

MUSCLE TEMPERATURE AND SWIM VELOCITY PROFILES DURING DIVING IN A WEDDELL SEAL, *LEPTONYCHOTES WEDDELLII*

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Summary

Locomotory muscle temperature and swim velocity profiles of an adult Weddell seal were recorded over a 21 h period. The highest temperatures occurred during a prolonged surface period (mean 37.3°C, s.d. 0.16°C). Muscle temperature averaged 36.8 and 36.6°C (s.d. 0.25°C, 0.19°C) during two dive bouts and showed no consistent fluctuations between dive and interdiving surface intervals. Swim velocities were also constant, near 1.3 ms⁻¹. These data indicate that past records of low aortic temperatures (35°C) during and after prolonged dives are not indicative of whole-body temperature changes, and that muscle temperature, even during dives as long as 45 min, remains near 37°C.

Introduction

Aortic temperature reductions of 1–3°C have previously been recorded during or after extended dives in Weddell seals, *Leptonychotes weddellii* (Kooyman *et al.* 1980; Hill *et al.* 1987). Such changes appeared to be consistent with the 1°C temperature decreases reported for multiple tissues during 15 min forced submersions of harbor seals, *Phoca vitulina* (Scholander *et al.* 1942). While hypometabolism has been considered to be a potential cause of such changes, increased conductive and convective heat loss, including alterations in skin and flipper blood flow, have also been suggested as possible mechanisms (Kooyman *et al.* 1980; Hill *et al.* 1987).

In view of these data, we now present the muscle temperature profile of a Weddell seal during diving. In addition, swim velocity is also reported, as an indicator of relative muscle work effort during diving.

Materials and methods

An adult, male seal *Leptonychotes weddellii* (Bonner) (448 kg) was captured near McMurdo Station, Antarctica, brought to an experimental hut, and weighed and

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anesthetized (1mgkg^{-1} intramuscular ketamine induction, and 1–3% isoflurane and oxygen for maintenance *via* a mask connected to a large-animal, semiclosed-circuit anesthesia machine). The seal was allowed entry into a dive hole below the hut 17h after the termination of anesthesia.

While the seal was anesthetized, an intramuscular temperature probe was inserted percutaneously into the longissimus dorsi-iliocostalis lumborum muscle complex. Measurements were recorded at 15s intervals by an attached microprocessor (MP). Depth and swim velocity were recorded at 15s intervals by the MP and an attached velocity meter, as previously described (Ponganis *et al.* 1990; Castellini *et al.* 1992b).

The temperature probe was a Yellow Springs Instruments thermistor, model 511, sensitive to 0.1°C , calibrated in a Lauda temperature bath. The factory-specified time constant of the thermistor (63% response time) was 0.2s. The probe calibration curve was generated by linear regression analysis.

Surface times and behavior between dives were recorded for correlation with the MP data. After the study, the seal was reanesthetized and the instruments removed without any apparent complications.

Data were stored, processed and prepared for analysis on Quattro Pro, Statistix and NCSS with the use of a customized Pascal program.

Results

Fig. 1 contains the swim velocity and muscle temperature profiles during the study period. Entry into the water occurred at 19:01h. During the first dive bout, dive profiles from 23:00–02:00h were considered to be characteristic of a foraging pattern (Castellini *et al.* 1992a), in that dive depths, durations and surface intervals were uniform at about 100m, 10min and 2min, respectively. Probable exploratory dives occurred at 02:25, 06:15 and 09:30h. These dives were 27, 36 and 45min in duration and were less than 50m in depth. The prolonged surface period of 78min began at 04:10h. The MP was disconnected and removed from the seal while it slept in the water at 28min into a second prolonged surface period.

Since consistent temperature oscillations between dive and interdiver surface intervals during dive bouts were not apparent (Fig. 1), all these temperatures were pooled and compared to the pooled temperatures recorded while the seal rested in the water (Table 1). The mean temperatures for these surface periods (SP) and dive periods (DP) were significantly different (Table 1, ANOVA, F ratio 979.9, $P > F = 0.0000$). The range of mean temperatures was 0.7°C ; Duncan's and Newman-Keul's range tests ($P = 0.05$) revealed that $\text{SP1} = \text{DP1}$, while Fisher's LSD test ($P = 0.05$) showed that $\text{DP2} = \text{SP3}$. All

Fig. 1. Muscle temperature of a Weddell seal during a 21h period. The first surface period (SP1) occurred primarily in the hut prior to water entry at 19:01h [start of first dive period (DP1)]. The prolonged surface period (SP2) between dive bouts occurred from 04:10 to 05:28h. At the end of the second dive period (DP2, 05:28–14:29h), the seal slept at the surface (SP3, 14:29h onwards), during which time the recorder was removed and disconnected from the animal.

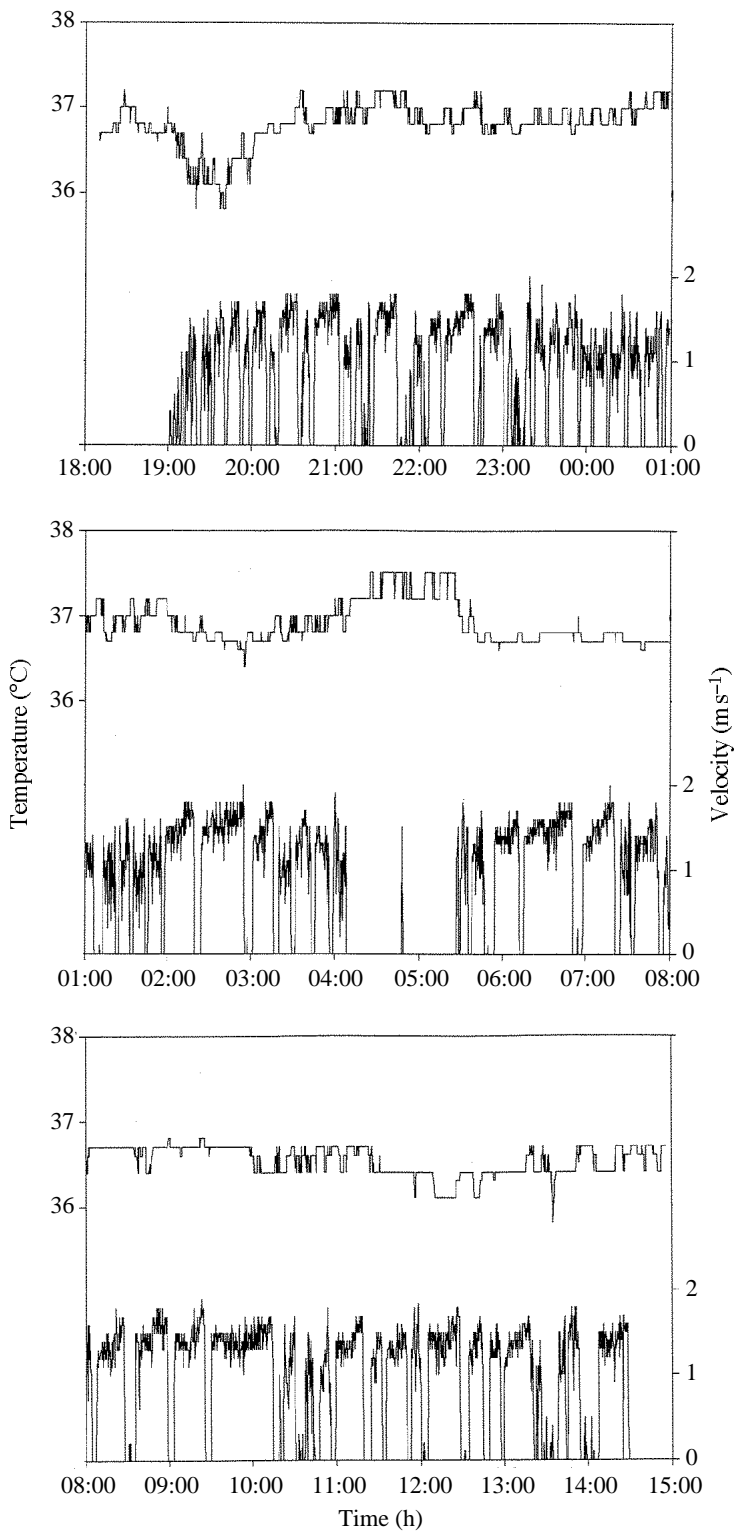


Fig. 1

Table 1. *Muscle temperature during diving and non-diving activity*

Activity	Temperature (°C)		
	Mean	S.D.	N
SP1	36.8	0.12	204
DP1	36.8	0.25	2188
SP2	37.3	0.16	312
DP2	36.6	0.19	2162
SP3	36.6	0.10	112

Data is taken from Fig. 1.

SP, surface period; DP, dive period.

other comparisons of mean surface period and dive period temperatures were not equal by these tests.

Overall, mean swim velocity was 1.3 ms^{-1} (S.D. 0.36 ms^{-1} , $N=3389$). During the three long extended dives, mean velocity was 1.5 ms^{-1} (S.D. 0.18 ms^{-1} , $N=441$).

Discussion

During this 21h record, the highest temperatures occurred during the prolonged surface period (SP2) between dive bouts. This temperature increase was similar to that previously observed in the arterial blood of diving Weddell seals (Kooyman *et al.* 1980; Hill *et al.* 1987). Such a temperature elevation during the surface period could be due to several factors: decreases in convective heat loss (Gallivan and Ronald, 1979), absence of cold prey ingestion (Imms and Lighten, 1989) and food-induced thermogenesis (FIT) (Costa and Kooyman, 1984). Why such an increase did not occur during the recorded portion of the last surface period (SP3) is unclear; however, the predominance of exploratory dives prior to SP3, the lower aortic temperatures during such long dives (Kooyman *et al.* 1980; Hill *et al.* 1987) and possibly decreased FIT (due to decreased or no food intake during exploratory dives), may contribute to such a pattern.

During diving, except for the initial temperature decrease soon after entry into the water, muscle temperature was nearly constant at about 37°C . Since some muscular work is necessary for the seal to swim continuously at 1.3 ms^{-1} , muscle temperature should rise, especially if its blood flow ceases or is intermittent. If muscle is completely ischemic and little or no heat is lost to surrounding tissue or through the blubber layer (Bryden, 1964), muscle temperature should rise in proportion to its metabolic rate by the following equation:

$$T = (\text{metabolic rate} \times 20.1 \times 0.8) \div \text{heat capacity},$$

where T is temperature in $^\circ\text{C}$, metabolic rate is tissue oxygen consumption in $\text{ml O}_2 \text{ kg}^{-1} \text{ musclemin}^{-1}$, heat capacity of muscle is assumed to be equivalent to that of blood and is $3846 \text{ J kg}^{-1} \text{ muscle}^\circ\text{C}^{-1}$ (Astrand and Rodahl, 1970), and a 20% metabolic energy efficiency is assumed. In this equation, the primary metabolic rate measurement is converted to joules ($1 \text{ ml O}_2 = 20.1 \text{ J}$, Schmidt-Nielsen, 1983). At a resting muscle

metabolic rate of $2\text{--}3\text{ ml O}_2\text{ kg}^{-1}\text{ muscle min}^{-1}$ (Connett *et al.* 1984), muscle temperature should rise at a rate of $0.008\text{--}0.013^\circ\text{C min}^{-1}$. Even at this resting metabolic rate, during total ischemia, muscle temperature should increase about $0.3\text{--}0.5^\circ\text{C}$ during a 40 min dive. However, this is probably an unrealistically low metabolic rate for working muscle. Given the diving metabolic rates measured in this species, a maximal locomotory muscle metabolic rate of $14\text{ ml O}_2\text{ kg muscle}^{-1}\text{ min}^{-1}$ has been estimated (Castellini *et al.* 1992b). At this rate, unperfused muscle should increase 2.2°C in temperature during a 40 min dive. Although such an extended dive should have resulted in the greatest reduction in muscle blood flow, no increase in temperature was recorded (Fig. 1). Either the muscle was extremely hypometabolic during active swimming at 1.5 ms^{-1} , or there was some muscle perfusion. Some muscle blood flow, increased in the latter portions of extended dives, would be consistent with the constant or even slightly lowered muscle temperature at the end of such dives (Fig. 1), with increased heart rates before surfacing (Hill *et al.* 1987), and with the increased plasma lactic acid concentration near the end of an extended dive (Guppy *et al.* 1986).

These muscle temperature measurements near 37°C during diving also suggest that no single site temperature is a satisfactory indicator of whole body metabolism or whole body temperature, as has been proposed in earlier reports (Kooyman *et al.* 1980; Hill *et al.* 1987). Although aortic temperatures near 35°C have been reported for extended dives (Kooyman *et al.* 1980; Hill *et al.* 1987), such a temperature decrease was not seen in locomotory muscle during this study. It appears that propulsive muscle temperature is regulated at a constant temperature during diving.

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