SKIN TEMPERATURES DURING FREE-RANGING SWIMMING AND DIVING IN ANTARCTIC FUR SEALS

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Summary

This study tests the hypothesis that an endothermic homeotherm should minimise heat flux in cold polar waters by minimising skin temperature. Temperature variability was measured at the surface of the skin of three Antarctic fur seals (*Arctocephalus gazella*) at intervals of 2 s over a total of 9.7 days while they were swimming and diving freely in polar waters at temperatures of 1.5–4 °C. The temperature difference (ΔT) between skin on the dorsal thorax and the water varied from more than 20 °C to close to equality over periods of less than 1 h. Shorter-term variations in ΔT of up to 5 °C occurred in association with diving, although these types of variations also occurred without diving. In general, ΔT began to decline during the descent phase of a dive and began to increase again during the ascent or at the end of the dive. One of the three individuals examined showed little variation in ΔT, which remained low (approximately 3 °C) throughout the experiment. In the other two fur seals, ΔT tended to decline during periods of sustained diving and usually increased during periods spent at the surface. Mean calculated heat flux varied from 95 to 236 W m^{-2} depending on the individual. Metabolic rates based on these calculated heat fluxes were towards the lower end of those measured in previous studies using different methodologies. The study has shown that Antarctic fur seal skin temperature is highly dynamic and suggests that the thoracic surface is an organ used for active thermoregulation.

Key words: thermoregulation, polar, low temperature, physiology, pinniped, Antarctic fur seal, *Arctocephalus gazella.*

Introduction

For an endotherm to maintain a constant body temperature in a cold environment, heat loss must be balanced by metabolic heat production. Endothermic vertebrates that inhabit aquatic environments, such as marine mammals and seabirds, are faced with the problem of retaining heat during immersion in cold water (Irving and Hart, 1957). These species have various anatomical adaptations that appear to reduce heat flux to the surrounding water; these include a surface covering of fur or feathers, layers of subcutaneous fat and counter-current heat exchangers in the circulation to appendages (Kanwisher and Sundness, 1965; Hampton and Whittow, 1976). Since sea water conducts heat 25 times more efficiently than air, the management of heat balance by these animals is likely to be one of the most important evolutionary challenges posed by an aquatic existence.

Evidence from diving pinnipeds suggests that muscle and core temperatures fluctuate little during submersion (Scholander et al., 1942; Ponganis et al., 1993), but aortic temperature reductions of 1–3 °C may indicate conductive and convective heat loss across the body surface (Kooyman et al., 1980; Hill et al., 1987). Amongst species of smaller body size, such as diving seabirds (Culik et al., 1996; Bevan et al., 1997; Handrich et al., 1997) and mustelids (Williams, 1986), core temperature may decline by up to 15 °C during immersion.

Several species compensate for reduced water temperatures by increasing heat production to maintain core temperature (Costa and Kooyman, 1982; for relationships between metabolic rate and water temperature in birds, see Bevan and Butler, 1992). These observations show that, in some cases, the response to the thermal challenges of submersion in cold water may be dealt with through heterothermy, whereas in others it is compensated by increased metabolic rate.

Reduced regional circulation during diving (Butler and Jones, 1997) may lead to regional heterothermy because heat lost, especially from peripheral tissues, may not be matched by transfer of core heat to the surface *via* the circulation. These physiological mechanisms used to reduce the rate of oxygen consumption during diving also have the potential to reduce the capacity to thermoregulate. This appears to occur during diving in dolphins in which heat flux across the skin is delayed until the end of the dive (Noren et al., 1999; Williams et al., 1999).

A balance between heat production and heat loss could be achieved by adjusting blood flow to the skin and extremities. Several models of heat balance in aquatic mammals during immersion have assumed the importance of skin temperature for the conduction of heat away from the surface into the water (Lavigne et al., 1990; Ryg et al., 1993; Boily, 1995; Hind and

Gurney, 1997). According to these approaches, both free and forced convection are highly sensitive to the temperature difference between the skin surface and the water so that the heat loss per unit area is proportional to the temperature differential.

In this study, I examine the temperature difference between the skin of a marine mammal, the Antarctic fur seal (*Arctocephalus gazella* Peters), and the surrounding water. The female Antarctic fur seal (30–50 kg) is a small marine mammal, but is large compared with those aquatic endotherms shown to be heterothermic. This species relies mainly upon a thick layer of fur to provide insulation (Bonner, 1981), but there is little information about how effective this is likely to be, especially during diving when hydrostatic pressure will tend to reduce the insulative capacity of fur. Since this species inhabits polar waters, I wished to test the hypothesis that these animals minimise heat flux to their environment by mininising skin temperature.

Materials and methods

The study was conducted at Bird Island, South Georgia (54°S 38°W), during November and December 1998. This site is convenient for examining aspects of fur seal behaviour because it supports a large breeding colony of 50 000–60 000 adult females. Between periods of 1–2 days spent nursing pups ashore, mothers spend 4–7 days foraging at sea. This provides an ideal opportunity to deploy instruments that can be recovered when the seals return to feed their pups.

Six adult females of *Arctocephalus gazella* Peters that were all feeding pups during the early stages of lactation were captured and fitted with archival data loggers. Individuals were approximately matched for mass and the stage of the breeding cycle (days 2–6 of lactation), and all appeared to be in good condition on the basis of body mass (see Table 1) and the condition of their pups. Capture and deployment techniques followed those used in previous recent studies that used the same experimental paradigm (Boyd et al., 1997). In the present study, two data loggers (Wildlife Computers MK7, Redmond, WA 98052, USA; mass <50 g, dimensions 5 cm×2 cm×2 cm) were deployed side-by-side on the back of each fur seal.

Because of the dense hair of fur seals, the prolonged immersion in sea water and the difficulties with making sensors sufficiently rugged to withstand the physically demanding environment of a seal colony, it was not possible to use heat flux sensors as was the case with short-term deployments on dolphins (Noren et al., 1999; Williams et al., 1999). However, the same principle applied in the sensors used in the dolphin studies was also used in the present study. This involves the simultaneous measurement of temperature by two thermistors separated by an insulation layer of known properties. Each thermistor was controlled by one of the data loggers. One data logger was used to measure and record skin temperature; its thermistor (thermistor 1, pre-calibrated in a water bath) was set within a small (2 mm×3 mm) knob of heat-conductive epoxy glue on a 10 cm stalk that trailed behind the instrument after it had been fitted to the animal and that lay flush with the fur on the back of the animal. The stalk was attached to the outer guard hairs of the fur using sparing amounts of 5 min epoxy glue RS Components, Corby, Northants, UK). Thermistor 1 sat on the dorsal mid-line approximately 10 cm anterior to the pelvis, an area of the animal that has no large blood vessel close to the surface. The guard hairs were clipped with scissors over a 1 cm×1 cm area, and the base of the mount of thermistor 1 was attached to the underfur with epoxy glue so that the thermistor was held firmly next to the skin. A 3 cm×3 cm patch of flexible, insulative polystyrene foam (Functional Foam, Beacon Products Ltd, Unit 10, EFI Industrial Estate, Merthyr Tydfil, UK; 1.3 cm thick, thermal conductivity 0.40 W m^{-1} K^{-1}, absorption less than 0.6 % vol over 28 days at STDP, permeability 0.82 ng Pa^{-1} s^{-1} m^{-1}, tensile strength 740 kPa) was placed over the top of the thermistor. The heat flux due to forced convection at this surface and with a temperature difference of 10 °C across the foam layer will be approximately 308 W m^{-2}. This patch was then tacked to the guard hairs and underfur using epoxy glue. This was not designed to prevent water ingress but was intended to minimise the rate of water turnover around the thermistor and to create a pocket of water around it.

The second instrument carrying thermistor 2 was used to measure and record water temperature 1 cm above the level of the fur of the back of the animal. In this case, the stalk was 0.5 cm in length, but otherwise the design was identical to that of the stalk-carrying thermistor 1, which was used to measure skin temperature. In this case, the thermistor was not attached to the hair but sat free within the water passing over the back of the animal. The stalk was sufficiently short and stiff to ensure that the thermistor was held 1 cm above the level of the fur.

In both data loggers, temperature was measured to the nearest 0.1 °C and the response time of the thermistor to a change in temperature of 1 °C of the surrounding medium was less than 2 s. For technical reasons, it was not possible to measure both skin and water temperature using the same data logger. Both data loggers also measured hydrostatic pressure and light level. All transducers were interrogated at 2 s intervals throughout deployments, and the resulting values were stored in the memory of each logger. The data within each logger were recovered when each fur seal was recaptured, and the data sets from each logger were combined on the basis of the time of each reading. The clocks of each instrument were synchronised to the nearest 1 s.

To examine the dynamics of the temperature gradient between the skin and the water in relation to diving activity, I fitted a simple heat balance model to patterns of temperature change. This was not fitted with a view to *a priori* prediction of variations in temperature gradients but to provide an insight into the physical processes involved in the variability in the temperature difference between the skin and the water, ΔT (where $\Delta T = T_{skin} - T_{water}$), in terms of underlying physiological processes. I assumed that the temperature of the small volume

of water enclosed between the foam insulation and the skin (which was, in effect, what was being measured by the thermistor) declined exponentially in the absence of heat influx. Similarly, in the presence of a constant heat influx and no efflux (i.e. perfect insulation), I assumed for this simple model that the temperature increased linearly up to a maximum equivalent to several degrees less than blood temperature. Other forms of the model were fitted that included sigmoid and asymptotic power functions. While these complex models gave improved fits to the data because of their greater parameterisation, they have not been illustrated in the present study because the additional variation explained was not justified by the additional model complexity. If heat influx is β_1 and efflux is β_2, t denotes a time, T_t is the temperature after time t and T_0 is the temperature at the start of an interval, then:

$$\frac{\mathrm{d}T}{\mathrm{d}t} = 0, \qquad \beta_1 - \beta_2 = 0 \ . \tag{1}$$

Therefore,

$$T_t = T_0\mathrm{e}^{-\beta_2 t} \begin{cases} \beta_1 = 0 \\ \tau = 0 \end{cases} \tag{2}$$

and

$$\lim_{T_t \to T_{max}} T_t = \beta_1 t + T_0 \begin{cases} \beta_2 = 0 \\ \tau = 1 \end{cases} \ . \tag{3}$$

The first step in the fitting procedure was to identify sections of the time series in which there were consistent positive and negative trends in the temperature gradient. On the basis of the hypothesis that during positive trends there was complete blood circulation to the skin, these were given a value of unity, i.e. $\tau = 1$. During negative trends when circulation was stopped,

$\tau = 0$. I also assumed there was an upper limit T_{max} to the skin temperature.

Results

Useable data were obtained from three of the six instrumented fur seals (Table 1). Data from the other three individuals had to be discarded because of failure of one of the thermistors. Deployments in the three individuals from which full data sets were obtained lasted 2.5–5 days, and these individuals differed little in terms of morphometrics (Table 1).

Diving, expressed in terms of mean depth per hour, took place mainly at night, and this pattern was consistent among individuals (Fig. 1). There was evidence of peaks in dive depth around dusk and dawn, although all individuals also had periods of diving during daylight. This shows that the behaviour of these individuals was consistent with that of Antarctic fur seals in general (Boyd and Croxall, 1992).

The overall mean temperature difference between the thermistor placed against the skin and the thermistor within the surrounding sea water (ΔT) was greatest in fur seal w1470 and smallest in fur seal w5875 (Table 1). There was a highly significant ($P<0.001$) difference between these mean values when tested using a one-way analysis of variance (ANOVA; $F_{2,258}=44.21$). Similarly, there was a highly significant difference ($P=0.004$) between the variance of ΔT in the three individuals (ANOVA, $F_{2,256}=5.64$). This is reflected in the hourly mean ΔT values plotted in Fig. 1. The contrast between the variance in ΔT for w1470 and w5871 (Fig. 1A,B) and for w5875 (Fig. 1C) shows the two quite different responses amongst the three individuals. Whereas w5875 maintained an almost constant low ΔT between the skin surface and the surrounding water, this was not true of the other two individuals. Although the response of w5875 could have been caused by water ingress under the foam insulation, this seems

Table 1. *Information about the fur seals that provided useable data*

	Seal number		
	w1470	w5871	w5875
Deployment date	17 November 1998	30 November 1998	2 December 1998
Recovery date	24 November 1998	9 December 1998	14 December 1998
Mass (kg)	46	42	46
Length (m)	1.28	1.36	1.36
Girth (m)	0.87	0.92	0.94
Mean T_{water} (°C)*	1.8±0.2	2.9±0.5	2.1±0.6
Mean T_{skin} (°C)*	9.6±5.1	7.4±4.6	2.7±1.2
Mean ΔT (ºC)*	7.7±5.1	4.5±4.5	3.1±1.3
Maximum ΔT (ºC)	21.0	19.7	23.4
Number of temperature readings	1.14×10^5	2.09×10^5	9.53×10^4
Metabolic rate estimated from heat flux (W)‡	264	155	106

*Values are means ± S.D.

‡Calculated from Kshatriya and Blake (1988, equation 1): $Q=(kS_w/d)\Delta T$, where Q is the heat loss (W), k is the thermal conductivity (W m^{-1} K^{-1}), S_w is the surface area and d is the thickness of the insulation (m). The surface area of a female Antarctic fur seal of similar size to those examined in the present study was 1.115 m^2 (Boyd and Croxall, 1996).

T_{water}, water temperature; T_{skin}, skin temperature; $\Delta T=T_{skin}-T_{water}$.
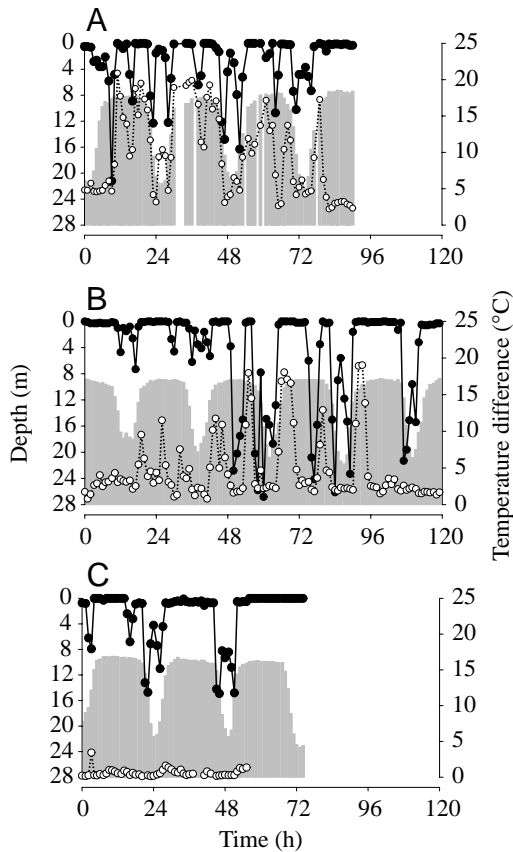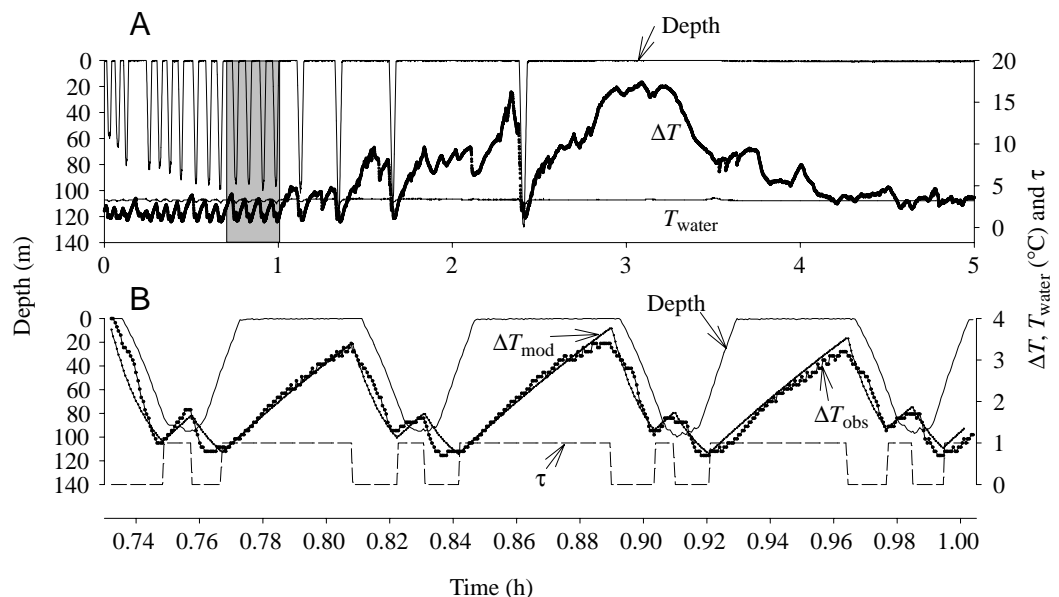
Fig. 1. Hourly mean dive depth (●), light level (histogram) and ΔT (the temperature difference between the skin and the water, ○) for three female Antarctic fur seals foraging during lactation. Data from w1470 (A), w5871 (B) and w5875 (C) are shown. No units are given for light level, which is presented as the raw output from the photometer. Photometer calibrations have shown that photometer response did not vary significantly between instruments and was linear across the range encountered in the present study.

unlikely because there were several short periods when ΔT did change (Fig. 1C), and this individual recorded the greatest maximum ΔT of the three seals (Table 1). In general, periods of diving were associated with low ΔT values and periods when there was no diving were associated with both low and high ΔT values. There was evidence from both w1470 and w5871 (Fig. 1A,B) that high ΔT values tended to occur in the few hours following a period of diving (e.g. Fig. 1A, hours 75–85; Fig. 1B, hours 60–75 and hours 80–100), although this pattern was not observed consistently (e.g. Fig. 1B, hours 96–120). There was an apparent diel variability in the temperature gradient in seal w1470, but this was most probably an effect of diel variation in diving activity that, in turn, influenced ΔT.

More detailed examination of sections of the activity/ temperature recordings for w1470 and w5871 that illustrate the dynamics of ΔT and, in particular, the response of ΔT to different types of diving behaviour are illustrated in Figs 2–5. These show that ΔT had complex dynamics that are to some extent related to diving behaviour.

Fig. 2 shows that short-term temperature variations were associated with deep diving (100 m) such that ΔT began to decline in advance of the beginning of a dive and declined during the descent phase of the dive to a minimum at approximately three-quarters of the way through the descent. Thereafter, ΔT increased briefly during the bottom section of the dive and then began to decline again during the early part of the ascent. ΔT then increased throughout the ascent and the following surface interval. The transitory increase in ΔT midway through a dive was particularly obvious in the detailed time series illustrated in Fig. 2B, but was present for all the other dives illustrated in Fig. 2A. In addition, Fig. 2A also illustrates how ΔT varied independently of diving behaviour.

A second section of the time series from w5871 is illustrated in Fig. 3 and shows the response to shallow dives (25–60 m). During hours 1.2–5, this also shows the comparatively large

Fig. 2. A 5 h section (A) and short subsection (B) of the depth and temperature record from w5871 illustrating the response to deep dives and different periods spent at the surface between dives. The shaded portion of A is the subsection that is expanded in B. ΔT is the temperature difference between the skin and the water. T_{water}, water temperature. The observed time series ΔT_{obs} and the modelled time series ΔT_{mod} are shown using different line styles. τ is the model parameter representing the on ($\tau=1$) and off ($\tau=0$) switch for circulation to the skin.

Fig. 3. A 5 h section (A) and short subsection (B) of the depth and temperature recording from w5871 illustrating the reponse to shallow dives and also the volatility of ΔT (the temperature difference between the skin and the water) in the absence of diving activity. The shaded portion of A is the subsection that is expanded in B. The observed time series ΔT_{obs} and the modelled time series ΔT_{mod} are shown using different line styles. τ is the model parameter representing the on ($\tau=1$) and off ($\tau=0$) switch for circulation to the skin. T_{water}, water temperature.
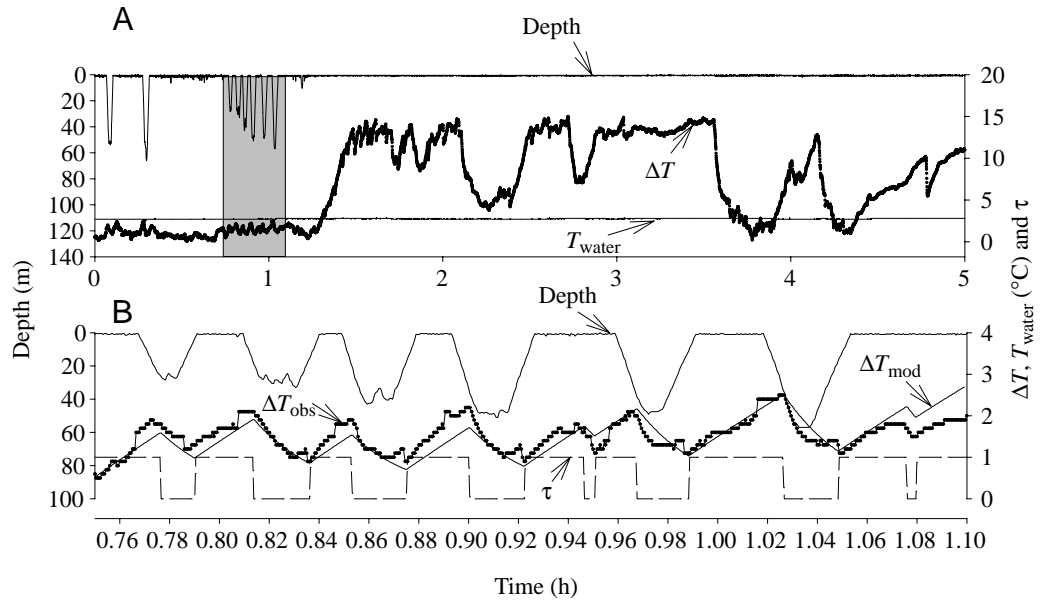
fluctuations in ΔT that occurred rapidly (over periods of 10 min) but with no apparent diving activity. The pattern of variation in ΔT during diving differed from the section of the time series shown in Fig. 2 because the decline in ΔT associated with diving occurred after the beginning of the dive. However, even though dives in this section of the time series were shorter than those in Fig. 2, they still showed a small (0.2–0.4 °C) increase in ΔT during the dive.

Two sections of the time series from w1470 are illustrated in Figs 4 and 5. These show a similar overall pattern to the illustrations from w5871, except that they show a longer-term systematic change in ΔT as well as the changes in ΔT in relation to diving to progressively increasing (Fig. 4) and declining (Fig. 5) depths. The detailed sections of these time series (Figs 4B, 5B) show that ΔT began to decline after the start of each dive. In Fig. 4B, the time series includes dives to

a wide range of depths and this shows that, for the shallower dives in the early part of the time series, ΔT began to decline close to the time that the fur seal had reached the bottom of the dive, whereas, for the deeper dives in the later part of the time series, ΔT began to decline when the fur seal was still in the descent phase of the dive. This difference reflected a consistent time lag between the beginning of the descent and the beginning of the decline in ΔT. In Fig. 4B, the beginning of the increase in ΔT coincided in each case with the end of the dive, but in Fig. 5B the increase in ΔT began at times between the beginning of the ascent and the end of the dive.

Considering all dives to a depth greater than 20 m for each of the three fur seals, ΔT declined in 88.5 % (177/200), 79.7 % (452/567) and 68.3 % (97/142) of dives for w1470, w5871 and w5875 respectively. There were also highly significant correlations ($r>0.6$ in all cases, $P<0.001$) between dive

Fig. 4. A 5 h section (A) and short subsection (B) of the depth and temperature record from w1470 illustrating the response of ΔT (the temperature difference between the skin and the water) to a bout of diving that progressed from shallow to deep dives. The shaded portion of A is the subsection that is expanded in B. The observed time series ΔT_{obs} and the modelled time series ΔT_{mod} are shown using different line styles. τ is the model parameter representing the on ($\tau=1$) and off ($\tau=0$) switch for circulation to the skin. T_{water}, water temperature.
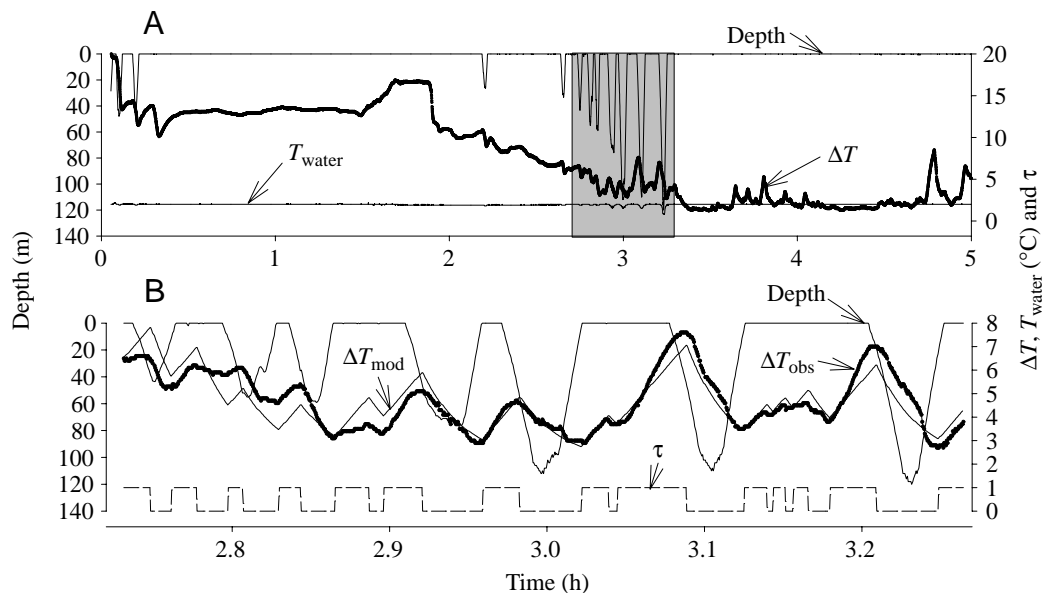
Fig. 5. A 5 h section (A) and short subsection (B) of the depth and temperature record from w1470 illustrating the response of ΔT (the temperature difference between the skin and the water) to a progressive decline in dive depth. The shaded portion of A is the subsection that is expanded in B. The observed time series ΔT_{obs} and the modelled time series ΔT_{mod} are shown using different line styles. τ is the model parameter representing the on ($\tau=1$) and off ($\tau=0$) switch for circulation to the skin. T_{water}, water temperature.
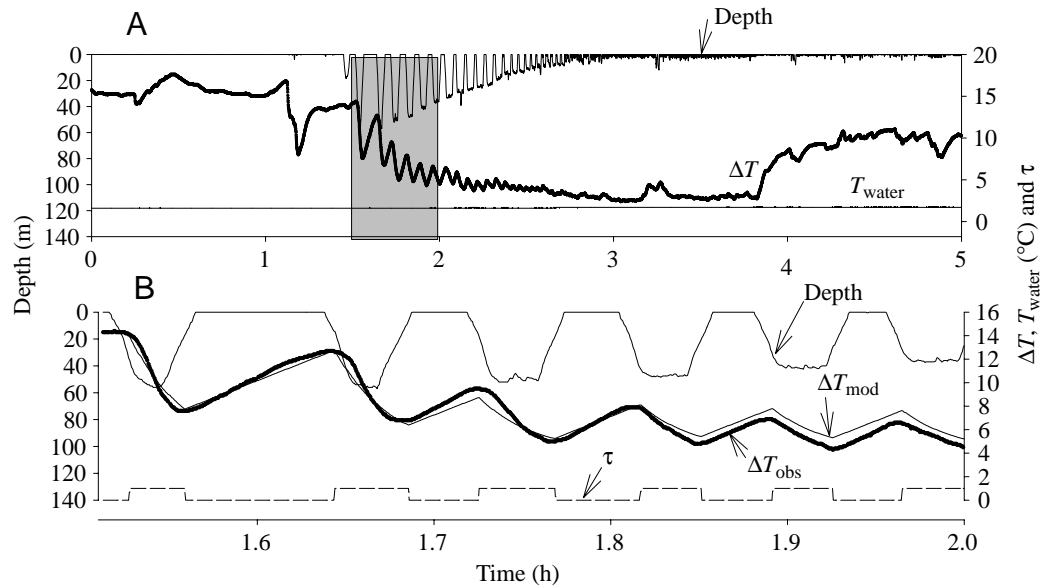
duration and the decline in ΔT between the start of dives and the point during dives when ΔT reached a minimum (ΔT_{min}) for w1470 and w5871 but not for w5875. The same pattern and level of significance were observed for the correlation between ΔT_{min} during dives and ΔT at the end of dives. This suggests that the changes in ΔT during dives are most likely to be principally a function of time submerged.

The results of the temperature-balance model fitted to the patterns of variation in ΔT are shown in Figs 2B, 3B, 4B and 5B. The principle by which the models were fitted assumed that there was a switch between two states, one in which there was full circulation to the skin (the 'on' phase) and the other in which there was no circulation (the 'off' phase) given by the value of τ. Since the purpose of fitting these models was to explore the underlying mechanisms driving the pattern of variability in ΔT rather than to be predictive, I attempted to balance the goodness of fit with a desire to retain model simplicity.

The model had mixed success at describing the pattern of variability in ΔT (Table 2). The overall pattern of variability was reasonably well represented in the four time series examined, but in those series illustrated in Figs 3B and 4B, the model was unable to represent underlying variability in the apparent rates of heat influx and efflux. Addition of a minimum

of $\Delta T=2\,°C$ improved the fit for data from w5871 (Figs 2, 3), but not for w1470 (Figs 4, 5). Experimentation with other forms of functions, including sigmoid and asymptotic power functions representing both the 'on' and 'off' phases, also led to an improved fit but at the expense of adding parameters that were of dubious biological significance. There was variation within and across examples of the apparent heat transfer rates (Table 2) suggesting that the on/off model of circulation to the skin is an oversimplification of the control process.

Discussion

Several important conclusions can be drawn from this study. First, the hypothesis examined, that fur seals in cold water minimise heat loss to the surrounding water by minimising skin temperature, is clearly not upheld by the present observations. Only one of the three individuals gave a pattern of ΔT that might have been expected had the fur seals been minimising their skin temperature, and it remains possible that water ingress under the insulation of the data logger could partly explain this observation. In the other two individuals, ΔT was shown to fluctuate over an amplitude of more than $20\,°C$ and across time scales of minutes to hours.

Second, even though the insulation surrounding the thermistor lying against the skin was at least as efficient as the normal fur in the animals, it is clear that some Antarctic fur seals must experience high heat flux to the surrounding water during immersion. Moreover, if one assumes that the variability in ΔT has some form of functional importance, the degree of heat flux appears to be regulated quite closely by the animal itself and was not always related to diving activity. The detailed analysis of the variations in ΔT in relation to diving also revealed that the variability was not simply a function of the pressure changes undergone during dives and any effects these may have had upon the quality of the insulating layer over the thermistor lying against the skin. This is because

Table 2. *Values of variables and coefficients for each of the models fitted to the time series examined in detail in Figs 2–5*

Variable or coefficient	Time series			
	w5871		w1470	
	Fig. 2	Fig. 3	Fig. 4	Fig. 5
β_1	0.021	0.012	0.022	0.017
β_2	0.022	0.010	0.010	0.009
r^2	0.903	0.591	0.755	0.955

β_1, heat influx; β_2, heat efflux.

patterns of variability in ΔT were inconsistent between dives of similar depth.

Third, although diving was the only form of behaviour measured in this study, there were rapid changes in ΔT in relation to diving activity. Given this observation, some of the other changes in ΔT that appeared to be unrelated to diving activity may have been related to other changes in behaviour and with the heat production associated with these changes. Similarly, the pattern of change during dives may result from heat production associated with the kinematics of swimming. For example, gliding during the descent and active swimming during the ascent (Davis et al., 1999; Williams et al., 1999) could have explained the patterns observed in this study.

These conclusions are based upon the assumption that the pattern of ΔT observed at a single site is similar to that present across the whole surface area of the animal. While it seems probable that, as found in dolphins, the skin temperature on the appendages may differ markedly from those measured on the dorsal thorax (Kanwisher and Sundnes, 1965; Williams et al., 1999) in the present study, there is no reason to believe that the amplitude of ΔT observed at the location measured is likely to differ from that on most other parts of the thoracic surface. In the case of diving, variability in ΔT conforms with the bradycardia observed during diving (Boyd et al., 1999) together with the presumed sympathetic reduction of circulation to peripheral tissues, including the skin (Butler and Jones, 1997). However, in the case of w5871, there was evidence of a temporary resumption of peripheral circulation in the middle of dives, possibly as a means of dissipating heat generated by work done during the descent phase of the dive (Figs 2B, 3B).

Measurement of heat loss in free-ranging animals may be used to examine metabolic heat production (McCafferty et al., 1998). If the measurements in the present study are representative of the temperature over much of the surface area of the animal, then it is possible to calculate the heat flux to the water assuming that this can be represented by a simple model of heat transfer through forced convection from a flat plate (Table 1). Fur seals in this study were losing heat to their environment at an average rate of 236, 139 and 95 W m^{-2} for w1470, w5871 and w5875 respectively. During some periods spent at the surface, this increased to more than 600 W m^{-2}, and during diving the rate declined to less than 30 W m^{-2}. Consequently, the minimum metabolic power required for these individuals to remain in thermal equilibrium would have been 5.7, 3.7 and 2.3 W kg^{-1} for w1470, w5871 and w5875 respectively (Table 1). This estimate will be less than the true value because of water leakage through and around the edges of the foam insulation covering the thermistor placed against the skin and as a result of respiratory and excretory heat loss. With the exception of the value for w5875, these estimates are within the range of metabolic rates for female Antarctic fur seals while swimming and diving measured using heart rate to estimate metabolic rate (Boyd et al., 1999). However, they are lower than those estimated from measurements made using doubly-labelled water (Costa et al., 1989; Arnould et al., 1996).

Further studies of skin temperature using different configurations of insulative patches and temperature measurements at multiple locations across the surface of the animal have the potential to provide an effective, simple and non-invasive method of estimating metabolic rate in Antarctic fur seals.

The model fitted to the observed time series of ΔT during examples of diving suggests that, in general, a square-wave pattern of circulation to the skin may sometimes be responsible for the pattern of variability in ΔT, but that there is also likely to be a more graded control process, perhaps associated with partial vasodilation or constriction. Overall, the model revealed that it was possible generally to track the variability in ΔT assuming that it was governed by two rate-limited processes, one warming and the other cooling.

The functions used to represent warming and cooling are highly simplified and could have been improved by including information about the properties of the overlying insulation and potential time lags due to the thermal properties of the adjacent body surface. However, since these properties were likely to vary with changes in hydrostatic pressure and with the degree of water exchange in the insulated layer immediately around the thermistor, on this occasion it would not have been practical to have fitted a more realistic physical model of the variation in ΔT.

Investigation of the energetics of swimming and immersion in animals lends itself to theoretical examination (e.g. Lavigne et al., 1990; Ryg et al., 1993; Boily, 1995; Hind and Gurney, 1997; Grémillet et al., 1998) mainly because the physical properties of convective and conductive heat flux across a boundary are reasonably well understood. Nevertheless, this study has shown that the thermal properties of that boundary (in this case the surface of the animal) cannot be assumed to be constant. Consequently, some theoretical examinations of the thermodynamics of aquatic animals and the way in which this has the potential to limit their range of activities are likely to be highly simplified representations of the true range of potential behaviours. On occasions, this has led to a degree of confusion and controversy (Lavigne, 1982; Lavigne et al., 1990).

Skin temperature, which is regulated by the delivery of heat from the core to the surface, is likely to be one of the most important single factors used to regulate metabolic rate in endothermic vertebrates immersed in cold water. The average heat flux found for fur seals in the present study was at least twice that of dolphins exercising in tropical waters (Noren et al., 1999; Williams et al., 1999), a difference that is likely to be due partly to the additional thermal challenge of cold polar waters but also to differences in body size between dolphins and fur seals.

This study has shown that skin temperature in a small marine mammal is highly labile, possibly indicating that these animals use their surface as a sophisticated organ for temperature control. It also highlights the significance of the management of heat flux across the body surface as a critical adaptation to an aquatic lifestyle.

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