

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/12796768>

The diving physiology of bottlenose dolphins (Tursiops truncatus). III Thermoregulation at depth

ARTICLE *in* JOURNAL OF EXPERIMENTAL BIOLOGY · NOVEMBER 1999

Impact Factor: 2.9 · Source: PubMed

CITATIONS

42

READS

25

6 AUTHORS, INCLUDING:



[Terrie M Williams](#)

University of California, Santa Cruz

164 PUBLICATIONS 5,706 CITATIONS

[SEE PROFILE](#)



[Dawn Noren](#)

National Oceanic and Atmospheric Administr...

45 PUBLICATIONS 612 CITATIONS

[SEE PROFILE](#)

THE DIVING PHYSIOLOGY OF BOTTLENOSE DOLPHINS (*TURSIOPS TRUNCATUS*)

III. THERMOREGULATION AT DEPTH

TERRIE M. WILLIAMS^{1,*}, D. NOREN¹, P. BERRY², J. A. ESTES³, C. ALLISON² AND J. KIRTLAND²

¹Department of Biology, Earth and Marine Science Building, A-316, University of California, Santa Cruz, CA 95064, USA, ²The Dolphin Experience, PO Box F42433, Freeport, Grand Bahama Island, Bahamas and ³Biological Resources Division, Earth and Marine Science Building, A-316, University of California, Santa Cruz, CA 95064, USA

*e-mail: williams@darwin.ucsc.edu

Accepted 26 July; published on WWW 30 September 1999

Summary

During diving, marine mammals initiate a series of cardiovascular changes that include bradycardia and decreased peripheral circulation. Because heat transfer from thermal windows located in peripheral sites of these mammals depends on blood flow, such adjustments may limit their thermoregulatory capabilities during submergence. Here, we demonstrate how the thermoregulatory responses of bottlenose dolphins (*Tursiops truncatus*) are coordinated with the diving response. Heart rate, skin temperature and heat transfer from the dorsal fin and flank were measured while dolphins rested on the water surface, stationed 5–50 m under water and floated at the surface immediately following a dive. The results showed that heat flow ranged from 42.9 ± 7.3 to $126.2 \pm 23.1 \text{ W m}^{-2}$ and varied with anatomical site and diving activity. Upon submergence, heat flow declined by

35% from the dorsal fin and by 24% from the flank. An immediate increase in heat flow to levels exceeding pre-dive values occurred at both sites upon resurfacing. Changes in heart rate during diving paralleled the thermoregulatory responses. Mean pre-dive heart rate ($102.0 \pm 2.6 \text{ beats min}^{-1}$, $N=26$) decreased by 63.4% during dives to 50 m and immediately returned to near resting levels upon resurfacing. These studies indicate that heat dissipation by dolphins is attenuated during diving. Rather than challenge the diving response, heat transfer is delayed until post-dive periods when the need for oxygen conservation is reduced.

Key words: dolphin, *Tursiops truncatus*, diving, heat flow, thermoregulation.

Introduction

Dolphins and whales are highly specialized marine mammals that spend their entire life at sea. One of the greatest physiological challenges to these marine endotherms is thermoregulation (Irving, 1969; Whittow, 1987). To counterbalance the high thermal conductivity of water, cetaceans have developed thick insulating blubber layers that encase the body. Thermal windows in poorly insulated peripheral areas permit the transfer of excess heat during periods of high activity or when the ambient water is warm (McGinnis et al., 1972). Integral to the function of these thermal windows is the vascular system, which plays an important role in the thermoregulatory responses of cetaceans (Fig. 1). For example, whales and dolphins maintain a counter-current arrangement of blood vessels in their flukes, dorsal fins and pectoral fins that provides fine control over the movement of warm blood between the body core and peripheral areas (Scholander and Schevill, 1955). Direct vascular links have also been reported for the dorsal fin and flukes of dolphins and for the temperature-sensitive reproductive organs (Rommel et al., 1994).

In addition to its thermoregulatory function, the vascular system of marine mammals plays a major role during the dive response. Marine mammals initiate a suite of physiological changes upon submergence to conserve oxygen and to support prolonged periods of breath-holding (Scholander, 1940; Elsner, 1969; Zapol et al., 1979; Kooyman, 1989). Collectively termed the dive response, these changes include a rapid, dramatic redistribution in blood flow that emphasizes the brain, lungs and heart. Apnea, bradycardia and a reduction in blood flow to peripheral sites (e.g. flippers and fins) are hallmarks of this response. These respiratory and cardiovascular adjustments, while facilitating oxygen conservation during submergence, may compromise the thermoregulatory function of thermal windows located in peripheral sites. Thus, an apparent conflict exists between oxygen conservation and heat dissipation during diving that results from the multiple roles played by the cardiovascular system of marine mammals.

To determine the effect of the dive response on

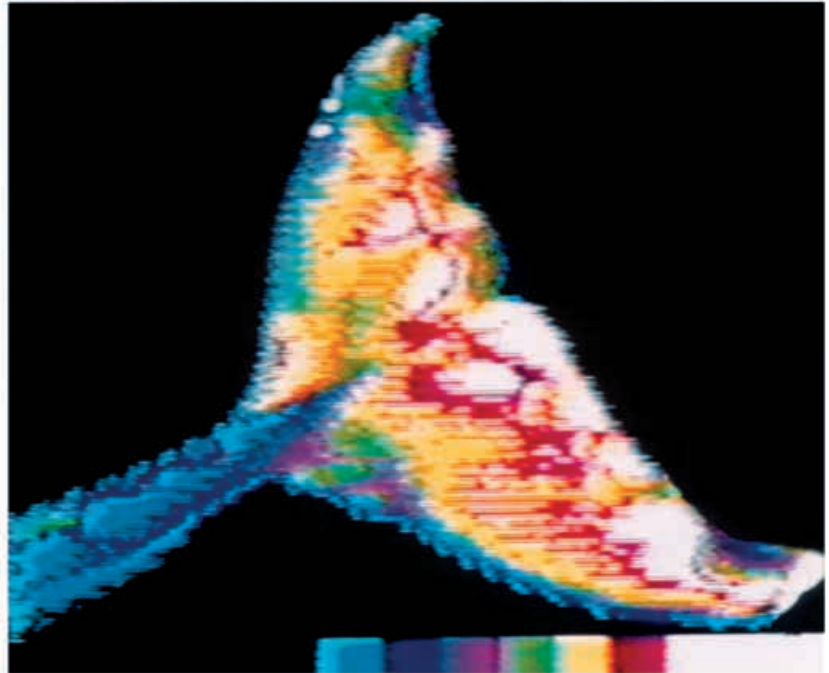


Fig. 1. Infrared thermograph of the fluke of a bottlenose dolphin. Warm areas (denoted by white and red) correspond to large blood vessels that traverse the width of the underside of the fluke. Note the comparatively cool peduncle area shown in blue. The color bar at the bottom denotes 0.1 °C differences in surface temperature per gradation.

thermoregulation in marine mammals, we monitored heat flow, skin temperature and heart rate during open ocean dives by trained bottlenose dolphins. These first recordings of heat transfer for an actively diving cetacean show that the thermoregulatory responses of dolphins depend on the phase of the dive. Heat flow from both peripheral and central sites was attenuated during submergence. The greatest period of heat transfer occurred immediately following a dive and corresponded to the release of the cardiovascular system from the dive response.

Materials and methods

Animals

Four adult Atlantic bottlenose dolphins (*Tursiops truncatus*, mean body mass 213 kg) were used in the heat flow studies. An additional immature dolphin was used for comparison during skin temperature measurements. The animals were maintained in large (15 m×15 m×4 m deep) saltwater enclosures connected to the open ocean in Freeport, Grand Bahama Island, Bahamas. Each animal was fed a daily diet of capelin, silversides and herring supplemented with multi-vitamins (Sea Tabs, vitamins C and B-12). Mean water temperature during the experimental period was 29.4 °C. Air temperature was 32.0 °C. Two adult, female Pacific bottlenose dolphins (*Tursiops tursiops gilli*, mean body mass 189 kg) were used in the diving heart rate tests. The animals were held in open-water, floating pens (7 m×7 m×3 m deep) in Kaneohe Bay, Oahu, Hawaii, and fed 2–3 times daily on mackerel, herring and smelt supplemented with vitamins. Average water temperature in the pens was 24.6 °C during the experimental period. Air temperature was approximately 28.0 °C.

Experimental design

Experiments were conducted on adult dolphins that had been acclimated to seasonally warm water temperatures ranging from 24 to 29 °C. Measurements were taken during three phases of the dive cycle: (1) at rest prior to diving, (2) during submergence, and (3) at rest on the water surface within 90 s of a dive. Resting measurements were made on quiescent animals as they floated near the water surface. Measurements on the diving dolphins were conducted in the open ocean approximately 1 nautical mile (1.85 km) offshore. On each experimental day, one or two dolphins followed a motorboat (17 or 21 foot Boston Whaler) from their enclosures to the dive site. Total swimming time was less than 15 min. During the heart rate studies, dolphins performed straight-line dives to a depth of 50 m while wearing a heart rate microprocessor placed on a harness. To avoid potential changes in thermal responses due to instrumentation (Wilson et al., 1986), heat flow and skin temperature measurements were conducted on separate dives. During the thermal studies, the dolphins accompanied a team of 3–4 SCUBA divers to depths ranging from 5 to 18 m. Trainers stationed the animal at depth and placed a heat flow/thermistor probe on the dorsal fin, fluke or flank. Experimental sessions lasted 20–50 min, depending on water depth. The dolphins periodically returned to the water surface to breathe between individual thermal measurements, while the SCUBA divers remained submerged for the entire session.

Heat flow and skin temperature

Heat flow across the skin of the dolphin to the surrounding water was measured using a 25 mm diameter disc-style heat flux transducer (Thermonetics Corp., San Diego, CA, USA) held against the stationary animal. The transducer was calibrated using a guarded heat plate procedure (ASTM C177)

prior to and after experimentation. Briefly, the transducers were placed on a central heater in which the power input was continuously monitored. Once stabilized, the heater output was compared with the millivolt output signal of the transducer. The heat flux transducer is impervious to water, and its calibration is stable for several years. Transducer calibrations changed by less than 8.2% over a 5 year period. Zero and range calibrations were conducted immediately before each experimental session; the zero calibration was rechecked during the dive by placing the probe in open water before measurements were taken. The accuracy of the instrument was ± 0.1 mV (0.8 W m^{-2}).

A thermistor implanted in the transducer permitted simultaneous measurement of skin temperature during the heat flow measurements. The thermistor was calibrated before and after the experimental period using a digital thermometer (Physitemp, model Bat-12) placed in an insulated water bath ranging in temperature from 15 to 40 °C. Both the thermistor and the digital thermometer were also calibrated against a National Bureau of Standards mercury thermometer. The accuracy of the thermistor was ± 0.1 °C. The accuracy of the thermistor was also tested against the digital thermometer placed on human skin and immersed in water. Thermistor readings on human skin were verified daily before each experimental session with dolphins.

The heat flux transducer/thermistor probe was mounted on a spring attached to a polyvinylchloride handle that allowed water to pass freely across the back of the transducer. The unit was held against the skin of the dolphin until the transducer stabilized and a steady-state signal was recorded for more than 20 s. Typical heat flow measurements required 1–2 min to complete and depended on the anatomical site. The response time of the thermistor was faster than that of the heat flux transducer and ranged from 10 to 50 s for stabilization depending on the temperature differential between the skin and water. Millivolt signals from the heat flux transducer and thermistor were recorded on two hand-held digital voltmeters (Micronta Multi-Mate). The voltmeters were placed in a weighted, clear acrylic waterproof box (Ikelite) when measurements were taken at depth. A 5 m line from the transducer probe handle was connected to the box and voltmeters by a submersible connector.

Anatomical sites representing peripheral thermal windows (dorsal fin, fluke, pectoral fin) and central areas (flank, peduncle) were measured. All measurements were taken with the probe completely submerged and represent skin temperatures and heat transfer from the surface of the animal to the water. For dolphins resting on the water surface either before or after a dive, the anatomical site of interest was submerged by approximately 12 cm during the measurements. Because of the equilibration time of the instruments and the breath-hold capability of the dolphins, it was not possible to measure heat flow and skin temperature for all sites during each dive session. Heat flow was recorded for the dorsal fin and flank during resting and diving. Skin temperatures were

recorded for five different sites during resting and for the dorsal fin, fluke and flank during diving.

Heart rate

During heart rate sessions, the dolphins wore a nylon harness containing a heart rate/dive depth microprocessor (2.5 cm diameter \times 15 cm long; Wildlife Computers, Inc.; Woodenville, WA, USA) and two cross-chest surface electrodes (Williams et al., 1993, 1999). The dolphins were trained to dive in a straight-line path between the boat and a submerged target positioned at a depth of 50 m. Heart rate from electrocardiographic signals was averaged over 10 s intervals throughout the dives. In addition, we monitored heart rate for 2 min periods immediately before and after the dives. Dive depth and duration were recorded simultaneously by the microprocessor at 1 s intervals. Data from the microprocessors were downloaded to a personal computer following each diving session and analyzed for changes in heart rate in relation to dive depth and duration using Dive-Analysis software (Wildlife Computers, Inc.; Woodenville, WA, USA). To ensure the accuracy of the heart rate microprocessor and electrode sensitivity, we periodically tested average heart rates from the microprocessor against values determined from electrocardiograph (ECG) waveforms (Birtcher Heart Rate Monitor, model 365) for dolphins resting on the water surface.

Statistical analyses

Data for skin temperature, heat flow and heart rate are presented as mean ± 1 standard error of the mean (S.E.M.) unless indicated otherwise. Differences between means for heat flow during resting and diving were tested by two-way analysis of variance (ANOVA). Differences in heat flow and skin temperature between anatomical sites were determined from Tukey pairwise comparisons or Student's *t*-tests according to Zar (1974) using statistical software (Sigma Stat 2.0, Jandel Scientific, Inc.). Heart rate was calculated by dividing the total number of ECG waveforms or fractions thereof by the test interval according to Chabot et al. (1989). Significance is set at $P < 0.05$ unless otherwise indicated.

Results

Heat flow

The level of heat flow from both central and peripheral sites depended on the phase of the dive cycle (Fig. 2). Heat flow from the surface of bottlenose dolphins ranged from $42.9 \pm 7.3 \text{ W m}^{-2}$ for the flank during diving to $126.2 \pm 23.1 \text{ W m}^{-2}$ for the dorsal fin immediately following a dive. In general, heat transfer was attenuated during submergence (two-way ANOVA factor dive, $F_{2,133} = 14.9$, $P < 0.001$), with transfer from the dorsal fin and flank decreasing significantly from pre-dive resting values (Tukey pairwise multiple-comparison test, pre-dive *versus* submerged, $P < 0.05$). Upon resurfacing, heat flow from both sites immediately increased to levels above resting. Heat flow from the dorsal fin, a thermal window, was consistently higher than for the flank

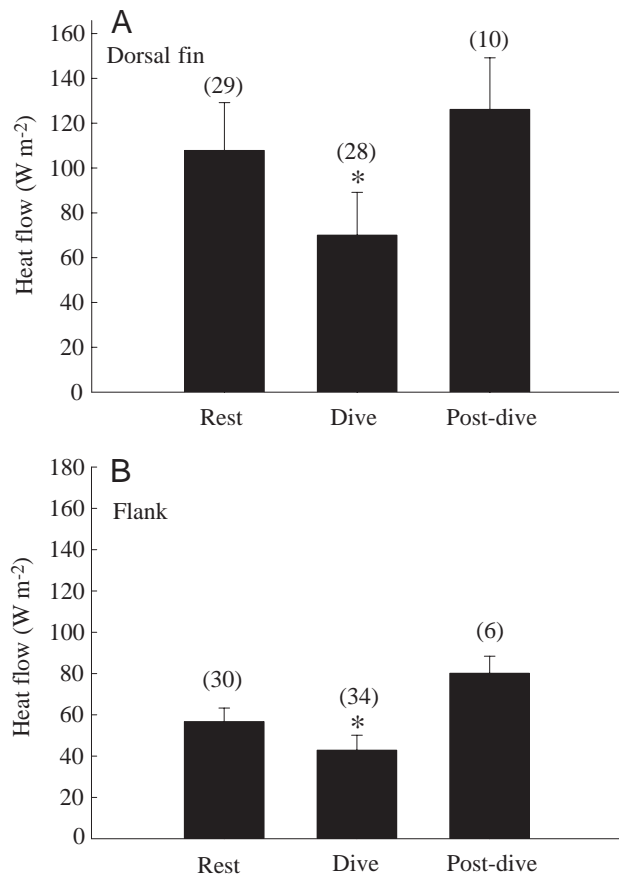


Fig. 2. Heat flow during resting, diving and post-dive periods for adult bottlenose dolphins. Values for the dorsal fin (A) and flank (B) are compared. Columns and vertical lines represent the mean values + s.e.m. Numbers in parentheses indicate the number of measurements in each data set for four dolphins. An asterisk denotes a significant decrease in heat flow between resting and diving values at $P < 0.05$.

during all phases of the dive ($P < 0.05$). In addition, the relative change in heat flow upon submergence was greater for the dorsal fin than for the flank (Fig. 2).

Skin temperature

Surface skin temperature of the dolphins remained within 1 °C of ambient water temperature (T_{water}) during resting and diving (Fig. 3). No significant difference (at $P < 0.05$) was found between skin temperatures measured for five different anatomical sites of dolphins resting on the water surface. Measurement sites included both insulated central areas (flank, peduncle) and peripheral thermal windows (fluke, dorsal fin and pectoral fin). In contrast to the resting condition, mean skin temperatures of the peripheral sites (fluke and dorsal fin) were 0.4–0.6 °C lower than measured for the flank of diving dolphins. However, the values for these sites were not statistically different for either the resting or diving ($P = 0.47$) dolphins.

Heart rate

Heart rate during the different phases of the dive changed in

parallel with heat flow (Fig. 4). During the pre-dive period, the heart rate of bottlenose dolphins ranged from 72 to 120 beats min^{-1} (102.0 ± 2.6 beats min^{-1} , $N = 26$). The variability in resting heart rate was attributed to the apneic respiratory pattern of dolphins (Williams et al., 1993). In dolphins freely diving to a depth of 50 m, average heart rate decreased to 37.4 ± 1.3 beats min^{-1} ($N = 47$) within 50 s of submergence. An anticipatory tachycardia during ascent was followed by a mean post-dive heart rate of 93.0 ± 3.1 beats min^{-1} ($N = 15$). This pattern of prompt bradycardia followed by an anticipatory tachycardia during free diving has been observed for a variety of marine mammals, including free-ranging elephant seals (Andrews et al., 1997), Weddell seals (Hill et al., 1987), sea lions (Ponganis et al., 1997) and grey seals (Thompson and Fedak, 1993) as well as Pacific bottlenose dolphins trained to

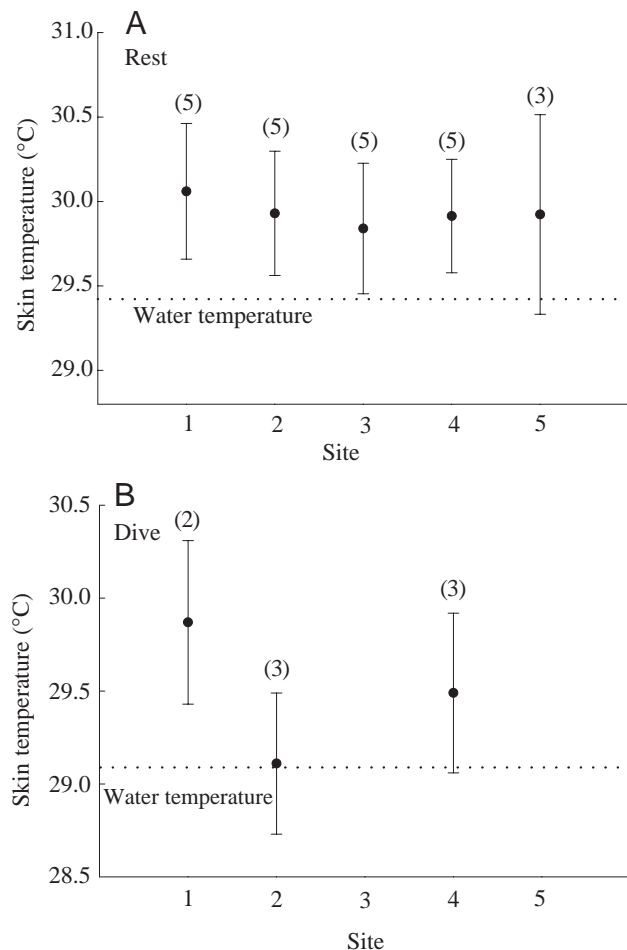


Fig. 3. Skin temperature for different anatomical sites of resting (A) and diving (B) bottlenose dolphins. Mean values ± 1 s.e.m. are presented. Numbers in parentheses represent the number of measurements in each data set for up to five dolphins. Anatomical sites are as follows: 1, dorsal fin; 2, mid flank; 3, mid peduncle; 4, underside of the fluke; and 5, underside of the pectoral fin. The horizontal dashed lines represent the water temperature at the measurement location (i.e. holding pen temperature for resting studies and ocean temperature at the dive site for the diving measurements).

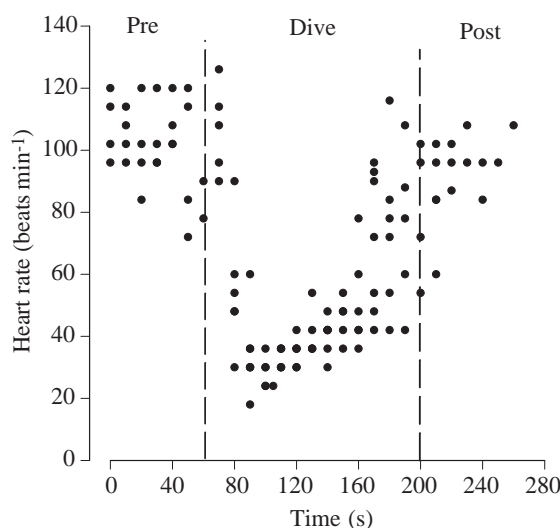


Fig. 4. Heart rate in relation to pre-dive, dive and post-dive intervals for two bottlenose dolphins. Data for six dives to a depth of 50 m are presented. Each point represents the average heart rate for 10 s intervals. Note the immediate bradycardia on submergence and the anticipatory tachycardia as the animal completes the dive.

dive in pools (Elsner et al., 1966) and the open ocean (Williams et al., 1999).

Discussion

The effects of diving on thermoregulatory responses in dolphins

Previous investigations of heat transfer in active cetaceans have focused primarily on the effects of water temperature or swimming exercise on heat loss (Hampton et al., 1971; McGinnis et al., 1972; Hampton and Whittow, 1976; Kasting et al., 1989; Ryg et al., 1993). In general, these studies have demonstrated that the dissipation of excess body heat in odontocetes (toothed whales) is greatest from peripheral areas, such as the dorsal fin, fluke and pectoral fins, and comparatively lower along the well-insulated flank. The difference in heat transfer between peripheral areas and insulated central sites depends on water temperature (McGinnis et al., 1972) and level of activity (Ryg et al., 1993). Interestingly, increased heat transfer occurs with relatively small changes in skin temperature (Fig. 3; see also Cuyler et al., 1992). Acclimation to ambient water temperatures also influences the level of heat transfer in cetaceans through changes in the thickness and quality of the insulating blubber layer (Worthy and Edwards, 1990; Williams et al., 1992). We find that the level of heat flow from the flank of warm-acclimated dolphins at $T_{\text{water}}=24\text{--}29\text{ }^{\circ}\text{C}$ (Fig. 2B) is similar to values for another odontocete, the killer whale (*Orcinus orca*), acclimated to $T_{\text{water}}=12\text{--}18\text{ }^{\circ}\text{C}$ (Kasting et al., 1989).

The results from this study demonstrate that diving activity introduces another important factor that influences the level of heat dissipation in odontocetes. Marked changes in heat flow occur upon submergence and resurfacing in diving dolphins

(Fig. 2). These changes presumably result from the initiation and termination of the dive response, as manifest by alterations in heart rate (Fig. 4). In view of this, the thermal costs of odontocetes can easily be overestimated if based solely on measurements taken while the animal is on the water surface.

The inter-dive surface interval appears to be an important thermoregulatory period for diving marine mammals. By coordinating periods of elevated heat transfer with the release from bradycardia between dives, these animals can maintain the metabolic benefits associated with the dive response while meeting thermoregulatory demands. The bottlenose dolphins in the present study used the surface interval between short dives to transfer excess heat quickly to the environment. Weddell seals use the same inter-dive period to dissipate heat and to reduce core body temperature prior to sustained dives (Hill et al., 1987). Calculations by these investigators indicate that a pre-dive decrease in core temperature below resting levels may reduce the rate of oxygen consumption of central organs by 10–20% in seals. As a result, the ability to transfer heat quickly while on the water surface may allow marine mammals to extend their total aerobic dive time.

Precise timing of heat transfer and the coincident control of organ temperatures during submergence are components of the thermoregulatory response of many diving marine endotherms. Weddell seals (Hill et al., 1987), bottlenose dolphins (Rommel et al., 1994) and king penguins (Handrich et al., 1997) show regional heterothermy and variable core temperatures associated with aquatic activity. As found for bottlenose dolphins in the present study, a temporal delay in thermoregulatory functions during the dive response allows many of these animals to accommodate two seemingly conflicting physiological requirements.

One consequence of the delay in heat transfer for diving bottlenose dolphins is a theoretical increase in core temperature during the course of the dive. Previous studies have shown that this odontocete exhibits rapid increases in core temperature during activity, especially under warm water conditions (McGinnis et al., 1972; Rommel et al., 1994; T.M.W., personal observation). Although it was not possible to monitor the core temperature of the dolphins in the present study, such an increase in core temperature during diving contrasts with other marine mammals. For example, it has been suggested that the low core temperatures of diving pinnipeds serve as a mechanism for reducing metabolic demands and conserving oxygen (Hill et al., 1987). Without data, it is difficult to know the magnitude of change in core temperature that may occur in diving dolphins. Larger size and shorter dive durations in comparison with those of phocid seals (Williams et al., 1999) and low activity levels facilitated by gliding during diving descents (Skrovan et al., 1999) may lead to only modest changes in core temperature. Obviously, further studies are needed to understand the effect of diving and delayed heat transfer on organ and core body temperatures in dolphins.

The thermoregulatory patterns of dolphins, like hypometabolism in diving marine mammals (Elsner and Wickham, 1988), may represent a specific example of a

generalized mammalian response to resource limitations. Although temporal scales differ, analogous delays in heat transfer may be found in large terrestrial mammals such as desert-dwelling camels. Common to these animals is the limited availability of a critical resource. For diving dolphins, cardiovascular changes to conserve oxygen (Scholander, 1940) subsequently reduce heat transfer from thermal windows during submergence (Fig. 2). Similarly, dehydrated camels will reduce heat transfer during daylight hours to conserve water that would otherwise be lost in evaporative processes. Excess heat is stored until evening, when transfer can occur via non-evaporative pathways (Schmidt-Nielsen et al., 1957). With the availability of the limiting resource (oxygen in the case of dolphins, water for desert camels), heat transfer is elevated. Thus, we find that average heat flow is only 65.0% of resting values for diving dolphins and 53.5% of resting values for camels without access to water. When the limiting resource is available, heat flow is increased to 117% and 168.3% of resting levels for the dolphin and camel, respectively. This strategy of alternating periods of suppressed and elevated heat transfer allows both species to delay heat transfer until it can be accomplished with the greatest economy in specific resources.

In summary, this study demonstrates that heat transfer in bottlenose dolphins is attenuated by the dive response. While these results are somewhat intuitive because of the well-known cardiovascular changes associated with submergence, they illustrate how two potentially conflicting physiological responses are coordinated in diving marine mammals. An important benefit of this coordination between physiological processes is the potential for conservation of limited oxygen reserves.

This series of papers on the diving physiology of dolphins was inspired by the work of Gerald L. Kooyman: they are dedicated to him in celebration of his remarkable research career and influence on all comparative physiologists. This study was supported by grants from the Office of Naval Research (N00014-95-1-1023) and UCSC COR to T.M.W. The authors also thank the trainers at the Dolphin Experience (Freeport, Grand Bahama Island) and NOSC (Kaneohe, HI) for assisting with the diving dolphins. R. Davis, R. Skrovan, S. Noren and D. Noren provided invaluable comments on various drafts of the manuscript. All experimental procedures involving animals followed NIH Guidelines and were evaluated and approved by institutional Animals Use Committees.

References

- Andrews, R. D., Jones, D. R., Williams, J. D., Thorson, P. H., Oliver, G. W., Costa, D. P. and LeBoeuf, B. J.** (1997). Heart rates of Northern elephant seals diving at sea and resting on the beach. *J. Exp. Biol.* **200**, 2083–2095.
- Chabot, D., Bayer, M. and de Roos, A.** (1989). The analysis of heart rate data: the effect of using interbeat intervals vs instantaneous heart rates. *Proceedings from the Eighth Biennial Conference on the Biology of Marine Mammals*. p. 11.
- Cuyler, C., Wiulsrod, R. and Øritsland, N. A.** (1992). Thermal infrared radiation from free living whales. *Mar. Mammal Sci.* **8**, 120–134.
- Elsner, R.** (1969). Cardiovascular adjustments to diving. In *The Biology of Marine Mammals* (ed. H. T. Andersen), pp. 117–145. New York: Academic Press.
- Elsner, R., Kenney, D. W. and Burgess, K.** (1966). Diving bradycardia in the trained dolphin. *Nature* **212**, 407–408.
- Elsner, R. and Wickham, L. I.** (1988). Implications from physiological studies of marine mammals. *Mar. Mammal Sci.* **4**, 34–43.
- Hampton, I. F. G. and Whittow, G. C.** (1976). Body temperature and heat exchange in the Hawaiian spinner dolphin, *Stenella longirostris*. *Comp. Biochem. Physiol.* **57A**, 196–197.
- Hampton, I. F. G., Whittow, G. C., Szekerces, J. and Rutherford, S.** (1971). Heat transfer and body temperature in the Atlantic bottlenose dolphin, *Tursiops truncatus*. *Int. J. Biometeorol.* **15**, 247–253.
- Handrich, Y., Bevan, R. M., Charrassin, J.-B., Butler, P. J., Putz, K., Woakes, A. J., Lage, J. and LeMaho, Y.** (1997). Hypothermia in foraging king penguins. *Nature* **388**, 64–67.
- 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.
- Irving, L.** (1969). Temperature regulation in marine mammals. In *The Biology of Marine Mammals* (ed. H. T. Andersen), pp. 147–174. New York: Academic Press.
- Kasting, N. W., Adderley, S. A. L., Safford, T. and Hewlett, K. G.** (1989). Thermoregulation in beluga (*Delphinapterus leucas*) and killer (*Orcinus orcus*) whales. *Physiol. Zool.* **62**, 687–701.
- Kooyman, G. L.** (1989). *Diverse Divers: Physiology and Behavior* (ed. D. S. Farner). Berlin: Springer-Verlag. 200pp.
- McGinnis, S. M., Whittow, G. C., Ohata, C. A. and Huber, H.** (1972). Body heat dissipation and conservation in two species of dolphins. *Comp. Biochem. Physiol.* **43A**, 417–423.
- Ponganis, P. J., Kooyman, G. L., Winter, L. M. and Starke, L. N.** (1997). Heart rate and plasma lactate responses during submerged swimming and trained diving in California sea lions, *Zalophus californianus*. *J. Comp. Physiol. B* **167**, 9–16.
- 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.
- Ryg, M., Lydersen, C., Knutsen, L. O., Bjorge, A., Smith, T. G. and Øritsland, N. A.** (1993). Scaling of insulation in seals and whales. *J. Zool., Lond.* **230**, 193–206.
- Schmidt-Nielsen, K., Schmidt-Nielsen, B., Jarnum, S. A. and Houpt, T. R.** (1957). Body temperature of the camel and its relation to water economy. *Am. J. Physiol.* **188**, 103–112.
- Scholander, P. F.** (1940). *Experimental Investigations on the Respiratory Function in Diving Mammals and Birds* (ed. Universitets Biologiske Laboratorium and Statens Institutt for Hvalforskning). Oslo: Hvalradets Skrifter 22. 131pp.
- Scholander, P. F. and Schevill, W. E.** (1955). Counter-current vascular heat exchange in the fins of whales. *J. Appl. Physiol.* **8**, 279–282.
- Skrovan, R. C., Williams, T. M., Berry, P. S., Moore, P. W. and Davis, R. W.** (1999). The diving physiology of bottlenose dolphins

- (*Tursiops truncatus*). II. Biomechanics and changes in buoyancy at depth. *J. Exp. Biol.* **202**, 2749–2761.
- Thompson, D. and Fedak, M. A.** (1993). Cardiac responses of grey seals during diving at sea. *J. Exp. Biol.* **174**, 139–164.
- Whittow, G. C.** (1987). Thermoregulatory adaptations in marine mammals: Interacting effects of exercise and body mass. A review. *Mar. Mammal Sci.* **3**, 220–241.
- Williams, T. M., Friedl, W. A. and Haun, J. E.** (1993). The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. *J. Exp. Biol.* **179**, 31–46.
- Williams, T. M., Haun, J. E., Friedl, W. A., Hall, R. W. and Bivens, L. W.** (1992). Assessing the thermal limits of bottlenose dolphins: a cooperative study by trainers, scientists and animals. *IMATA Soundings Fall 1992*, 16–17.
- Williams, T. M., Haun, J. E. and Friedl, W. A.** (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*). I. Balancing the demands of exercise for energy conservation at depth. *J. Exp. Biol.* **202**, 2739–2748.
- Wilson, R. P., Grant, W. S. and Duffy, D. C.** (1986). Recording devices on free-ranging marine animals: does measurement affect performance? *Ecology* **67**, 1091–1093.
- Worthy, G. A. J. and Edwards, E. F.** (1990). Morphometric and biochemical factors affecting heat loss in a small temperate cetacean (*Phocoena phocoena*) and a small tropical cetacean (*Stenella attenuata*). *Physiol. Zool.* **63**, 432–442.
- 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.
- Zar, J. H.** (1974). *Biostatistical Analysis*. Englewood Cliff, NJ: Prentice Hall, Inc. 620pp.