# Temperature regulation of the testes of the bottlenose dolphin (*Tursiops truncatus*): evidence from colonic temperatures

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**Abstract.** Dolphins possess a countercurrent heat exchanger 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 flukes. A rectal probe housing a linear array of five 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 countercurrent heat exchanger. Colonic temperatures adjacent to the countercurrent heat exchanger were maximally 1.3 °C cooler than temperatures measured outside this region. Temporary heating and cooling of the dorsal fin and flukes affected temperatures at the countercurrent heat exchanger, but had little or no effect on temperatures posterior to its position. These measurements support the hypothesis that cooled blood is introduced into the deep abdominal cavity and functions specifically to regulate the temperature of arterial blood flow to the dolphin testes.

**Key words:** Thermoregulation – Countercurrent heat exchange – Testis – Clinical assessment – Dolphin, *Tursiops*

## Introduction

A streamlined body shape is important for maintaining low energetic costs of swimming in dolphins [reviews: Fish and Hui (1991), Williams et al. (1992)]. Anatomical adaptations for streamlining include a fusiform body, reduced appendages, and intra-abdominal testes. It has

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remained a question as to how dolphins produce and store sperm with intra-abdominal testes, since most mammals require below core $T_b$ for viable sperm production and maturation (Moore 1926; Cowles 1958, 1965; VanDemark and Free 1970; Waites 1970; Bedford 1977; Carrick and Setchell 1977). We recently described a CCHE in delphinids, including the bottlenose dolphin (*Tursiops truncatus*) that could cool arterial blood to the testes: the CCHE receives cooled blood from the peripheral surfaces of the dorsal fin and flukes (Rommel et al. 1992).

The CCHE lies in the posterior abdominal cavity and is formed by a spermatic arterial plexus juxtaposed to a lumbo-caudal venous plexus (Fig. 1). The arterial plexus is a single layer of approximately 40 parallel vessels that extend ventro-laterally from the dorsal aorta. The venous plexus is a single layer of irregularly anastomosed, thin-walled vessels. The blood that supplies the venous plexus returns from superficial veins that drain the dorsal fin and flukes and can be cooled by exposure to ambient $T_w$ (Scholander and Schevill 1955). These veins leave the fin and flukes and remain superficial to the body core (i.e., just deep to the blubber layer and superficial to vertebral muscles) until they feed directly into the lateral and posterior borders of the lumbo-caudal venous plexus. Thus, cooled blood can be introduced directly into the deep posterior abdominal cavity. The juxtaposition of this venous plexus to the spermatic arterial plexus, the vessel dimensions, and the opposite directions of blood flow through the plexuses suggest that dolphins use a CCHE to regulate the temperature of the blood reaching the testes (Rommel et al. 1992).

To date, there exist no published measurements of testis temperatures in any cetacean. Because the CCHE flanks a region of the colon (Fig. 1), we hypothesized that the introduction of cooled blood, via the lumbo-caudal venous plexus, would influence colonic temperatures. $T_c$, 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. We fashioned a rectal probe housing a linear array of thermocouples designed to measure $T_c$ simultaneously at positions anterior to, within, and posterior to the region of the colon flanked by the CCHE (Fig. 1c).

## Materials and methods

A linear array of five copper-constantan thermocouples (Omega Teflon-coated, 30 gauge wire) were aligned on a 3 mm outside diameter flexible plastic tube. This array was then covered with thin-walled, heat-shrink tubing. A tapered plug was fitted on the probe's anterior end and the entire assembly was heated to shrink the wrap, thus making the probe waterproof and electrically nonconductive. The final outside diameter of the probe was 5 mm. The dimensions of the probe and relative positions of the thermocouples were based on anatomical measurements from dissections of stranded bottlenose dolphin carcasses, approximately 2.20 m in total length. In an animal of this length the anterior border of the CCHE lies approximately 35 cm anterior to the anus, and flanks a region of colon 15–20 cm long. A flexure in the colon, approximately 50 cm deep to the anus, determined maximum probe length. With animal safety foremost, we conservatively limited the length of the probe to 40 cm. The thermocouples were positioned within the colon at the following distances anterior to the anus: #1 – 40 cm, #2 – 35 cm, #3 – 30 cm, #4 – 25 cm, and #5 – 15 cm. The probe was designed to position thermocouple #1 anterior to the CCHE, thermocouples #2–4 within the CCHE, and thermocouple #5 posterior to the CCHE, in a 2.20 m dolphin as schematized in Fig. 1c. The posterior-most thermocouple (#5) was 15 cm deep to the anus, and was considered too shallow to measure a true deep core temperature (Ridgway 1972; Sweeney and Ridgway 1975).

$T_c$ was measured in two peripubescent male bottlenose dolphins (total length 2.40 m and 2.41 m; bw 152 kg and 157 kg, respectively), and one sexually mature male bottlenose dolphin (total length 2.62 m; bw 234 kg). The schematic 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 also Fig. 2). The sexually mature male used in the study was 40 cm longer than the stranded carcasses we dissected; thus, there was a relative posterior shift in probe position that placed thermocouples #1–3 within the CCHE, and #4 and #5 posterior to the region of the CCHE.

Temperatures of the peripubescent males were taken under three experimental conditions: while the animals rested in (1) seawater pens at $T_w = 28.6$ °C ($n = 2$), (2) constant temperature baths at $T_w = 32$–33 °C ($n = 5$), and (3) hauled out on soft foam mats ($n = 4$). Temperatures in the sexually mature male were measured while the animal was positioned on mats next to its seawater pen in full sun, where $T_{air} = 27$–29 °C ($n = 3$); $T_c$s in the sexually mature male were also taken while we manipulated the temperatures of the dorsal fin and flukes. This male was positioned on mats and its flanks sprayed with sea water for the duration of the experiment (approximately 35 min). To manipulate the temperatures of the extremities, a fluke-shaped neoprene glove was fitted over the flukes and water compresses were applied to the dorsal fin. These devices were filled with warm (approximately 40 °C) or cool (approximately 5 °C) water as the experimental protocol dictated.

Temperatures were continuously sampled at 0.5- or 1.0-min intervals (Fluke, multi-channel Hydra Data Logger) and transferred for storage to a laptop computer. After probe insertion, temperatures stabilized within 2 min; we conservatively did not use the first 4 min of data collected after probe insertion in the following analyses. The probe was calibrated in a copper tube to ensure uniform thermal conditions. The copper tube was placed in an ice-water bath at 0.0 °C and in an insulated chamber at 20.0 °C. At these temperatures all five channels in the data logger registered exactly the same values for the thermocouple array.
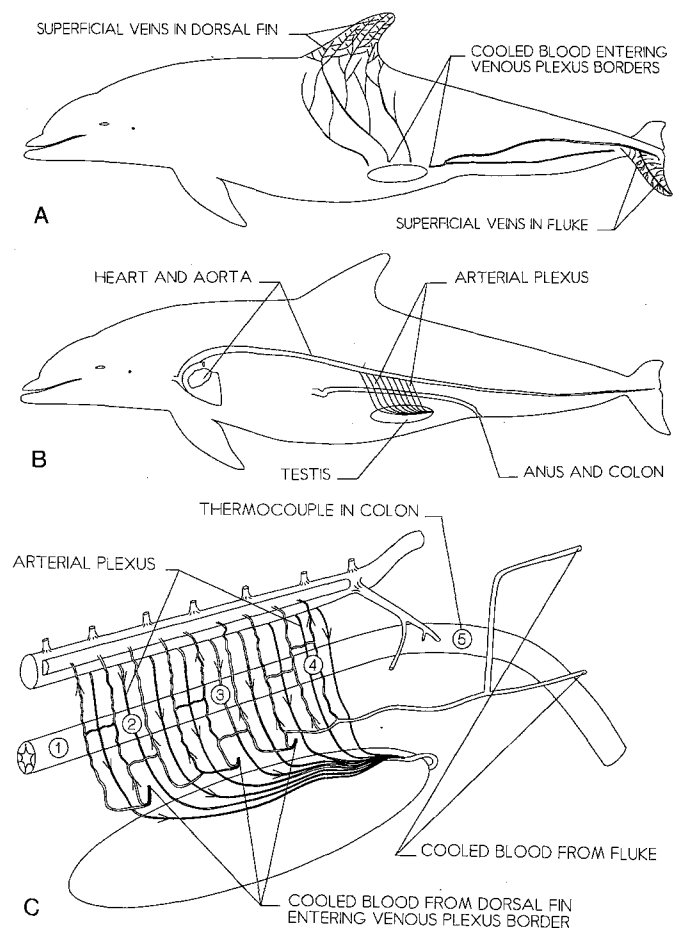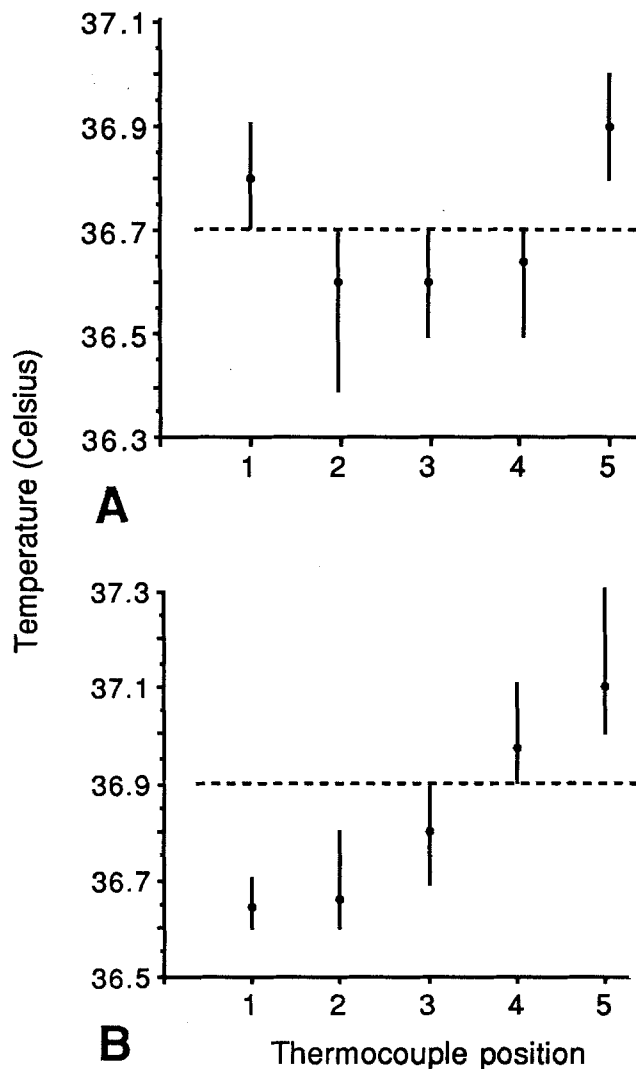


**Fig. 1A–C.** Schematized topography of vascular structures associated with countercurrent heat exchange at the dolphin testes: **A** blood from the superficial veins of the dorsal fin and flukes is cooled by exposure to ambient water. These extremities are drained by relatively thick-walled large caliber veins that remain superficial (i.e., just deep to the blubber layer and superficial to vertebral muscles) as they coalesce and course towards the abdominal cavity. These large 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 could be introduced into the deep posterior abdominal cavity near the testis; **B** the spermatic arterial plexus is an unique arrangement of arteries that extend 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 direction of flow. Cut ends at the lateral border of the lumbo-caudal venous plexus are where the superficial veins from the dorsal fin enter the abdominal cavity (**A**). Note the countercurrent heat exchanger flanks a region of lumbar aorta and colon in the posterior abdominal cavity. Numbers 1–5 represent placement of thermocouples in the colon of a peripubescent male (see Materials and methods)
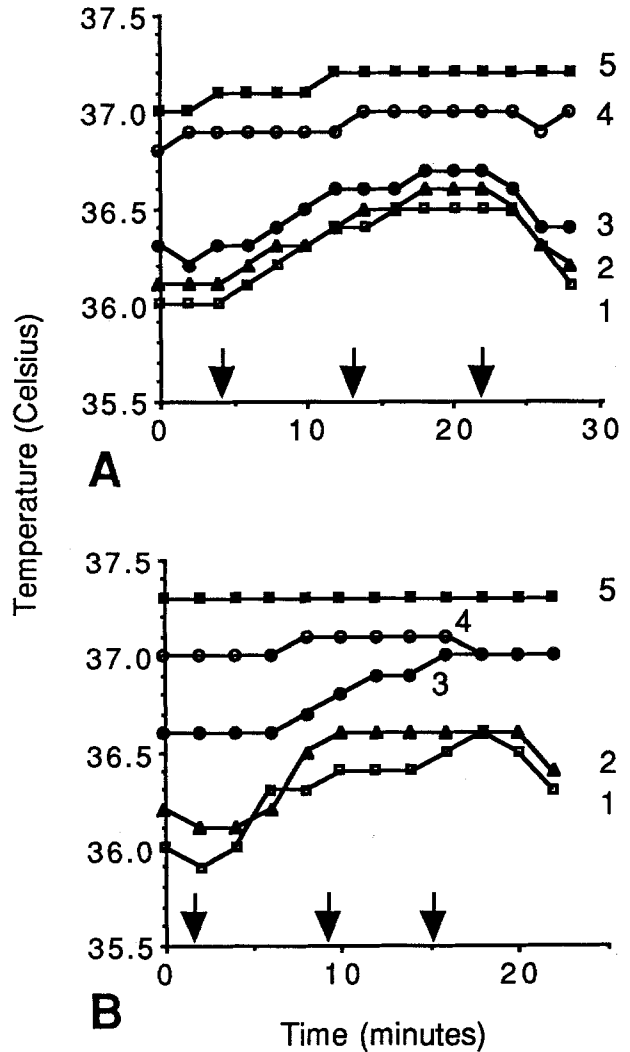
## Results and discussion

$T_c$ in dolphins is position dependent (Fig. 2). The peripubescent dolphins maintained stable temperature gradients along the colon while resting in their seawater pens or in constant-temperature water baths. Under these conditions, $T_c$s at the CCHE were 0.2–0.7 °C cooler than temperatures recorded anterior and/or posterior to this region. Temperature gradients along the colon were less stable in the peripubescent males than in the sexually mature male. Temperature gradients were not evident in the peripubescent males when they were positioned on soft mats next to their pens. However, in the sexually mature male resting on foam mats temperatures measured in the region of the colon·flanked by the

CCHE were 0.9–1.3 °C cooler than temperatures re corded posterior to this region. Under these conditions the sexually mature male always displayed a stable tem perature gradient along the colon.



**Fig. 3A, B.** Changes in colonic temperature coincident with therma manipulations of the dorsal fin and fluke surfaces of sexually mature male bottlenose dolphin. Thermocouples #1, 2, and 3 are positioned within the CCHE; thermocouples #4 and 5 are posterior to the CCHE. **A** and **B** represent two experimental sessions The *first arrow* indicates time at which a fluke-shaped neoprene glove was fitted over the flukes and filled with warm (approximately 40 °C) water. The *second arrow* indicates time at which the dorsal fin was cooled with ice water compresses. At the *third arrow* the flukes and dorsal fin were uncovered and all surfaces sprayed with sea water at 28–29 °C. Temperatures at thermocouples #1, 2, and 3 increased in response to warming the flukes. As we continued to warm the flukes and began to cool the dorsal fin these temperatures continued to increase, but more slowly. For both experiments, temperatures at thermocouples #1 and 2 decreased when these surfaces were exposed and sprayed with sea water; in experiment A thermocouple #3 also decreased in temperature. Temperatures at thermocouples #4 and 5 experienced small or no increases during the manipulations of the fin and fluke surfaces, but did not uniformly decrease in temperature when the dorsal fin and flukes were exposed



**Fig. 2A, B.** Regional differences in colonic temperatures of peripubescent male bottlenose dolphins immersed in water at 32 °C. Mean and maximum range of temperatures for each position sampled continuously over a 120-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 #1–3 are within the CCHE, and #4 and #5 are posterior to the region of the CCHE

Although we had predicted from anatomical data gathered from stranded bottlenose dolphins that thermocouple #1 would be anterior to the CCHE in both peripubescent males, only the smallest male presented a relatively higher temperature at thermocouple #1. This implies that in the larger peripubescent male thermocouple #1 was not positioned anterior to the CCHE. A shift of even a few centimeters in the relative placement of the thermocouple array in the colon would place thermocouple #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).

We designed the probe to position the posterior-most thermocouple 15 cm deep to the anus – a position considered too shallow to register a true deep core temperature (Ridgway 1972; Sweeney and Ridgway 1975). We assumed that the temperature measured at this thermocouple would be cooler than temperatures measured anterior to this position. Interestingly, in the sexually mature male and in the peripubescent males resting in their seawater pens or in constant temperature water baths, $T_c$s measured at the CCHE were always cooler than temperatures measured at the more shallow, posterior-most thermocouple.

Cooled blood supplying the lumbo-caudal venous plexus is returned from the superficial vasculature of the dorsal fin and flukes (Rommel et al. 1992). Warming and cooling the dorsal fin and flukes of the sexually mature male elicited temperature changes noticeably greater within the region of the colon flanked by the CCHE than temperatures measured simultaneously at the posterior-most position (Fig. 3). We could always elicit a temperature increase at the CCHE when we warmed the flukes. Subsequent cooling of the dorsal fin variably slowed this temperature increase or had no effect. We interpret these results in two ways: we potentially interfered with normal function of the superficial vasculature of the dorsal fin (i.e., closed down the superficial veins) with the application of cold compresses. Alternatively, in this larger male, we may have been measuring temperatures of the posterior CCHE, where blood from the flukes enters the CCHE. A redesigned probe and continued experimentation will help clarify these results.

The existence of a relatively cool region of colon, and the ability to effect the temperatures in that region by influencing the surface temperatures of the dorsal fin and flukes, supports the hypothesis that cooled venous blood is entering the deep posterior abdominal cavity. Although the temperature differences appear to be small, we are assaying the effect of the CCHE at its medial border and through the colon wall. In an idealized countercurrent heat exchanger heat is transferred at low temperatures at one end and at progressively higher temperatures towards the opposite end (Schmidt-Nielsen 1990). The blood in the veins and arteries will be coolest at the lateral border of the CCHE, i.e., farthest from the midline, where the superficial veins enter the abdominal cavity. Thus, while we would expect temperatures to approach those of the environment at the lateral border of the CCHE, the medial border would have temperatures approaching that of the core.

The relatively large differences that we measured between $T_c$ within and posterior to the CCHE in the older male suggests that this system may not be fully functional in the peripubescent males. We know from dissections of stranded bottlenose dolphins that the CCHE of sexually mature males is more well developed than that of younger males.

Some clinicians prefer not to use "rectal" temperature because it is too variable (Geraci 1981). We believe that this variability is due to local influences on colonic temperatures by the CCHE. The suggested position for measuring rectal temperatures is 20–30 cm deep to the anus, which positions the probe within a region of colon flanked by the CCHE (Sweeney and Ridgway 1975). The CCHE influence on bowel temperature may also explain abrupt excursions in deep $T_b$ in the posterior colon that have been observed with remote telemetry of ingested radio pills (McGinnis et al. 1972; Hampton and Whittow 1976).

The array of thermocouples within the probe offers a safe and relatively non-invasive means of assessing the effects of changes in peripheral blood flow on dolphin deep $T_b$s. Our anatomical data, coupled with $T_c$ data, support the hypothesis that cooled blood is being introduced into the deep abdominal cavity via the lumbo-caudal venous plexus. The juxtaposition of this venous plexus to the spermatic arterial plexus supports the interpretation that dolphins use a CCHE to regulate testis temperature and, thus, to compensate for the potentially detrimental effects of abdominal temperatures on sperm viability.

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