer (Beckman Coulter Co., Hialeah, FL), and RBC shape by light microscopy of dilute wet mounts. Human blood samples were collected, following informed verbal consent, from the antecubital vein of six healthy, adult individuals (five male, one female) and were anticoagulated with 15 IU/ml of heparin. Hematological and hemorheological measurements of both whale and reference human bloods were completed within four hours after sample collection.

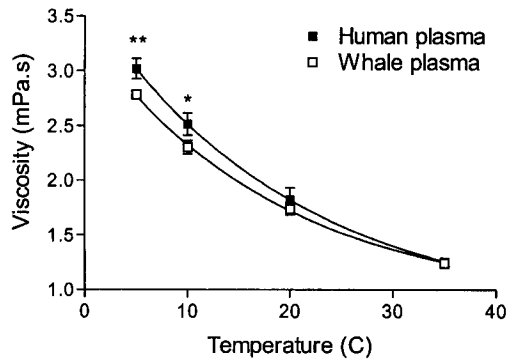


Figure 1. Effect of temperature on mean whale ( $n = 2$ ) and human ( $n = 6$ ) plasma viscosity. Error bars correspond to one standard deviation. Difference between human and whale values by two-way ANOVA: \*  $P < 0.05$ , \*\*  $P < 0.01$ .

Blood viscosities were determined with a Wells-Brookfield cone-plate rotational viscometer (model RVTDV-200, Brookfield Engineering Labs, Middleboro, MA) at shear rates between 75 and 750  $\text{sec}^{-1}$  and at 5°, 10°, 20°, and 35°C. Plasma viscosities were determined with this viscometer at the same temperatures at 1,500  $\text{sec}^{-1}$ . For comparing whale and human bloods, the hematocrit of all blood samples was adjusted to 0.5 L/L by adding or removing a calculated amount of autologous plasma obtained by centrifugation at  $4,000 \times g$  for 10 min.

Hematocrit values of the blood samples collected from the two whales were 0.58 and 0.64 L/L, MCV values were 176 and 177 fL, and MCHC values were 344 and 339 g/L. The mean hematocrit value for the six human samples was 0.44 L/L (range 0.38–0.48). Nominal human ranges are 85–95 fL for MCV and 320–340 g/L for MCHC (Rapaport 1987). Microscopic examination of whale red blood cells indicated that the cells were smooth biconcave disks, similar in appearance to human RBC, with diameters slightly greater than human RBC.

Plasma viscosity values were essentially identical for whale and human samples at 35°C, whereas whale plasma viscosity was significantly lower than human at 10° and 5°C as tested by two-way ANOVA (Fig. 1). Both whale and human plasma viscosity increased over the range from 5° to 35°C, consistent with values for water over the same temperatures.

Both whale and human blood behaved as non-Newtonian suspensions, with viscosity decreasing as the shear rate is increased (Fig 2). However, at lower temperatures, the degree of non-Newtonian behavior was less for whale blood. At 5° and 10°C, a decrease of shear rate from 750 to 75  $\text{sec}^{-1}$  resulted in a 74% increase for human blood but only a 29% increase in viscosity of whale blood, whereas at 20° and 35°C the increase in viscosity was similar for both species.

Direct comparisons between whale and human blood viscosities indicate differences that are shear rate and temperature dependent. Statistical analysis by two-way ANOVA indicated that when measured at 5° or 10°C and at lower shear rates, whale blood has a significantly lower viscosity: at 5°C, whale blood is about 30% less viscous than human blood at a shear rate of 75  $\text{sec}^{-1}$ , yet differs by less than 4%

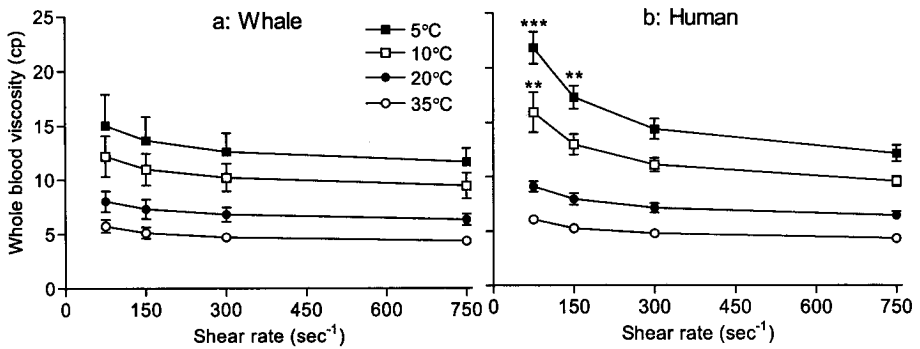


Figure 2. Mean  $\pm$  1 SD whole blood viscosity determined at 5°, 10°, 20°, and 35°C in (a) whale blood and (b) human blood. Samples adjusted to hematocrits of 0.5 L/L, whale blood ( $n = 2$ ), human blood, ( $n = 6$ ). Difference from whale values by two-way ANOVA: \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

at 750  $\text{sec}^{-1}$  (Fig. 3). Conversely, at 35°C, the ratio is independent of shear rate over the entire range (mean =  $0.98 \pm 0.02$  SD).

Our preliminary study suggests that at 35°C, approximating the core temperatures of bowheads and humans, both the absolute values of viscosity and the shear rate dependence of viscosity for blood at a 0.5 L/L hematocrit are essentially identical for these two species. (Fig. 2, 3). By contrast, at 5°C, a temperature approximating that of peripheral circulation within the whale's flukes, the effect of this reduced temperature is shear rate dependent (Fig. 3). At a high shear rate, 750  $\text{sec}^{-1}$ , the viscosities do not differ, whereas at the lowest employed in the present study, 75  $\text{sec}^{-1}$ , whale blood had a 30% lower viscosity. Further, based upon the trend indicated in Figure 3, it is possible that even greater differences in temperature sensitivity might be observed at shear rates less than 75  $\text{sec}^{-1}$ . Lower shear rates may exist in the low-flow regions of the whale's circulation, since for a wall shear of 75  $\text{sec}^{-1}$  in a 1-mm diameter vessel, the average blood flow velocity is still relatively brisk at 1 cm/sec (Chien 1975). Reductions of flow would yield even lower shear rates.

Both bowhead whale and human blood behave as non-Newtonian fluids (Fig. 2), viscosity decreasing with increasing shear rate. At higher rates of shear, important determinants of viscosity are hematocrit, plasma viscosity, and RBC deformability (Chien 1975). Given that all RBC suspensions were adjusted to a hematocrit of 0.5 L/L, that plasma viscosities were similar (Fig. 1), and that high shear viscosities were essentially identical (Fig. 3), it can be inferred that the deformability of whale and human RBC do not differ significantly and that this similarity exists over 5°–35°C. However, some caution is required with respect to this conclusion. RBC deformation depends upon the magnitude of the applied deforming force, and blood viscosity data obtained at high levels of applied fluid shear forces, 750  $\text{sec}^{-1}$ , tend to reflect the limiting ability of the RBC to deform (Baskurt and Meiselman 1997). Therefore, high shear viscometric data may be insensitive to subtle changes of deformability, whereas at more moderate levels of shear, differences of RBC

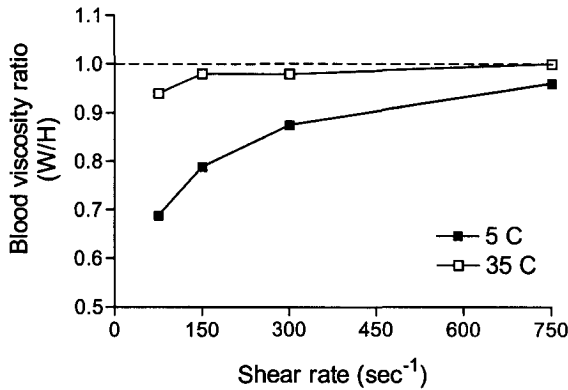


Figure 3. Effect of shear rate on the mean ratio of whale (W) to human (H) blood viscosity at 5° and 35°C. Data from Figure 2. Horizontal dashed line represents a ratio of one.

deformability may become more evident (Baskurt and Meiselman 1997). Thus, the lower viscosity for whale blood at 5°C and at moderate shear rates (Fig. 3) suggests the possibility of greater deformability for whale RBC under these conditions.

In summary, our results indicate that while the flow behavior of bowhead whale blood is similar to human blood at or near deep body temperature, it is markedly less viscous and less sensitive to shear rate at lower temperatures of 5°–10°C. These lower temperatures are consistent with regions within the bowhead tail where circulatory thermal exchange occurs. It thus appears likely that this reduced temperature dependence of blood viscosity contributes to the maintenance of blood flow serving temperature regulation.

#### ACKNOWLEDGMENTS

This research was supported by NIH Research Grants HL15722, HL 48484, and FIRCA IR03 TW01295. We thank whaling captains, Arnold Brower and George Ahmaogak, who provided the opportunities for blood sampling from whales. The Barrow Arctic Science Consortium provided laboratory space and general assistance. Karen St. John, Barrow Alaska Native Hospital, and Cyd Hanns, North Slope Borough Veterinary Clinic, gave generous help in numerous ways. We are grateful for the field assistance of Matt Irinaga and Victoria Woshner, North Slope Borough Dept. of Wildlife Management, and of Sharon and Ben Meiselman. Mike Castellini graciously loaned us a temperature regulator when ours failed. We are also grateful for the helpful comments of reviewers. This work was performed under NMFS Marine Mammal Permit No. 932-1489.

#### LITERATURE CITED

- BASKURT, O. K., AND H. J. MEISELMAN. 1997. Cellular determinants of low-shear blood viscosity. *Biorheology* 34:235–247.
- BURNS, J. J., J. J. MONTAGUE AND C. J. COWLES, EDS. 1993. The bowhead whale. Special Publication No. 2, The Society of Marine Mammalogy, Lawrence, KS.

- CHIEN, S. 1975. Biophysical behavior of red cells in suspensions. Pages 1031–1133 in D. M. Surgenor, ed. *The red blood cell*. Academic Press, New York, NY.
- CLARKE, J., AND S. NICOL. 1993. Blood viscosity of the little penguin, *Eudyptula minor*, and the Adélie penguin, *Pygoscelis adeliae*: Effects of temperature and shear rate. *Physiological Zoology* 66:720–731.
- ELSNER, R., J. PIRIE, D. W. KENNEY AND S. SCHEMMER. 1974. Functional circulatory anatomy of cetacean appendages. Pages 143–159 in R. J. Harrison, ed. *Functional anatomy of marine mammals*. Volume 2. Academic Press, London and New York.
- HOKKANEN, J. E. I. 1990. Temperature regulation of marine mammals. *Journal of Theoretical Biology* 145:465–485.
- RAND, P. W., E. LACOMBE, H. E. HUNT AND W. H. AUSTIN. 1964. Viscosity of normal human blood under normothermic and hypothermic conditions. *Journal of Applied Physiology* 19:117–122.
- RAPAPORT, S. I. 1987. *Introduction to hematology*. J. B. Lippincott, Philadelphia, PA.
- SCHMID-SCHÖNBEIN, H. 1988. Fluid dynamics and hemorheology in vivo: The interactions of hemodynamic parameters and hemorheological “properties” in determining the flow behavior of blood in microvascular networks. Pages 129–219 in G. D. O. Lowe, ed. *Clinical blood rheology*. CRC Press.
- SCHOLANDER, P. F., AND W. E. SCHEVILL. 1955. Countercurrent vascular heat exchange in the fins of whales. *Journal of Applied Physiology* 8:279–282.

Received: 24 May 2003

Accepted: 9 October 2003