

## THERMOREGULATION OF THE INTRA-ABDOMINAL TESTES OF THE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*) DURING EXERCISE

D. A. PABST<sup>1</sup>, S. A. ROMMEL<sup>1</sup>, W. A. McLELLAN<sup>1</sup>, T. M. WILLIAMS<sup>2,\*</sup> AND T. K. ROWLES<sup>3</sup>

<sup>1</sup>Department of Biology, James Madison University, Harrisonburg, VA 22807, USA, <sup>2</sup>Naval Oceans Systems Center Hawaii Laboratory, PO Box 997, Code 511, Kailua, HA 96734, USA and <sup>3</sup>Department of Animal Science, University of Tennessee, Knoxville, TN 27901-1071, USA

Accepted 22 August 1994

### Summary

Dolphins possess a vascular countercurrent heat exchanger (CCHE) that functions to cool their intra-abdominal testes. Spermatic arteries in the posterior abdomen are juxtaposed to veins returning cooled blood from the surfaces of the dorsal fin and tail flukes. In this study, we investigated the effect of exercise on CCHE function in the bottlenose dolphin. The CCHE flanks a region of the bowel in the posterior abdomen and influences colonic temperatures. A rectal probe housing a linear array of seven copper–constantan thermocouples was designed to measure colonic temperatures simultaneously at positions anterior to, within and posterior to the region of the colon flanked by the CCHE. Immediately after vigorous swimming, temperatures at the CCHE decreased relative

to resting and pre-swim values: post-swim temperatures at the CCHE were maximally 0.5 °C cooler than pre-swim temperatures. These data suggest that the CCHE has an increased ability to cool the arterial blood supply to the testes when the dolphin is swimming. This ability could offset the increased thermal load on the testes in an exercising dolphin. To the best of our knowledge, this is the first report of deep body cooling in an exercising mammal that is not undertaking a dive.

Key words: bottlenose dolphin, countercurrent heat exchange, energetics, exercise, locomotion, testes, thermoregulation, *Tursiops truncatus*.

### Introduction

Most mammals require below core body temperatures for viable sperm production and maturation (for a review, see Bedford, 1977; Carrick and Setchell, 1977; Cowles, 1958, 1965; Moore, 1926; VanDemark and Free, 1970; Waites, 1970). Dolphins possess intra-abdominal testes surrounded by robust swimming muscles that could potentially be exposed to core, or above core, body temperatures when the dolphin is exercising. They also possess a vascular countercurrent heat exchanger (CCHE) that functions to regulate the temperature of their intra-abdominal testes (Rommel *et al.* 1992). The CCHE is formed by a venous plexus returning cooled blood from the surfaces of the dorsal fin and tail flukes juxtaposed to a spermatic arterial plexus supplying the testis (Fig. 1).

The CCHE flanks a region of the bowel in the posterior abdomen and influences colonic temperatures (Rommel *et al.* 1994). In bottlenose dolphins (*Tursiops truncatus*) under resting conditions, colonic temperatures measured in the region of the CCHE are cooler than temperatures measured anterior or posterior to this region. The influence of the CCHE on colonic temperatures is dependent upon a number of variables. For example, temperatures at the CCHE were 0.2–0.7 °C lower

than those at positions anterior to and/or posterior to the CCHE in peripubescent males and were 0.9–1.3 °C lower in a sexually mature male (Rommel *et al.* 1994). Temporary heating and cooling of the dorsal fin and tail flukes increased temperatures at the CCHE, but had little or no effect on temperatures posterior to its position. These results demonstrate that, under resting conditions, cooled blood is introduced into the deep abdominal cavity in a position to regulate the temperature of arterial blood flow to the dolphin testis.

The intra-abdominal testes of the bottlenose dolphin are literally wedged between two robust locomotor muscles, the m. hypaxialis and the m. rectus abdominus (Arkowitz and Rommel, 1985; Pabst, 1990) (Fig. 2). The position of the testes suggests that they could be exposed to local increases in temperature as the dolphin swims. In some terrestrial mammals, countercurrent heat exchangers work more efficiently during exercise (for example, Baker and Chapman, 1977; Caputa *et al.* 1976, 1991; Taylor and Lyman, 1972). To date, there exist no data on the effect of exercise on CCHE function in the bottlenose dolphin. The goal of this study was to investigate thermoregulation of the dolphin intra-abdominal testes during exercise.

\*Present address: Department of Biology, University of California at Santa Cruz, Santa Cruz, CA 95064, USA.

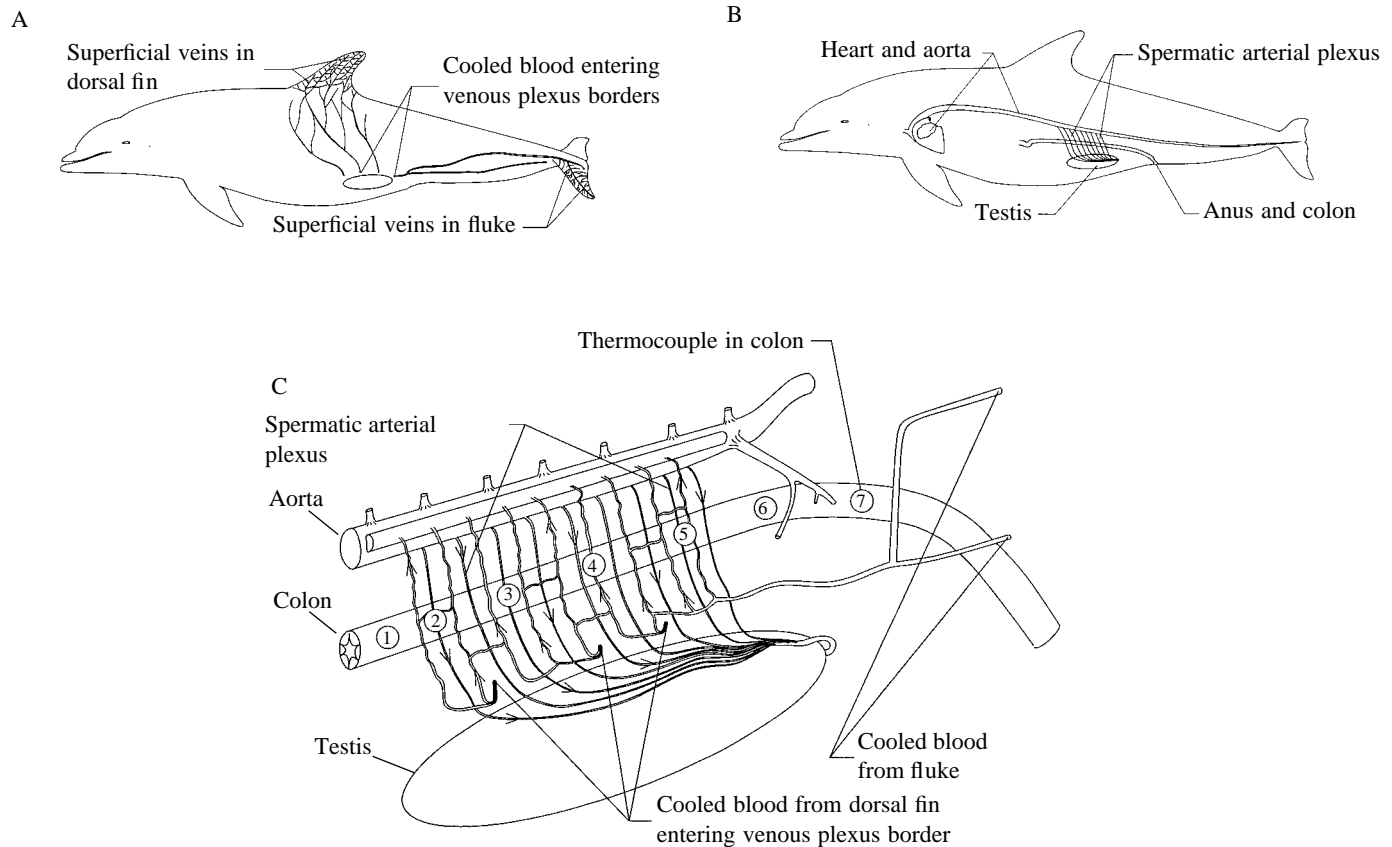


Fig. 1. Schematic topography of the countercurrent heat exchanger at the dolphin testis. (A) Blood in the superficial veins of the dorsal fin and the tail flukes is cooled by exposure to ambient water. Blood from these extremities is drained by relatively thick-walled, large veins that remain superficial (i.e. just beneath the blubber layer and superficial to the vertebral muscles) as they coalesce and course towards the abdominal cavity. These veins enter the posterior abdominal cavity, near the pelvic vestiges, and feed directly into the lateral and posterior margins of the lumbo-caudal venous plexus. Thus, relatively cool blood can be introduced into the deep posterior abdominal cavity near the testes. (B) The spermatic arterial plexus is a unique arrangement of arteries extending ventro-laterally from the lumbar aorta. The vessels are organized into a single layer and are oriented roughly parallel to each other. At the distal margin of the plexus, the arteries coalesce to form a cone-shaped structure, from which a single testicular artery continues posteriorly to enter the testis. (C) Oblique lateral view of the left half of the countercurrent heat exchanger. The juxtaposition of the lumbo-caudal venous plexus to the spermatic arterial plexus suggests that dolphins use countercurrent heat exchange to regulate the temperature of arterial blood flow to the testis. Arrowheads indicate the direction of blood flow. Cut ends at the lateral border of the lumbo-caudal venous plexus show where the superficial veins from the dorsal fin enter the abdominal cavity (see A). Note that the countercurrent heat exchanger flanks a region of colon in the posterior abdominal cavity. Numbers 1–7 represent the placement of thermocouples in the colon of a peripubescent male (see Materials and methods).

### Materials and methods

Colonic temperature, taken with a rectal probe, is often used as a clinical assessment of dolphin health (Sweeney and Ridgway, 1975). We chose this as a safe, relatively non-invasive, method for assaying the thermal effects of the CCHE. A linear array of seven copper–constantan thermocouples (Omega Teflon-coated, 30 gauge wire) were aligned on a 0.003 m outside diameter flexible plastic tube. This array was then covered with thin-walled, heat-shrink tubing. A rounded tip was fitted on the anterior end of the probe and the entire assembly was heated to shrink the wrap, thus making the probe completely waterproof and electrically non-conductive. The final outside diameter of the probe was 0.005 m. The dimensions of the probe and the relative positions of the thermocouples were based on anatomical measurements from dissections of stranded bottlenose dolphin carcasses,

approximately 2.20 m in total length. A flexure in the colon, approximately 0.50 m deep to the anus, determined maximum probe length. With animal safety foremost, we conservatively limited the length of the probe to 0.43 m. A band of surgical tape placed at 0.43 m marked the inserted probe depth and allowed us to inspect probe placement visually while temperatures were being measured. The thermocouples were positioned within the colon at the following distances anterior to the anus: no. 1, 0.42 m; no. 2, 0.40 m; no. 3, 0.35 m; no. 4, 0.30 m; no. 5, 0.25 m; no. 6, 0.20 m; and no. 7, 0.15 m. Fig. 1C illustrates the placement of the rectal probe relative to the CCHE in a 2.20 m bottlenose dolphin. The posterior-most thermocouple (no. 7) was 0.15 m deep to the anus, a position considered too shallow to measure a true deep core temperature (Sweeney and Ridgway, 1975; Ridgway, 1972).

Colonic temperatures were measured on two peripubescent

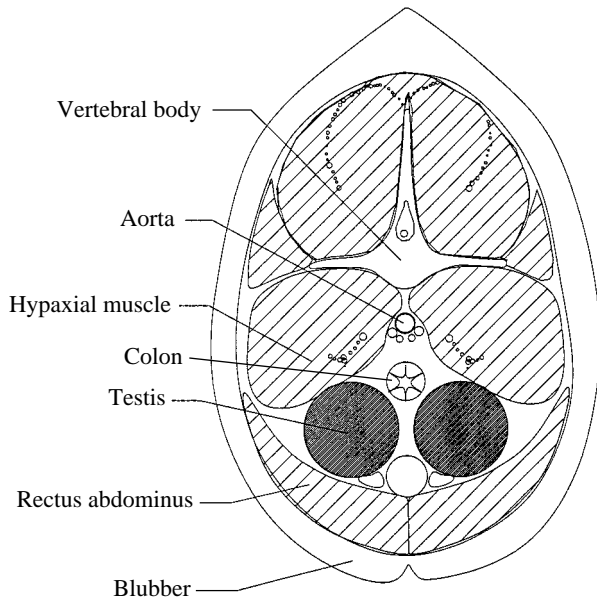


Fig. 2. Schematic representation of a cross section through a bottlenose dolphin at the level of the testes. The m. hypaxialis lumborum and the m. rectus abdominus surround the testes, suggesting that the testes could be exposed to local increases in temperature when these muscles are active during swimming.

male bottlenose dolphins (total length 2.33 m and 2.41 m; body mass 149 kg and 141 kg respectively) and one sexually mature male bottlenose dolphin (total length 2.62 m; body mass 232 kg). The diagram of the probe placement in Fig. 1C approximates the morphology of the peripubescent males based on morphological data gathered from dissections of stranded carcasses (see Fig. 3). The sexually mature male used in the study was 0.4 m longer than the dolphin used to determine the length of the probe; thus, there was a relative posterior shift in probe position in this animal that placed thermocouples 1–4 within the CCHE and thermocouples 5–7 posterior to the region of the CCHE.

Temperatures were measured under two experimental conditions: (1) while the animals rested in their seawater pens ( $N=4$ ) or were hauled out on soft foam mats ( $N=2$ ), and (2) immediately before and after open-water swims ( $N=4$ ). All experiments were conducted at an ambient water temperature of 25–26 °C. For swimming experiments, the two peripubescent dolphins were trained to swim beside, and at the same speed as, a motorboat (see Williams *et al.* 1992). The dolphins swam outside the boat wake at 2.5–3 ms<sup>-1</sup> for 8–10 min during each experiment used in this analysis. Temperatures were taken pre- and immediately post-swim while the animal rested in the water beside the boat.

Temperatures were continuously sampled at 3 s intervals (Fluke, multi-channel Hydra Data Logger) and transferred to a laptop computer for storage. After probe insertion, temperatures stabilized within 2 min; we conservatively did not use the first 4 min of data collected after probe insertion. The probe was calibrated in a copper tube to ensure uniform thermal conditions. The copper tube was placed in an iced-

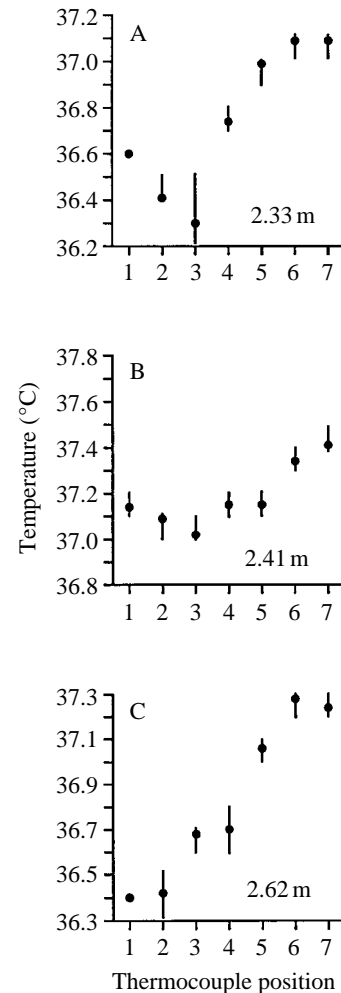


Fig. 3. Regional differences in colonic temperatures of two peripubescent (2.33 m, A, and 2.41 m, B) and one sexually mature (2.62 m, C) male bottlenose dolphin under resting conditions. Mean (●) and maximum range (indicated by bar length) of temperatures are reported for each position sampled continuously over a 5–15 min period. (A) In the smaller peripubescent male, thermocouple positions correspond to the numbers in Fig. 1C. (B) In the larger peripubescent male, thermocouple positions appear to be shifted posteriorly: thermocouples 1–5 are within the CCHE and thermocouples 6 and 7 are posterior to the region of the CCHE. (C) In the sexually mature male, the thermocouple positions are further shifted posteriorly: thermocouples 1–4 are within the CCHE and thermocouples 5–7 are posterior to the region of the CCHE.

water bath at 0 °C and in an insulated chamber at 20 °C. At these temperatures, all seven channels in the data logger registered exactly the same values for the thermocouple array.

## Results

Dolphins displayed a gradient of colonic temperatures while at rest (Fig. 3). In the peripubescent males, colonic temperatures at the CCHE were 0.1–0.8 °C cooler than temperatures recorded anterior and/or posterior to this region. In the sexually mature male, colonic temperatures in the region of the CCHE were

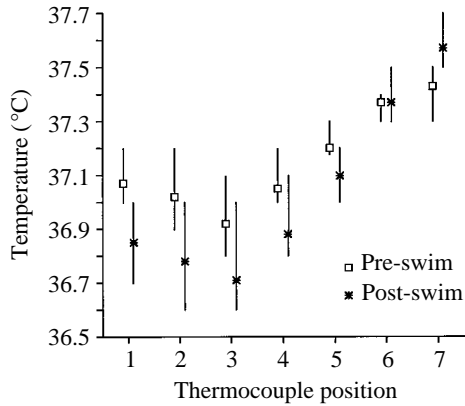


Fig. 4. Regional differences in colonic temperatures of the peripubescent 2.41 m dolphin before and after swimming reported as means and ranges. Results are pooled from four exercise sessions: periods of swimming activity ranged from 8 to 10 min at speeds of 9–12 km h<sup>-1</sup>. Temperatures in the region of the CCHE (thermocouples 1–5) decrease with exercise. Temperatures at the posterior-most thermocouple increase with exercise.

0.2–0.9 °C cooler than temperatures recorded posterior to this position. Although we had predicted from anatomical data gathered from stranded bottlenose dolphins that thermocouple no. 1 would be anterior to the CCHE in both peripubescent males, only the smallest male presented a relatively higher temperature at thermocouple no. 1. This implies that, in the larger peripubescent male, thermocouple no. 1 was not positioned anterior to the CCHE. A shift of even a few centimetres in the relative placement of the thermocouple array in the colon would place thermocouple no. 1 within the region of the CCHE and, thus, potentially decrease the temperature recorded at this thermocouple. The posterior shift in probe placement that we predicted in the larger, sexually mature male is evident from the temperature profiles (Fig. 3).

The effect of exercise on colonic temperature was position-dependent (Fig. 4). Data presented here are for the 2.41 m male only, because the 2.33 m male did not maintain the level of exercise performance required to be included in this study. Temperatures within the region of the colon flanked by the CCHE decreased after the dolphin swam vigorously. Thermocouples 1, 2 and 3 experienced the largest decreases in temperature; mean post-swim readings at these positions were 0.2 °C cooler than mean pre-swim temperatures. Temperature decreases in the region of the CCHE appeared to be dependent upon the dolphin's level of activity during exercise. Temperatures at thermocouples 1 and 2 decreased by 0.5–0.6 °C after the dolphin's most strenuous exercise period (10 min at 13 km h<sup>-1</sup>). Mean temperatures at the posterior-most thermocouple increased by 0.1 °C with exercise, while the reading at thermocouple 6 remained unchanged.

Unlike temperature gradients displayed during rest, colonic temperatures were not stable after exercise. When the dolphin was allowed to rest beside the boat for longer than 4–6 min after exercise, colonic temperatures at the region of the CCHE increased slowly (Fig. 5).

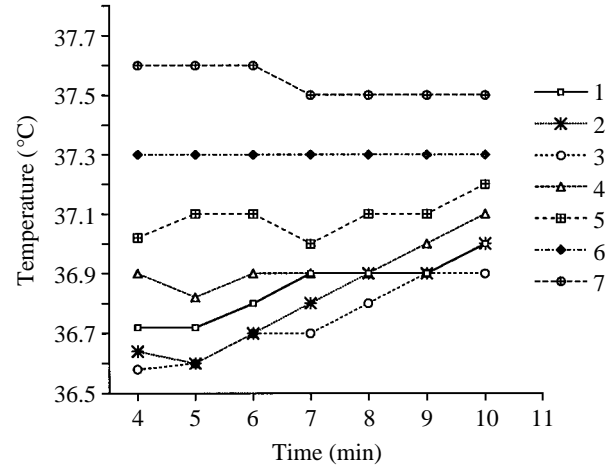


Fig. 5. Changes in colonic temperatures after exercise in the peripubescent 2.41 m dolphin. Results are from one exercise period. Immediately after swimming, temperatures at the CCHE decreased (thermocouples 1–5). If the dolphin had a prolonged rest period after swimming, colonic temperatures slowly increased within the region of the CCHE and approached pre-swim temperatures within 10 min. The temperature at the posterior-most thermocouple also decreased with time.

## Discussion

Temperatures in the region of the colon flanked by the CCHE decrease with exercise. These data suggest that the CCHE has an increased ability to cool the arterial blood supply to the testes, and may thermally isolate the testes from adjacent locomotor muscles, when the dolphin is swimming vigorously. We hypothesize that the maximal cooling observed is due to increased flow of relatively cool venous blood through the CCHE during exercise.

The venous blood supplying the CCHE returns from the surfaces of the dorsal fin and flukes (see Fig. 1). These appendages have two venous returns. Circumarterial (also defined as peri-arterial by Elsner *et al.* 1974) venous channels are found deep within the fin and have been suggested to act as the heat-conserving, countercurrent heat exchanger (Scholander and Schevill, 1955). The superficial venous system may be a shunt for the deep countercurrent heat exchanger; blood routed through this venous system would be cooled by exposure to ambient water (Kanwisher and Sundnes, 1966; Scholander and Schevill, 1955). Scholander and Schevill (1955) hypothesized that the mechanism for routing blood through these venous systems was 'semiautomatic'. If the dolphin needed to conserve heat, the rate of blood flow through the fin would be slow, and venous blood would be preferentially returned *via* the deep peri-arterial venous channels. If, however, the animal needed maximal cooling, blood flow through the fin would increase. The increased flow would swell the nutrient arteries, occlude the deep venous return and force blood through the superficial venous system.

Exercising dolphins, swimming at 2.5–3.0 m s<sup>-1</sup>, experience increased heart rates relative to resting dolphins (Williams *et al.* 1992), suggesting that blood flow rates through the radiating

surfaces of the dorsal fins and flukes could be increased during exercise. Heat loss from blood in the superficial veins would increase by increased convective heat exchange (Schmidt-Nielsen, 1990) at higher swimming speeds. Thus, changes in blood flow patterns through the dorsal fin and tail flukes, coupled with increased convective heat loss from the venous blood returning through the CCHE, may allow maximal cooling of the intra-abdominal testes during exercise.

Baker and Chapman (1977) described a similar result in exercising dogs that use a countercurrent heat exchanger to control brain temperature: brain temperature decreased at the onset of heavy exercise. The maximal cooling of the brain observed during exercise in dogs was attributed to increased respiratory ventilation (Baker and Chapman, 1977). The countercurrent heat exchanger is formed as the carotid artery, which supplies blood to the brain, travels through the cavernous venous sinus, which receives cooled blood from the oral and nasal cavities (reviewed in Baker, 1979). Increased respiratory ventilation accelerates evaporative heat loss in the venous blood draining the oral and nasal passages and supplying the venous sinus.

Some terrestrial mammals can use countercurrent heat exchangers selectively to cool temperature-sensitive brain tissue during exercise, while their core temperatures increase with locomotor activity (Baker, 1979; Baker and Chapman, 1977; Elkhawad, 1992; Taylor and Lyman, 1972). Only marine mammals undertaking a dive appear to be able to locomote and concomitantly decrease their core temperatures. Although not necessarily indicative of whole-body temperature (see Ponganis *et al.* 1993), Weddell seals (*Leptonychotes weddellii*) can decrease their aortic temperature by 1–3 °C during an extended voluntary dive (Kooyman *et al.* 1980; Hill *et al.* 1987). Decreases in core temperature during diving in the Weddell seal could be due to metabolic changes that occur during diving and/or to changes in blood flow that might increase heat loss from the body (Kooyman *et al.* 1980; Hill *et al.* 1987).

The marine mammals used in this study were exercising at the surface. Because their respiration rate was 5–7 breaths min<sup>-1</sup>, we assume they were not invoking a dive response (see Williams *et al.* 1992). The cooled blood returning from the dorsal fin and tail flukes is introduced into the deep abdomen in a position to cool the arterial blood reaching the testes, but it is also returning to the core at a lower temperature than under pre-exercise conditions. To the best of our knowledge this is the first report of deep body cooling in an exercising mammal that is not undertaking a dive. Like the mechanism hypothesized by Scholander and Schevill (1955) for shunting blood through the fins, whole-body cooling in these mammals appears to be ‘semiautomatic’. Colonic temperatures measured at the CCHE experienced the largest decrease after the dolphin’s most strenuous exercise period. Redistribution of blood through the radiating surfaces of the dorsal fin and tail flukes during exercise potentially allows dolphins to be ‘self-cooling’, i.e. to achieve maximum whole-body cooling during vigorous exercise.

It should be emphasized that our results are based on four exercise sessions on a single peripubescent male. It would be interesting to investigate the effect of exercise on CCHE function in a sexually mature male. Morphological data demonstrate that the CCHE is more developed in sexually mature males than in younger males (Rommel *et al.* 1992). Additionally, under resting conditions, colonic temperatures in the region of the CCHE in a mature male can be up to a 1.3 °C cooler than temperatures measured outside this region (Rommel *et al.* 1994); this temperature differential is larger than that measured in either of the resting peripubescent males in this study. We hypothesize that sexually mature males may demonstrate an increased ability, relative to peripubescent males, to cool their reproductive systems during exercise.

Core temperature is an important index of health. Marine mammals, though, can display different ‘core’ body temperatures, depending on the position where the core temperature is taken (Geraci, 1981; Ponganis *et al.* 1993; Rommel *et al.* 1994). Our data demonstrate that colonic temperatures of bottlenose dolphins are positionally dependent and respond dissimilarly to exercise. Might these temperatures also respond dissimilarly to fever? Which, if any, of these positions should be considered as ‘core’ in dolphins? Vascular adaptations of marine mammals allow them to redistribute blood volumes (Scholander and Schevill, 1955; Zapol *et al.* 1979) and heat throughout their body. This suggests that one core temperature is not sufficient to represent whole-body temperature, to predict whole-body metabolism (Ponganis *et al.* 1993) or to determine animal health. Further studies are required to determine which temperatures are indicative of metabolic status in marine mammals.

We thank L. Bottaro-Lamy, T. Dunham and R. Yamada for invaluable assistance with the experiments. F. Crozier, A. Freeman, E. Huber, K. Keller, M. Magee, P. Miller, P. Nachtigall, E. Rawitz, S. Shippee and C. Wongdock also contributed greatly to this study. We thank W. Friedl for his continued support. All experimental procedures were evaluated and approved according to animal welfare regulations specified under NIH guidelines. We thank C. Coogan and two anonymous reviewers for their helpful comments on our manuscript. This work was supported by ONR Grant no. 000149310751.

## References

- ARKOWITZ, R. AND ROMMEL, S. A. (1985). Force and bending moment of the caudal muscles in the shortfin pilot whale. *Mar. Mamm. Sci.* **1**, 203–209.
- BAKER, M. A. (1979). A brain-cooling system in mammals. *Scient. Am.* **240**, 130–139.
- BAKER, M. A. AND CHAPMAN, L. W. (1977). Rapid brain cooling in exercising dogs. *Science* **195**, 781–783.
- BEDFORD, J. M. (1977). Evolution of the scrotum: the epididymis as the prime mover? In *Reproduction and Evolution* (ed. J. H. Calaby

- and C. H. Tyndale-Biscoe), pp. 171–182. Canberra City: Australian Academy of Science.
- CAPUTA, M., KADZEILA, W. AND NAREBSKI, J. (1976). Significance of cranial circulation for the brain homeothermia in rabbits. II. The role of cranial venous lakes in the defense against hyperthermia. *Acta neurobiol. exp.* **36**, 626–638.
- CAPUTA, M., KAMARI, A. AND WACHULEC, M. (1991). Selective brain cooling in rats resting in heat and during exercise. *J. therm. Biol.* **16**, 19–24.
- CARRICK, F. N. AND SETCHELL, B. P. (1977). The evolution of the scrotum. In *Reproduction and Evolution* (ed. J. H. Calaby and C. H. Tyndale-Biscoe), pp. 165–170. Canberra City: Australian Academy of Science.
- COWLES, R. B. (1958). The evolutionary significance of the scrotum. *Evol.* **12**, 417–418.
- COWLES, R. B. (1965). Hyperthermia, aspermia, mutation rates and evolution. *Q. Rev. Biol.* **40**, 341–367.
- ELKHAWAD, A. O. (1992). Selective brain cooling in desert animals: the camel (*Camelus dromedarius*). *Comp. Biochem. Physiol.* **101A**, 195–201.
- ELSNER, R., PIRIE, J., KENNEY, D. P. AND SCHEMMER, S. (1974). Functional circulatory anatomy of cetacean appendages. In *Functional Anatomy of Marine Mammals*, vol. 2 (ed. R. J. Harrison), pp. 143–159. New York, London: Academic Press.
- GERACI, J. R. (1981). *Marine Mammal Care*. Ontario: University of Guelph.
- HILL, R. D., SCHNEIDER, R. C., LIGGINS, G. C., SCHUETTE, A. H., ELLIOTT, R. L., GUPPY, M., HOCHACHKA, P. W., QVIST, J., FALKE, K. J. AND ZAPOL, W. M. (1987). Heart rate and body temperature during free diving of Weddell seals. *Am. J. Physiol.* **253**, R344–R351.
- KANWISHER, J. W. AND SUNDNES, G. (1966). Thermal regulation in cetaceans. In *Whales, Dolphins and Porpoises* (ed. K. S. Norris), pp. 379–409. Berkeley: University of California Press.
- KOORYMAN, G. L., WAHRENBROCK, E. A., CASTELLINI, M. A., DAVIS, R. W. AND SINNETT, E. E. (1980). Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *J. comp. Physiol. B* **138**, 335–346.
- MOORE, C. R. (1926). The biology of the mammalian testis and scrotum. *Q. Rev. Biol.* **1**, 4–50.
- PABST, D. A. (1990). Axial muscles and connective tissues of the bottlenose dolphin. In *The Bottlenose Dolphin* (ed. S. Leatherwood and R. R. Reeves), pp. 51–67. San Diego: Academic Press.
- PONGANIS, P. J., KOORYMAN, G. L., CASTELLINI, M. A., PONGANIS, E. P. AND PONGANIS, K. V. (1993). Muscle temperature and swim velocity profiles during diving in a Weddell seal, *Leptonychotes weddellii*. *J. exp. Biol.* **183**, 341–348.
- RIDGWAY, S. H. (1972). Homeostasis in the aquatic environment. In *Mammals of the Sea: Biology and Medicine* (ed. S. H. Ridgway), pp. 590–747. Springfield: Charles C. Thomas.
- ROMMEL, S. A., PABST, D. A., MCLELLAN, W. A., MEAD, J. G. AND POTTER, C. W. (1992). Anatomical evidence for a countercurrent heat exchanger associated with dolphin testes. *Anat. Rec.* **232**, 150–156.
- ROMMEL, S. A., PABST, D. A., MCLELLAN, W. A., WILLIAMS, T. M. AND FRIEDL, W. A. (1994). Temperature regulation of the testes of the bottlenose dolphin (*Tursiops truncatus*): evidence from colonic temperatures. *J. comp. Physiol. B* **164**, 130–134.
- SCHMIDT-NIELSEN, K. (1990). *Animal Physiology: Adaptation and Environment*, 4th edn. New York: Cambridge University Press.
- SCHOLANDER, P. F. AND SCHEVILL, W. E. (1955). Countercurrent vascular heat exchange in the fins of whales. *J. appl. Physiol.* **8**, 279–282.
- SWEENEY, J. C. AND RIDGWAY, S. H. (1975). Procedures for the clinical management of small cetaceans. *J. Am. vet. Med. Ass.* **167**, 540–545.
- TAYLOR, C. R. AND LYMAN, C. P. (1972). Heat storage in running antelopes: independence of brain and body temperatures. *Am. J. Physiol.* **222**, 114–117.
- VANDEMARK, N. L. AND FREE, M. J. (1970). Temperature effects. In *The Testis*, vol. III (ed. A. D. Johnson, W. R. Gomes and N. L. VanDemark), pp. 233–312. New York: Academic Press.
- WAITES, G. M. H. (1970). Temperature regulation and the testis. In *The Testis*, vol. I (ed. A. D. Johnson, W. R. Gomes and N. L. VanDemark), pp. 241–279. New York: Academic Press.
- WILLIAMS, T. M., FRIEDL, W. A., FONG, M. L., YAMADA, R. M., SEDIVY, P. AND HAUN, J. E. (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* **355**, 821–823.
- ZAPOL, W. M., LIGGINS, G. C., SCHNEIDER, R. C., QVIST, J., SNIDER, M. T., CREASY, R. K. AND HOCHACHKA, P. W. (1979). Regional blood flow during simulated diving in the conscious Weddell seal. *J. appl. Physiol.* **47**, 968–973.