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ORIGINAL PAPER

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Thermoregulation during swimming and diving in bottlenose dolphins, *Tursiops truncatus*

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Abstract Heat transfer from the periphery is an important thermoregulatory response in exercising mammals. However, when marine mammals submerge, peripheral vasoconstriction associated with the dive response may preclude heat dissipation at depth. To determine the effects of exercise and diving on thermoregulation in cetaceans, we measured heat flow and skin temperatures of bottlenose dolphins (*Tursiops truncatus*) trained to follow a boat and to dive to 15 m. The results demonstrated that skin temperatures usually remained within 1 °C of the water after all exercise levels. Heat flow from peripheral sites (dorsal fin and flukes) increased over resting values immediately after exercise at the water surface and remained elevated for up to 20 min. However, post-exercise values for heat flow from the flukes and dorsal fin decreased by 30–67% when dolphins stationed at 15 m below the surface. The pattern in heat flow was reversed during ascent. For example, mean heat flow from the flukes measured at 5 m depth, $40.10 \pm 2.47 \text{ W} \cdot \text{m}^{-2}$, increased by 103.2% upon ascent. There is some flexibility in the balance between thermal and diving responses of dolphins. During high heat loads, heat transfer may momentarily increase during submergence. However, the majority of excess heat in dolphins appears to be dissipated upon resurfacing, thereby preserving the oxygen-conserving benefits of the dive response.

Key words Thermoregulation · Diving · Exercise · Dolphin · Heat flow

Abbreviations T_a ambient air temperature · T_s skin temperature · T_w ambient water temperature · RPM revolutions per minute

Introduction

The high thermal conductivity and heat capacity of water poses a unique thermoregulatory challenge for active marine mammals that differs from that of terrestrial mammals. During exercise, terrestrial mammals increase both heat production and muscle blood flow (Mitchell 1977). Excess heat generated by the active muscles during exercise may be dissipated by increased blood flow through dilated vessels of the skin (Berger 1982; Franklin et al. 1993; Kellogg et al. 1993). Ultimately, the heat is transferred to the surrounding environment by four different pathways, conduction, convection, radiation, and/or evaporation (Mitchell 1977; Berger 1982; Brooks and Fahey 1984). In comparison, the primary thermal adaptation in phocid seals and cetaceans is a thick blubber layer that insulates against heat loss to the water (Kanwisher and Sundnes 1966; Irving 1969; Ryg et al. 1993). Poorly insulated peripheral areas are utilized as thermal windows which permits the transfer of excess heat via conduction and convection during exercise or when ambient water is warm (McGinnis et al. 1972; Kanwisher and Ridgway 1983).

To limit heat transfer at the peripheral sites, cetaceans maintain a counter-current arrangement of vessels in their fins and flukes (Scholander and Schevill 1955; Hampton and Whittow 1976). During periods of elevated activity, however, the counter-current heat exchanger is bypassed and blood flow through superficial veins near the skin increases to provide maximum cooling (Scholander and Schevill 1955). Cetaceans take advantage of cooled blood from these peripheral sites to

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regulate temperature-sensitive organs such as the intra-abdominal testes (Rommel et al. 1992, 1994; Pabst et al. 1995).

Little is known about the use of these specialized thermal windows during different levels of activity in cetaceans. Previous studies have telemetered deep body temperatures of bottlenose and Hawaiian spinner dolphins during rest, surface swimming, and leaps and spins in pools (Hampton et al. 1971; McGinnis et al. 1972; Hampton and Whittow 1976; Whittow 1987). Heat flow and skin temperatures (T_s) of Hawaiian spinner dolphins during rest (McGinnis et al. 1972; Hampton and Whittow 1976) and an Atlantic bottlenose dolphin exercising in a pool (Hampton et al. 1971) have also been investigated. As expected, activity resulted in an increase in deep body temperature of Hawaiian spinner dolphins (Hampton and Whittow 1976; Whittow 1987) and a Pacific bottlenose dolphin (McGinnis et al. 1972). Heat flow from the tip of the pectoral fin of the Atlantic bottlenose dolphin increased three to four-fold after swimming at a speed of $1 \text{ m} \cdot \text{s}^{-1}$ for 6–7 min (Hampton et al. 1971), presumably to counteract an increase in core temperature with activity. Variation in heat flow from different regions of the body was considerable (Hampton et al. 1971; Hampton and Whittow 1976), however, as was variation in heat flow between animals (Hampton and Whittow 1976). In contrast, external T_s at all measurement sites were fairly uniform and greater than, but within $1 \text{ }^\circ\text{C}$, of the surrounding water temperature (Hampton et al. 1971; Hampton and Whittow 1976).

The details of cetacean thermoregulation during swimming and diving in the open ocean remain unknown. Because blood flow to peripheral regions is reduced during diving to conserve total body oxygen (Scholander 1940), the amount of blood available for heat dissipation at peripheral thermal windows may be compromised during subsurface activity. Thus, there appears to be a direct conflict between the cardiovascular requirements for thermoregulatory and diving responses in marine mammals (Whittow 1987).

This study examines thermoregulation in active bottlenose dolphins in the open ocean. Specifically, changes in heat flow and T_s were measured for swimming and diving animals. By conducting the studies under warm water conditions in the Bahamas we were able to investigate mechanisms for dissipating excess heat in an environment that poses a thermoregulatory challenge. To determine the effects of the dive response on post-exercise heat transfer, we compared the levels of heat flow for animals stationed at the water surface and submerged. The results of the study demonstrate that heat flow increases at peripheral thermal windows in response to increased swimming activity. However, this response is attenuated when the animal is diving. Rather than challenge the dive response, dolphins are able to delay the dissipation of excess heat until the post-dive recovery period.

Materials and methods

Animals

Three adult Atlantic bottlenose dolphins (*Tursiops truncatus*) were used in these studies (Table 1). Blubber thickness was measured on the flank by a portable ultrasound unit (Scanoprobe II) to assess the general condition of insulation for each animal. The animals were housed in large ($15 \text{ m} \times 15 \text{ m} \times 4 \text{ m}$ deep), salt-water pens connected to the open ocean via a channel near Port Lucaya, Grand Bahama Island. All animals were acquired from the wild and had been maintained at the facility for over 8 years.

The dolphins were fed daily a diet of capelin and herring supplemented with multi-vitamins (Sea Tabs, vitamin C, B-12, and B complex). Mean water temperature (T_w) during the experimental period from August through mid-September was $29.8 \text{ }^\circ\text{C}$; mean air temperature (T_a) was $28.6 \text{ }^\circ\text{C}$.

Experimental design

Local T_s and heat flows of two dolphins were measured under three conditions: (1) during rest on the water surface, (2) post-exercise on the water surface, and (3) post-exercise at a dive depth of 15 m. To assess temporal changes in the thermoregulatory response during a dive, we measured heat flow continuously as one dolphin ascended from a depth of 5 m to the water surface. Measurement sites for heat flow and T_s (Fig. 1) were chosen to include peripheral thermal windows (dorsal fin and fluke blade) and a well insulated region of the body (flank).

Resting measurements were made on two male dolphins trained to float next to a deck prior to exercise sessions. The effects of exercise on heat flow and T_s were also determined on these two dolphins. Post-exercise measurements were taken as the animals stationed on the water surface immediately following a 12–22 min swim at $3.7 \text{ m} \cdot \text{s}^{-1}$ or an 11–13 min swim at $4.3 \text{ m} \cdot \text{s}^{-1}$. Additional measurements were taken during the recovery period at 10-min intervals for up to 30 min following the cessation of swimming.

During swimming, the dolphins remained on or near the water surface and matched their swim speed to that of a 5-m Boston whaler. Brief periods ($< 1 \text{ min}$) of wave-riding in the bow or stern wake were observed. Speed of the boat was determined by videotaping (Sony Handicam Hi 8) a known distance between two fixed points as the boat was running at a constant RPM (revolution per minute). The range of speeds in this study ($3.7\text{--}4.3 \text{ m} \cdot \text{s}^{-1}$) were determined by digital analysis of the video tape (Peak Performance software) and the calculated relationship between RPM and timed distances. The two swim speeds used in this study were well above the minimum cost of transport speed of $2.1 \text{ m} \cdot \text{s}^{-1}$ determined for bottlenose dolphins (Williams et al. 1992, 1993) and were considered moderate to high exercise loads for these animals.

The effect of the dive response on post-exercise heat flow and T_s was determined by repeating the measurements on dolphins sta-

Table 1 Morphological characteristics of the bottlenose dolphins used in this study. Lengths are straight line measurements from the tip of the rostrum to the notch in the flukes. Mass was estimated from measured length and maximum circumference. Age was determined from approximate age at time of capture and duration of captivity. Blubber depths are mean values measured for the flank (see Fig. 1). (F female, M male)

Dolphin	Sex	Age (years)	Length (cm)	Mass estimate (kg)	Blubber depth Mean \pm SE (mm)
1	M	14	252.0	227	11.8 ± 0.3
2	M	14	259.0	236	13.2 ± 0.3
3	F	14	238.0	172	12.0 ± 0.0

tioned at 15 m depth. The dolphins swam at $4.3 \text{ m} \cdot \text{s}^{-1}$ for 11–13 min, as above, to the dive site approximately 3 km offshore of Port Lucaya, Grand Bahama Island. At the dive site each dolphin accompanied a trainer to the sandy bottom. Measurements were taken from the three sites in a random order immediately upon the animal reaching the station position at 15 m. Generally, two anatomical sites were measured before the animal had to return to the surface to breathe. Measurements continued when the animals returned to the trainer.

To assess temporal changes in heat flow associated with the dive response without prior exercise, we continuously monitored heat flow from one female dolphin ascending from a 5-m dive. Steady-state measurements were recorded while the animal stationed at depth in a shallow channel and following the initial breath after ascent. Only the dorsal fin and fluke blade were measured during these experimental sessions. After the submerged measurement, scuba divers ascended with the dolphin, keeping the heat flow/thermistor probe fixed on the measurement site. One anatomical site was measured for each submergence and subsequent breath.

Heat flow

Heat flow across the skin of the dolphin to the water was measured with a 2.54-cm diameter circular model heat flux transducer (Thermonetics). The internal surface of the transducer was held underwater against the skin of the stationary animal until it stabilized and a steady state signal was recorded for more than 15 s. Most heat flow measurements required 1–2 min to complete. To ensure that ambient water flowed freely on the external side of the transducer, it was mounted on a spring and open pore PVC handle. Zero and range calibrations were conducted during each experimental session. Accuracy for the instruments was $\pm 7.10\text{--}7.89 \text{ W} \cdot \text{m}^{-2}$ depending on the instrument used.

Voltage (mV) from the transducer was measured on a hand-held Auto Range Digital Multimeter (Radio Shack model no. 22-166A or Micronta model no. 22-166A). For measurements at depth, the multimeters were housed in a clear acrylic waterproof box (Ikelite). A 5-m line from the transducer probe handle was connected to the box by an underwater connector.

Skin temperature

T_s was determined using a thermistor implanted on the surface of the heat flow disk (Thermonetics). During dives, the thermistor was attached to a second multimeter which allowed continuous, simultaneous monitoring of T_s and heat flow. T_s from the thermistor was recorded when the heat flow value was stable. The thermistor was calibrated against a digital thermometer (Physitemp) in an insulated water bath prior to experiments. Calibration temperatures of the thermistor ranged from 18.6 °C to 36.6 °C and spanned the range of experimental temperatures. Accuracy was found to be within ± 0.1 °C.

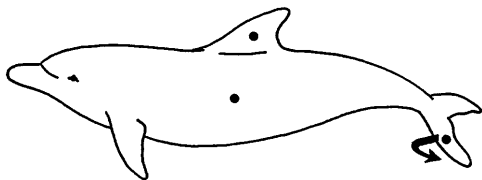


Fig. 1 Measurement sites for heat flow and skin temperature (T_s) of bottlenose dolphins. The dots designate the three sites (dorsal fin, flank, and the underside of the fluke blade) where the hand-held transducers were placed on the animals. Blubber thickness was measured on the flank only

Analyses

T_s and heat flow data were analyzed using Sigma Stat software (Jandel Scientific 1995) and were pooled when there were no significant differences in the data from individuals (t -tests: $P > 0.05$). One-way repeated measures ANOVA on ranks was used for the analyses of T_s data. One-way repeated measures ANOVA with Student-Newman-Keuls pairwise multiple comparison method was used for the analyses of heat flow data during rest on the water surface, post-exercise on the water surface, and post-exercise at depth. Significant changes in heat flow before and after a 5-m ascent from depth were determined from paired t -tests. Linear regressions were from least squares methods using Sigma Plot software (Jandel Scientific 1995) with significances determined through analysis of variance using Sigma Stat (Jandel Scientific 1995). All statistical results were deemed significant when $P \leq 0.05$. Means are presented as ± 1 SE unless otherwise indicated.

Results

Skin temperature

T_s did not vary significantly between the two dolphins ($P > 0.05$); therefore, the results were pooled (Fig. 2). Values for T_s ranged from 28.74 °C to 31.61 °C and were correlated to T_w (Fig. 2).

Most T_s , irrespective of body site, remained within 1 °C of T_w during rest and throughout the post-exercise recovery period. In general, the lowest T_s were found for resting and post-exercise submerged dolphins when compared to post-exercise dolphins measured at comparable T_w on the water surface (Fig. 2). However, these differences were not significant ($P > 0.05$).

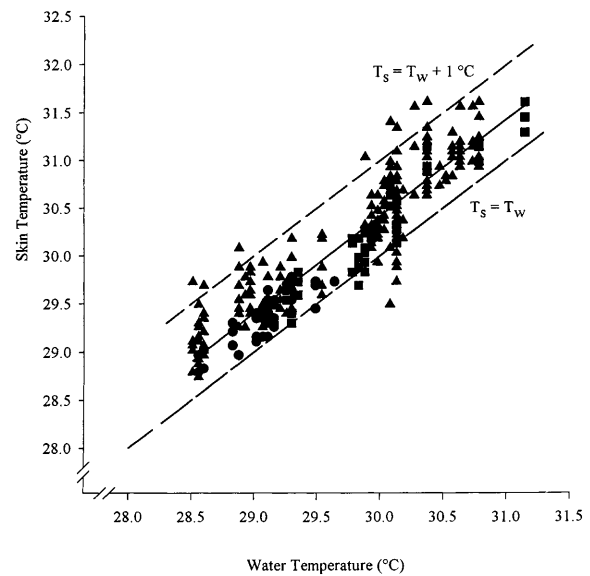


Fig. 2 T_s from three anatomical sites of two adult male bottlenose dolphins during rest on the water surface (■), post-exercise on the water surface (▲), and post-exercise submergence to 15 m (●). The dashed lines show $T_s = \text{ambient water temperature } (T_w)$ and $T_s = T_w + 1$ °C. The solid line denotes the least squares regression through the data points. T_s was correlated to T_w according to the relation: $T_s = 1.012 + 0.980 T_w$ ($n = 314$; $r^2 = 0.850$; $F = 1770.214$; $df = 1$; $P < 0.001$)

Heat flow on the water surface

Heat flow of dolphins resting on the water surface ranged from $7.89 \text{ W} \cdot \text{m}^{-2}$ to $134.13 \text{ W} \cdot \text{m}^{-2}$, and depended on both the animal and measurement site. Although differences in heat flow between the three sites were not significant, heat flow from the dorsal fin tended to be the highest ($72.24 \pm 9.63 \text{ W} \cdot \text{m}^{-2}$ for dolphin 1; $69.17 \pm 4.91 \text{ W} \cdot \text{m}^{-2}$ for dolphin 2), while heat flow from the flank tended to be the lowest ($50.85 \pm 5.94 \text{ W} \cdot \text{m}^{-2}$ for dolphin 1; $43.15 \pm 4.74 \text{ W} \cdot \text{m}^{-2}$ for dolphin 2).

All sites showed an increase in heat flow from rest following surface swimming at $3.7 \text{ m} \cdot \text{s}^{-1}$, with significant increases ($P < 0.05$) at the two thermal windows, the dorsal fin and fluke blade (Fig. 3). Heat flow from the dorsal fin was 2.2 times the resting value after 12 min of exercise and 2.5 times resting after 22 min of exercise. The maximum heat flow measured for this site was $180.38 \pm 15.86 \text{ W} \cdot \text{m}^{-2}$ immediately after swimming for 22 min. Heat flow from the fluke blade was 1.9 times the resting heat flow value immediately after 12 min of exercise and 2.3 times resting immediately after 22 min of exercise. The maximum heat flow measured from the

fluke blade was $122.52 \pm 12.93 \text{ W} \cdot \text{m}^{-2}$ immediately after swimming for 22 min. Heat flow from the peripheral sites remained significantly elevated above resting values for at least 10 min during recovery and usually did not decrease significantly below the initial post-exercise heat flow values until 20 min into the recovery period (Fig. 3).

Both peripheral sites showed significantly greater heat flow than the flank at 0 min ($F = 12.16$, $df = 2$, $P < 0.001$), 10 min ($F = 7.02$, $df = 2$, $P = 0.010$), and 20 min ($F = 10.23$, $df = 2$, $P = 0.002$) of recovery following a 12 min swimming bout. The trend was similar after 22 min of swimming but significant only for the dorsal fin.

Heat flow at depth

Diving immediately after an 11–13 minute swim at $4.3 \text{ m} \cdot \text{s}^{-1}$ resulted in a reduction in heat flow when compared to values measured on the water surface after the same exercise speed and duration. Reductions of 30–67% were observed from the two peripheral sites at depth for both dolphins (Figs. 4, 5). Heat flow from both the dorsal fin and the fluke blade were significantly lower during a post-exercise dive than during post-exercise on

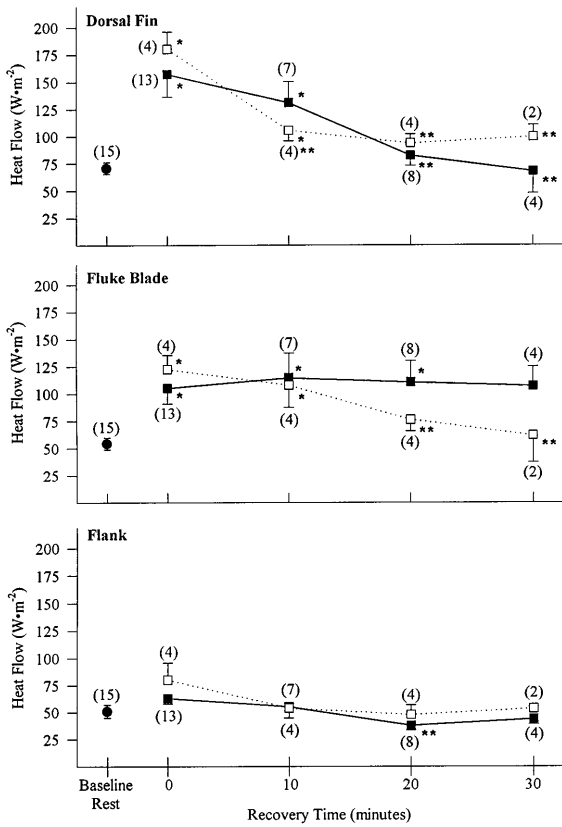


Fig. 3 Heat flow during post-exercise recovery in bottlenose dolphins. Heat flow from the dorsal fin, fluke blade, and flank during rest (●) and after 12 min (■) and 22 min (□) of swimming at $3.7 \text{ m} \cdot \text{s}^{-1}$ are presented. Values significantly greater than resting (*) and significantly less than 0 min post-exercise (**) are indicated. Data are pooled for two dolphins. Numbers in parentheses indicate the total number of trials. Mean values during the post-exercise recovery period are presented with SE bars in one direction only for clarity

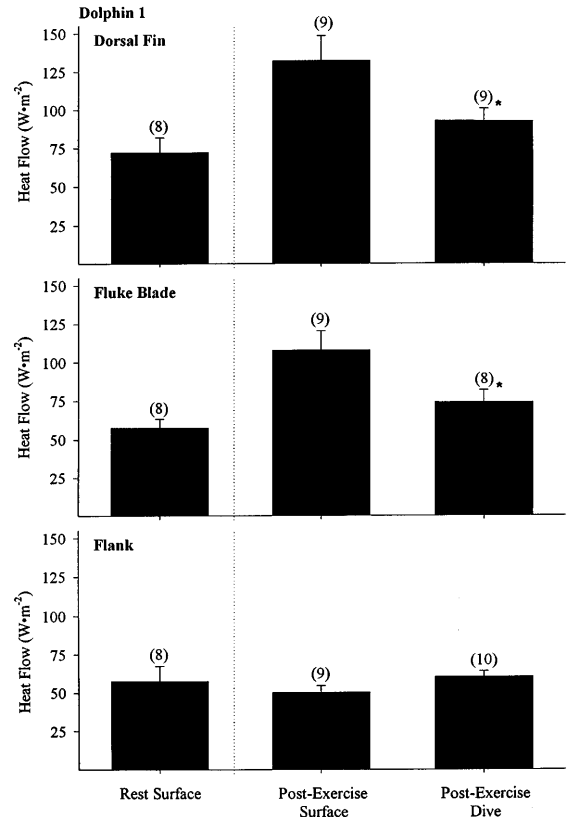


Fig. 4 Heat flow for three activity levels in dolphin 1. Post-exercise measurements at the surface and at 15 m depth were after 11–13 min of swimming at $4.3 \text{ m} \cdot \text{s}^{-1}$. Mean heat flow from the dorsal fin, fluke blade, and flank are shown with SE bars. Numbers in parentheses indicate the number of trials at each activity level. Post-exercise dive values significantly less than post-exercise surface are indicated by *

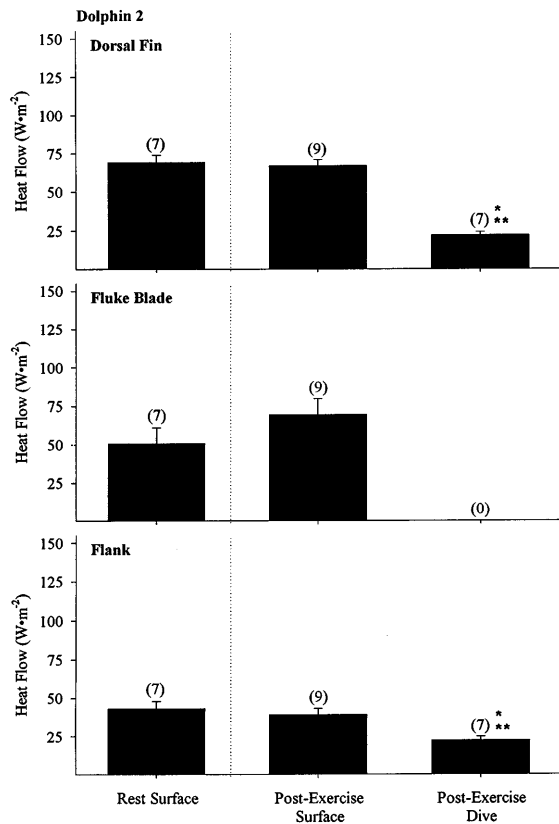


Fig. 5 Heat flow for three activity levels in dolphin 2. Post-exercise measurements at the surface and at 15 m depth were after 11–13 min of swimming at $4.3 \text{ m} \cdot \text{s}^{-1}$. Mean heat flow from the dorsal fin, fluke blade, and flank are shown with SE bars. Numbers in parentheses indicate the number of trials at each activity level. Note that it was not possible to obtain fluke blade measurements on this animal during diving. Post-exercise dive values significantly less than post-exercise surface are indicated by *; post-exercise dive values significantly less than rest on the water surface are indicated by **

the water surface ($P < 0.05$). The change in heat flow during a post-exercise dive was especially marked for dolphin 2 (Fig. 5). In addition to a reduction in heat flow from the dorsal fin, we found that heat flow from the flank of dolphin 2 was significantly less during a post-exercise dive than both rest and post-exercise at the water surface ($P < 0.05$) (Fig. 5).

Although the typical trend at depth was a reduction in heat flow, in one test, an unusually high measurement of $244.6 \text{ W} \cdot \text{m}^{-2}$ was obtained from the dorsal fin of dolphin 1 stationed at 15 m depth. In addition to the exercise period before the dive, this animal had completed multiple jumps out of the water immediately before the measurements were taken.

Temporal changes in heat flow

Mean heat flow during submergence to 5 m was $44.83 \pm 6.65 \text{ W} \cdot \text{m}^{-2}$ for the dorsal fin and $40.10 \pm 2.47 \text{ W} \cdot \text{m}^{-2}$ for the fluke blade of dolphin 3 (Fig. 6). During ascent, heat flow from the sites increased gradually, until the animal was 1 m below the water

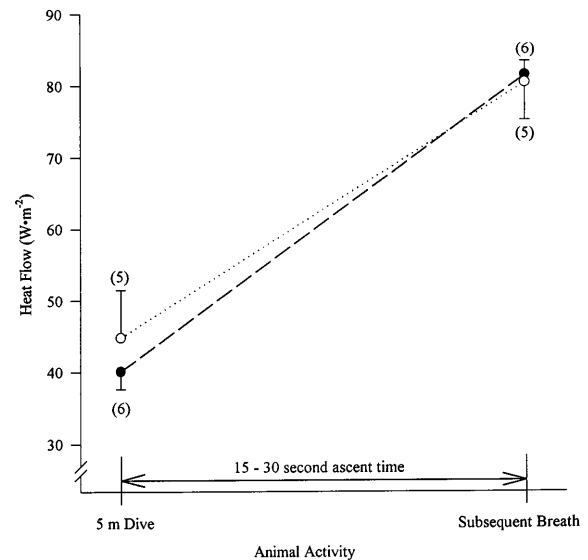


Fig. 6 Heat flow from the fluke blade (●) and dorsal fin (○) during a 5-m dive and subsequent breath. Numbers in parentheses designate the number of trials. Mean values are presented with SE bars in one direction only for clarity. Dashed lines connect the value at depth to the value during the breath for each measurement site, but they do not represent values measured between the two data points

surface. The maximum heat flow response occurred as the animal surfaced and breathed. Heat flow during the initial breath was significantly greater than the submerged value for the dorsal fin ($t = -18.78$, $df = 4$, $P < 0.001$) and fluke blade ($t = -16.20$, $df = 5$, $P < 0.001$). Mean values for heat flow from the dorsal fin increased by 79.3% while mean values from the fluke blade increased by 103.2% during the 15–30 s ascent.

Discussion

The typical mammalian response to exercise involves a redistribution of blood to the skin for enhanced heat transfer (reviewed in Brooks et al. 1996). In mammals adapted for aquatic living such as the bottlenose dolphin, this exercise response is complicated by the circulatory adjustments associated with diving. Bradycardia and decreased peripheral blood flow are important components of the dive response (Scholander 1940) but appear in direct conflict with the circulatory changes that occur with exercise. As a result, the active diving mammal must balance the peripheral circulation to accommodate thermoregulation that requires increased blood flow and oxygen conservation that demands decreased blood flow. In this study we find a hierarchy in the responses, with heat transfer from peripheral thermal windows being attenuated by the dive response in bottlenose dolphins.

The primary sites of heat loss in the bottlenose dolphin are the peripheral thermal windows located at the dorsal fin and flukes. During exercise, heat flow increases at these sites and remains elevated during recovery (Fig. 3). Similar results have been found for a

variety of cetacean species, including the harbor porpoise (Kanwisher and Sundnes 1965), the Hawaiian spinner dolphin (McGinnis et al. 1972; Hampton and Whittow 1976), and the Pacific (McGinnis et al. 1972) and Atlantic (Kanwisher and Sundnes 1966; Hampton et al. 1971) bottlenose dolphins.

Despite the high thermal conductivity of water, the dolphins in this study required a recovery period of at least 20 min to achieve resting heat flow values for all sites following swimming exercise. This recovery time is similar in duration to those reported for many terrestrial mammals exercising in air (Brown et al. 1993; Hodgson et al. 1993). Because heat transfer is 20–25 times faster in water than in air at comparable temperatures, the extended post-exercise recovery period for dolphins was not expected. However, several factors may have contributed to these results. First, the temperature differential between the water and core body was less than 8 °C in this study, resulting in a relatively small gradient for heat transfer. Second, the peripheral thermal windows represent only 30% of the total surface area of the Atlantic bottlenose dolphin (calculated from data in Hampton et al. 1971) which will limit the absolute heat loss from the body. Third, forced convective cooling, an important mechanism for increasing heat transfer during active swimming (Pabst et al. 1995), is reduced in sedentary animals during the recovery period. Therefore, the overall rate of heat dissipation may have been lower when the dolphins stopped swimming.

Heat transfer associated with exercise was also modified during diving. This was evident in the significant reductions in post-exercise heat flow during submergence when compared to post-exercise heat flow measured on the water surface (Figs. 4, 5). Although heart rate and blood flow were not measured in this study it is likely that cardiovascular changes associated with the dive response contributed to the observed reduction in heat flow (T.M. Williams, D.P. Noren, P. Berry, J.A. Estes, C. Allison, J. Kirtland, personal observation).

Like the dive response (e.g., Scholander 1963; Kooyman and Campbell 1972; Zapol et al. 1979; Hill et al. 1987; Kooyman 1989; Cherepanova et al. 1993; Guyton et al. 1995), thermoregulatory responses during submergence may not be an all-or-none phenomenon for marine mammals. The results from this study indicate that specific thermal demands alter the balance between diving and thermoregulatory responses. Previous studies on restrained harbor seals (Hammel et al. 1977) and ducks (Johansen 1964) show an override of the dive response during heat stress. Similarly, flexibility in the thermoregulatory response occurred during natural dives in the open ocean for the dolphins in the present study. Each of the dolphins showed variability in heat flow between the three measurement sites, with heat flow during a dive preferentially dissipated from the dorsal fin. There also appeared to be variability in heat dissipation strategies between the individual dolphins. For example, dolphin 2 showed significant reductions in post-exercise heat flow from the flank and dorsal fin

during a dive (Fig. 5). In comparison, dolphin 1 showed significant reductions in post-exercise heat flow only from the two peripheral sites during a dive; the flank remained unchanged (Fig. 4). For dolphin 2 heat flow levels during diving were significantly less than resting values. Dolphin 1 maintained heat flow above resting values when submerged, indicating an ability to partially reduce the thermal load during a dive.

The level of activity, and hence heat production, has an additional effect on heat transfer during submergence. The unusually high value of $244.6 \text{ W} \cdot \text{m}^{-2}$ from the dorsal fin of dolphin 1 at 15 m depth was obtained immediately after this animal had completed multiple jumps out of the water. Either a full dive response had not yet been initiated or the thermoregulatory responses of dolphins may be adjusted even during submergence. Such adjustments in the dive response to allow momentary increases in heat flow would allow a partial reduction in exercise-induced thermal loads without a complete override of the dive response and consequent increase in oxygen utilization (Gallivan and Ronald 1979).

We were unable to measure core body temperature in the current study. Other studies, however, have reported conflicting results regarding the effects of submergence on core body temperature. Reductions in core and aortic temperatures of freely diving pinnipeds at depth have been observed (Kooyman et al. 1980; Andrews et al. 1994) as well as temperature reductions at the water surface between dives (Hill et al. 1987). Harp seals diving in a pool showed no decrease in core temperatures with submergence (Gallivan and Ronald 1979). Another diving endotherm, the king penguin, shows marked regional heterothermy during diving (Handrich et al. 1997). Clearly, further investigation concerning the relationship between submergence and core temperature is needed for endothermic animals. In particular, the balance between peripheral heat flow and maintenance of a stable core temperature in diving cetaceans warrants further study.

An interesting result from the present study is the temporal change in heat transfer during ascent and the post-dive period. Significant increases in heat flow were measured from the dorsal fin and fluke blade upon the dolphin's first breath following a dive (Fig. 6). The thermal response associated with emergence from a dive parallels changes in heart rate for bottlenose dolphins (T.M. Williams, D.P. Noren, P. Berry, J.A. Estes, C. Allison, J. Kirtland, personal observation). Heart rate gradually increases in dolphins during ascent and is maximized when hyperventilation occurs upon emergence (Elsner et al. 1966). Although heart rate could not be monitored concurrently with heat flow in the present study, the temporal patterns suggest a link between cardiovascular and thermal events during and after a dive by dolphins.

In general, the thermoregulatory status of dolphins is dependent on activity level and state of submergence. During rest, there is minimal heat dissipation. Exercise on the water surface results in an increase in heat flow from all sites, with the largest changes occurring at the

thermal windows, the dorsal fins and fluke blades. Diving attenuates the exercise response and delays heat transfer to accommodate the dive response. The results of this study suggest that there is flexibility in the balance between these two apparently conflicting physiological responses. Under conditions of intense activity, and presumably high heat loads, heat transfer may increase momentarily during submergence. However, the majority of heat transfer usually occurs when the dolphin resurfaces, thereby preserving the oxygen-sparing benefits of the dive response.

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