Changes in body temperatures in king penguins at sea:
the result of fine adjustments in peripheral heat loss?

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Abstract

To investigate thermoregulatory adjustments at sea, body temperatures (the pectoral muscle and the brood patch) and diving behavior were monitored during a foraging trip of several days at sea in six breeding king penguins *Aptenodytes patagonicus*.

During inactive phases at sea (water temperature: 4-7°C), all tissues measured were maintained at normothermic temperatures. The brood patch temperature was maintained at the same values as those measured when brooding on shore (38°C). This high temperature difference causes a significant loss of heat. We hypothesize that high energy expenditure associated with elevated peripheral temperature when resting at sea is the thermoregulatory cost that a post-absorptive penguin has to face for the restoration of its subcutaneous body fat.

During diving, mean pectoral temperature was 37.6 ± 1.6°C. While being almost normothermic on average, the temperature of the pectoral muscle was still significantly lower than during inactivity in five out of the six birds, and underwent temperature drops of up to 5.5°C.

Mean brood patch temperature was 29.6 ± 2.5°C during diving and temperature decreases of up to 21.6°C were recorded. Interestingly, we observed episodes of brood patch warming during the descent to depth suggesting that in some cases, king penguins may perform active thermolysis using the brood patch. It is hypothesized that functional pectoral temperature may be regulated through peripheral adjustments in blood perfusion.

These two paradoxical features, i.e. lower temperature of deep tissues during activity, and normothermic peripheral tissues while inactive, may highlight the key to the energetics of this diving endotherm while foraging at sea.

**Keywords**: thermoregulation, marine endotherm, *Aptenodytes patagonicus*, temperature decreases, pectoral muscle, brood patch, adjusted heat loss, energy expenditure, diving, resting.

**List of symbols and abbreviations:**

- $T_{PM}$: pectoral muscle temperature
- $T_{BP}$: brood patch temperature
- $\Delta T$: temperature change (either for the brood patch: $\Delta T_{BP}$, or the pectoral muscle: $\Delta T_{PM}$)
- GI and GD: gradual increase and gradual decrease of maximal dive depth
- MR and RMR: metabolic rate and resting metabolic rate
- Neg$_{PM}$: selection of dive cycles showing a final negative $\Delta T_{PM}$
- Pos$_{PM}$: selection of dive cycles showing a final positive $\Delta T_{PM}$
- Early$_{BP}$: selection of dive cycles showing a positive $\Delta T_{BP}$ at the beginning of the dive
- Late$_{BP}$: selection of dive cycles showing a positive $\Delta T_{BP}$ in the late descent phase of the dive
Introduction

Low ambient temperatures increase the energetic costs required for the maintenance of homeo-endothermy. For some small birds, or species living in extreme environments, the metabolic rate and heat production that would be required for maintenance of core temperature reaches such levels that they adopt thermoregulatory adjustments (cyclic torpor or hypothermia) that permit energy reserves to last throughout the night or the winter season (39, 40, 46). For aquatic species, the maintenance of core temperature is even more costly because the thermal conduction of water is 25 times that of air (29, 36), and also because of the drastic reduction of plumage insulation in water (19, 49). Logically, prevention of body cooling should therefore represent a substantial part of the total energy expenditure in endothermic homeotherms in water. A decrease in peripheral body temperatures well below the core temperature lowers the difference in temperature between the body shell and its surroundings and consequently reduces peripheral heat loss. Low peripheral temperatures result from a combination of low environment temperature, compression of air in the feathers at depth and speed, and peripheral vasoconstriction (32), whereby the warm blood bypasses the cold exposed tissues and increases their cooling. Consequently, internal tissues are isolated and the core temperature is maintained at minimal cost.

King penguins (*Aptenodytes patagonicus*) forage at sea with alternating long, deep dives (up to 8min and 300m depth) and short surface intervals (generally less than 3min), several hours a day (12). While foraging, air-breathing species are limited in their apnoeic capacity by the amount of oxygen they can store and their overall metabolic rate at sea (9, 38). In king penguins, as well as in emperor and the gentoo penguins, the calculated aerobic dive limit, cADL (32), i.e. the total usable oxygen stores divided by the rate of oxygen usage while under water, is less than the duration of up to 50% of observed dives (7, 16, 22, 33, 35). Moreover, between two long dives, the short surface intervals do not seem sufficient to permit
the recovery from lactate accumulation associated with an increasing reliance on anaerobic metabolism (32). Even if the behavioral component may shorten or prolong the theoretical dive duration, the large number of dives exceeding the cADL makes this paradoxical physiological state unsustainable over several hours, as observed during common diving activity in the king penguin.

The cADL calculated from these studies must therefore have been underestimated, either due to overestimation of the diving metabolic rate (DMR) or erroneous assessment of available oxygen stores. However, estimation of the latter is considered to be reliable and reasonably accurate (1, 32, 37, 42). Furthermore, studies that have tried to identify possible energy-sparing strategies developed by diving birds to lower DMR have pointed to the possibility of physiological adjustments allowing a reduction of core temperature (4, 5, 17, 25). This hypothesis is controversial as it contradicts the classical theory of a highly regulated core temperature in endothermic homeotherms (9, 32, 48).

Nevertheless, temperature drops have been recorded during diving in king penguins, even in deep tissues (17, 25). In these studies, temperature sensors situated just under the liver (upper abdomen, 17) or between the liver and the apex of the heart (thoracic temperature, 24) recorded temperature drops of 12°C and 2.7°C, respectively. Subsequent debate has focused on the functional significance of these temperature drops. On the one hand, they may represent core temperature and cause a reduction in overall metabolic rate via the Q10 effect (48). On the other hand, they may not be representative of deep tissues and may, therefore, only be exterior to the thermal core of the body. In fact, studies on emperor penguins (Aptenodytes forsteri) diving from an isolated ice hole, reported no significant temperature changes in the inferior vena cava (43), the pectoral muscle, the stomach or the axillary/brachial veins (44), thus indicating the maintenance of body core temperature.
Unpublished data (Handrich, Y.) indicate an increase in skin temperature during the descent phase of dives in king penguins, which is unexpected in the context of the heat conservation hypothesis. Indeed, during the progression to depth, a decrease is observed in both water temperature and the air volume trapped in the feathers. Consequently, the descent to depth increases the temperature difference between the body and ambient temperature and the effectiveness of insulation is reduced. In addition, moving through the water increases convective heat transfer. Thus, swimming towards the sea bottom causes an increase in heat loss and a decrease in peripheral body temperatures. Birds showing a higher peripheral temperature when progressing to depth increase the body-ambient temperature difference, and thereby undergo greater heat loss. These observations therefore suggest that in some circumstances, king penguins seem to favor adjusted peripheral heat loss.

The aim of the present work is to clarify aspects of thermoregulation and the mechanisms of possible temperature and heat loss adjustments in free ranging king penguins at sea. We examined body temperature characteristics from the scale of daily activities to the finer temporal scale of the single dive cycle in organs having opposite thermal balances. Firstly, we examined the pectoral muscle (*Musculi pectoralis*) because of its primary contribution to overall heat production (50) and therefore the likelihood that this major locomotive muscle is the warmest during active swimming. Secondly, we examined the brood patch (*Area incubationis*), which is a bare and highly vascularised area of skin and possibly a preferential location for heat loss.

Based on the hypothesis of reduced body temperatures during sustained diving, our objectives were: 1) to investigate differential thermoregulatory strategies in relation to activity at sea, i.e. the maintenance of high and stable body temperatures when resting at sea, and the attainment of lowered body temperature during diving, especially at the level of a very active and energetically demanding tissue, the pectoral muscle, 2) to investigate whether temperature
reductions are regulated through active processes of peripheral adjustments in heat loss, or whether they are the passive consequences of diving in cold water.

**Materials and methods**

This study was carried out at Possession island, Crozet Archipelago, southern Indian Ocean (46°25’S, 51°45’E) at the 'Grande Manchotière’ colony of king penguins. This colony consisted of around 28 000 breeding pairs (52), during the 2001 breeding season.

**Technical information and measured variables**

Birds were equipped with modified Mk7 data loggers (Wildlife computers, USA). Due to the different characteristics of the loggers, penguins were equipped with 1 or 2 units in order to measure simultaneously on each bird the brood patch temperature ($T_{BP}$), the pectoral muscle temperature ($T_{PM}$), and environmental variables such as ambient temperature ($T_a$) and pressure. The sampling interval (SI) was respectively SI= 2s for $T_{BP}$ and SI= 4s for $T_{PM}$ for bird 1, 2, 3 and 4. Birds 5 and 6 recorded body temperatures with SI= 8s for $T_{BP}$ and $T_{PM}$.

These two additional birds were excluded from some of the results (bout fraction and dive cycle, see below) because the SI was inappropriate with short time scale analysis. In all birds, SI= 30s for $T_a$, and SI= 2s for pressure. With this sample protocol, the 2 Mb of memory within each logger allowed recording for 18 to 21 days (birds equipped with two loggers in combination). The thermistor measurement ranges were 0-50°C for ambient temperature (seawater) and 17-42°C for body temperatures; measurement accuracy was 0.2 and 0.1°C, respectively. Coated thermistors (YSI model 44017, 15 x 1 mm) had a time constant of 2.5 s (90% response in 5.7 s). The pressure sensor measurement range was –2 to 49 bars, and the
sensor response was temperature corrected. Measurement precision near the surface (0-1 bar) and at depth was 0.05 and 0.2 bar, respectively. On birds equipped with two loggers, the synchronization of the units was checked according to the 2 depth profiles and corrected when required (< 0.5 s per day).

**Bird equipment and surgical procedure**

The capture/release and surgical procedures received the approval of the ethics committee of the French Polar research institute (IPEV) and of the French ministry of the environment. Description of the general procedure is presented in Froget et al. (2004). Details concerning the use of temperature data loggers and positioning of temperature probes is given below.

On singly equipped birds, loggers were glued to lower back feathers. From the unit, two thermistor electrodes were channeled under the skin towards the pectoral muscle and the brood patch. Sensors inside the logger measured pressure and water temperature. For birds equipped with two units, one logger was implanted under the skin on the right flank, at the level of the thigh. From this logger, two thermistor electrodes were channeled under the skin towards the pectoral muscle and the brood patch. The second logger was glued to the lower back feathers to measure pressure and ambient temperature. The fixing of the electrode under the skin of the brood patch was undertaken without local opening the skin. The two thermistors were located just under the epidermis of the intact brood patch and four centimeters vertically into the pectoral muscle.

**Characterization of activities and data analysis**

All behaviors were categorized into one of three general activities:
• Brooding on shore: birds warm the chick with their brood pouch and defend their territories.

• Inactive period at the surface during inter bout: due to increased convective heat loss when moving, even in the absence of diving events (over the limit of the sensor resolution) we hypothesized traveling and shallow diving when body temperatures where fluctuating during inter bout periods. Thus, inactive phases, or resting, were defined as the complete absence of diving events and the stabilization of all body temperatures during at least one hour.

• Dive bouts: the succession of at least 3 deep dives (≥50m) with recovery periods at the surface of less than 15 minutes.

The visualization of dive profiles and temperature records was achieved using specifically designed software (V46, Jensen Software). Data were analyzed using custom-made programs (FoxBase+, Fox Software). Automated programs corrected unit oscillation (pressure sensor noise) near the surface in a linear value. This correction was necessary for accurate detection of the beginning and end of dives. Programs automatically extracted the different temperatures and the pressure at various time scales, and calculated their average value, absolute change (ΔT) and dynamics (ΔT/time, °C/s) over a period of time. During dive bouts, the variables we tested to explain body temperature changes were: maximal and average depth, dive frequency, percentage of time spent under water or on the surface and the ratio of these two variables, dive bout duration, temporal index of the dive bout in the trip (e.g. 50% means that the bout starts at the middle of the trip), initial temperatures and temperature differences between the different tissues and/or sea water. Regarding the brood patch, some dive bouts were excluded from the analysis when this tissue reached values below the thermistor range (<17°C, bird 1 & 3: n= 4 bouts). For the analysis of changes in temperature on a shorter time scale, the dive bout was divided into elementary components i.e. individual
dive cycles. We defined the dive cycle as a deep dive (≥ 50m) and the following post-dive period (characterized by resting at the surface or shallow dives) ending with the next deep dive. For the dive cycle analysis, we also took account of the 12 or 14 s (depending on the tissue-sampling interval) before the first positive pressure measurement of a deep dive, in order to record possible events relying on the preparation of the dive (personal observations). The post-dive period ended when the pre-dive period of the subsequent dive cycle started (see Fig. 1). The dive cycle was further separated into five phases (Fig. 1A): the pre-dive period, the descent to depth, the bottom time (13), the ascent to the surface and the post-dive period separating two deep dives. Initial, final, minimal and maximal temperatures and their respective positions in time were extracted for all the different defined periods (Fig. 1B, example given for the bottom phase).

At the scale of the dive cycle, analyses were made using the temperature changes between two points. This permitted the pooling of temperature profiles showing the same trend inside the dive cycle. Therefore, initial temperatures shown on Figures 4, 5 and 6 correspond to the mean temperature obtained from all birds.

Statistics

Reported values are means ± SD. Data sets were verified for normality and equality of variance before test choice. Mean comparisons were followed by post hoc tests i.e. multiple comparison Tukey test (q) for parametric data and Dunn’s (different sample size) / SNK (same sample size) post test (Q) for nonparametric data. Temperature changes were tested versus the null hypothesis; a randomized data set between -0.1 and +0.1°C (confidence interval of the thermistors).

Results
Because of technical problems (battery failure & broken probes) and atypical behaviors (i.e. intermediate return to shore), results presented in this study concern six birds out of the 9 birds originally equipped with data loggers.

At the end of the field season, breeding was successful in 6 of the 9 couples followed. Failures in incubation (one case) and chick rearing (two cases) were attributed, respectively, to an over-extensive foraging trip, causing egg abandonment, and to extreme meteorological conditions (storm).

The six penguins accomplished foraging trips of $21.0 \pm 4.6$ days, which shows no difference from published results for unbanded birds from the same colony and the same year (18). As far as their behavior at sea is concerned, all dive characteristics (bimodal frequency distribution of dive depth, maximal dive depth, dive duration, number of deep dives per day) were in accordance with published results (12, 16, 34). Individual trip and bout durations are summarized in Table 1.

1. **Body temperatures while brooding onshore**

The number of days for which temperatures were collected on shore ranged from 7 to 8 per penguin. Table 2 reveals that both measured body temperatures were homogenous. $T_{PM}$ and $T_{BP}$ on shore were not significantly different in three out of the six birds. Averaged $T_{BP}$ among the six birds ($38.0 \pm 0.6^\circ C$) was in accordance with previous results on incubating king penguins ($38.2^\circ C$, (24)).

2. **Body temperatures at sea**

   a. **While inactive**
Inactive or resting phases at sea, as defined, mainly occurred at night but were also recorded between two dive bouts during daylight hours (05:00 / 20:00). All measured body temperatures reached high and stable values (see Table 2). The pectoral muscle was the warmest measured tissue during these periods at $38.6 \pm 0.9^\circ C$ among the four birds. $T_{BP}$ was $37.3 \pm 0.7^\circ C$ on average and was significantly lower ($-1.3 \pm 0.5^\circ C$) than the pectoral muscle ($p_{min}= 0.002$ for bird 1). Average $T_{BP}$ when inactive at sea was no different from that measured in the colony ($38.2^\circ C$). Resting temperatures remained constant during the entire foraging trip. Neither total time spent at sea nor sea surface temperature had any effect on resting temperatures, despite the fact that the latter varied from $7^\circ C$ around the island to $4^\circ C$ near the Polar front.

### b. During dive bouts

The data set analyzed here corresponds to a cumulative duration of 126 days at sea, totaling 1264 hours of deep diving activity divided into 155 dive bouts (Table 1). Dive bouts occurred only during daylight hours. Dive bouts usually started with a gradual increase (GI) and finished with a gradual decrease (GD) of maximal dive depth (from shallow to deep dives over 100m, (34)).

#### i. The pectoral muscle

Mean $T_{PM}$ during dive bouts was $37.6 \pm 1.6^\circ C$ among the six birds (see range in Table 2). In five out of the six penguins, $T_{PM}$ during diving was significantly lower than during resting in water ($p<0.05$ for bird 1, 3, 4, 5 and 6). In bird 2, mean $T_{PM}$ also showed a decrease during diving but was not significantly different from resting values ($Q=1.05$, NS). Overall mean $T_{PM}$ during dive bouts was not different from brooding on shore since $T_{PM}$ was found to be lower during diving than during on shore in two birds (bird 5 and 6, $p<0.05$), not
significantly different in three birds (bird 1, 3 and 4), and finally higher during diving versus on shore in one bird (bird 2, p<0.05).

After several deep dives, $T_{PM}$ showed significant temperature drops. The average maximal change in pectoral temperature ($\Delta T_{PM}$) when bouts and birds were pooled was -2.0 ± 1.3°C (-0.5 to -4.0°C among birds). During a given bout, $\Delta T_{PM}$ was as high as -5.5°C (see Table 2). The average and maximal $\Delta T_{PM}$ during a dive bout were not correlated with bout duration. This is because the lowest $T_{PM}$ values were rarely reached at the end of the bout due as episodes of warming occurred at any point in time (Fig. 2). These positive $\Delta T_{PM}$ episodes lasted from 3.3 to 33.8 min (1-5 dive cycles), and ranged from +0.1 to +0.7°C. We were unable to correlate these episodes of warming with any of the numerous recorded environmental or physiological parameters tested. However, the GI and GD periods of transition between shallow and deep dives at the two extremities of each bout were always characterized by episodes of positive $\Delta T_{PM}$.

**ii. Brood patch**

Average $T_{BP}$ during dive bouts was 29.6 ± 2.5°C among the six birds. Typically, $\Delta T_{BP}$ throughout the dive bout was negative, and the lowest $T_{BP}$ values were consistently reached at the end of the dive bout. Maximal $\Delta T_{BP}$ during dive bouts ranged among birds from -9.2 ± 6.9°C to -17.0 ± 3.1°C. $T_{BP}$ attained at the end of the dive bout was significantly, positively correlated with the cumulative time spent at depth ≥ 50m ($r_{Spmin}$ = -0.588, n=22, p=0.004 for bird 4, illustrated in Fig. 3).

Birds 5 and 6 were excluded from further analysis because of the sampling interval (8 s) of body temperatures that did not permit analysis at a fine temporal resolution.

$\Delta T_{BP}$ during dive bouts usually followed an exponential decay curve. However, during the course of this decrease, the slope of $\Delta T_{BP}$ seemed to be associated with diving effort. Each
dive bout was then separated into phases on the basis of the speed of $\Delta T_{BP}$ ($\Delta T_{BP}/dt$, see Fig 2). For the four birds, $\Delta T_{BP}/dt$ correlated best with the mean depth of the bout fraction (data includes zero values of the surfacing period, $r_{S_{\text{min}}} = -0.317$, $n=76$, $p=0.005$ for bird 1. Other variables that were significantly correlated with $\Delta T_{BP}/dt$ are, in decreasing order, % of time spent at depth $> 50$m, time at depth $> 50$m divided by time at the surface and frequency of deep dives.

c. During the dive cycle

Mean duration of the dive cycles was $453 \pm 185$ s ($n=2389$), with diving and resting periods lasting $286 \pm 64$ s and $153 \pm 154$ s, respectively (Table 1).

Temperature trends during a dive cycle are presented in Figure 4 (bird 1, 2, 3 and 4 are pooled, $n=2389$), and are defined as the typical trends for each tissue. The typical trend for $T_{PM}$ was a brief decrease ($-0.14 \pm 0.32^\circ C$) during the first $15 \pm 7$ s of the dive cycle. Thereafter, $\Delta T_{PM}$ was positive until almost halfway through the bottom phase ($+0.34 \pm 0.46^\circ C$). At this stage, maximal $T_{PM}$ within the dive cycle was attained. $T_{PM}$ then remained constant until the end of the ascent phase. During the post-dive period, $\Delta T_{PM}$ was negative ($-0.16 \pm 0.26^\circ C$). Finally, $\Delta T_{PM}$ over the whole dive cycle was not significantly different from 0 ($-0.02 \pm 0.13^\circ C$).

The typical pattern for $T_{BP}$ was a brief increase ($+0.11 \pm 0.24^\circ C$, lasting $15 \pm 6$ s) at the beginning of the dive cycle. Thereafter, $\Delta T_{BP}$ was negative throughout practically all of the duration of the dive ($-0.91 \pm 0.99^\circ C$). The end of the ascent phase and the post-dive period were always characterized by a positive $\Delta T_{BP}$ ($+0.41 \pm 0.93^\circ C$). Finally, $\Delta T_{BP}$ over the whole dive cycle was a significant decrease of $-0.40 \pm 0.90^\circ C$ ($p<0.001$).

i. Selection of dive cycles showing negative or positive $\Delta T_{PM}$
Since $T_{PM}$ was observed to decrease or re-increase progressively during dive bouts, we compared two selections of dive cycles showing either a significant negative $\Delta T_{PM}$ ($\text{Neg}_{APE}$, $-0.23 \pm 0.07^\circ C$, $n=407$) or positive $\Delta T_{PM}$ ($\text{Pos}_{APE}$, $+0.22 \pm 0.06^\circ C$, $n=252$). Selections are represented in Figure 5A & 5B, respectively. Between these two selections, $\text{Neg}_{APE}$ cycles showed longer dive and post-dive durations than $\text{Pos}_{APE}$ ($317 \pm 66\, \text{s} \text{Vs} 282 \pm 60\, \text{s}$, $p<0.001$ and $185 \pm 168\, \text{s} \text{Vs} 178 \pm 207\, \text{s}$, $p<0.001$, respectively). Maximal dive depth was also greater in $\text{Neg}_{APE}$ cycles ($176 \pm 50\, \text{m} \text{Vs} 147 \pm 52\, \text{m}$, $p<0.001$). The positive $\Delta T_{PM}$ that occurred during the descent and the bottom phase was found to be the same in both selections ($\text{Neg}_{APE}$: $+0.41 \pm 0.58^\circ C$, $\text{Pos}_{APE}$: $+0.42 \pm 0.47^\circ C$). However, during the short period of cooling that occurs within the first seconds of the dive cycle (Fig. 5), the drop in $T_{PM}$ was two-fold higher in $\text{Neg}_{APE}$ cycles than $\text{Pos}_{APE}$ cycles ($-0.28 \pm 0.45^\circ C$ Vs $-0.14 \pm 0.34^\circ C$, respectively). In addition, $\text{Neg}_{APE}$ cycles showed a decrease of $T_{PM}$ throughout the ascent and the post-dive phases ($-0.15 \pm 0.29^\circ C$ and $-0.21 \pm 0.33^\circ C$ respectively), whereas $\text{Pos}_{APE}$ cycles were characterized by a $\Delta T_{PM}$ not different from 0 during the same phases. Importantly, in both selections initial $T_{PM}$ and $T_{BP}$ were found to be within the whole range of temperatures measured for each tissue. Consequently, no $T_{PM}$ or $T_{BP}$ threshold, for example the attainment of a minimal temperature or a minimal temperature difference between tissues and the environment, was identified to explain whether $\Delta T_{PM}$ was positive or negative after one dive cycle. In both selections, $\Delta T_{BP}$ showed no difference with the typical pattern presented in Figure 4.

\text{ii. Underwater episodes of brood patch warming}

Within the 2389 analyzed dives ($n=4$ birds), 21% of dive cycles (evenly distributed among birds) showed episodes of positive $\Delta T_{BP}$ during the descent to depth. The selection of
dives cycles showing episodes of warming was made with respect to measurement precision (± 0.1°C). Consequently, only temperature events showing an increase of at least +0.2°C were considered as significant and thus selected. These paradoxical temperature events were found to occur either at the beginning of the dive (Early\textsubscript{ABP}, n=293, 12.3% of all dives) or in the second half of the descent to depth (Late\textsubscript{ABP}, n=199, 8.3% of all dives, see Figures 6A & 6B respectively). Only 19 dive cycles (0.8% of all dives) included both observed warming up events.

Early\textsubscript{ABP} cycles were characterized by a positive $\Delta T_{BP}$ that started during the pre-dive period (+0.17 ± 0.18°C) and continued during the first 12 ± 8 s of the immersion (+0.26 ± 0.10°C). Thereafter, the $T_{BP}$ trend and final $\Delta T_{BP}$ was not different from the typical trend presented in Figure 4. $T_{PM}$ variation during Early\textsubscript{ABP} cycles was characterized by a low and not significant temperature drop (-0.07 ± 0.16°C) at the beginning of the dive cycle and a continuous positive $\Delta T_{PM}$ until birds reached the surface. However, final $\Delta T_{PM}$ after Early\textsubscript{ABP} cycles was not significantly different from 0.

In Late\textsubscript{ABP} cycles, the positive $\Delta T_{BP}$ (+0.26 ± 0.11°C) took place after 34 ± 33s of progression underwater i.e. at a mean depth of 49 ± 52m. During the bottom phase, the ascent and the post-dive phases, the $T_{BP}$ profile and final $\Delta T_{BP}$ were similar to the general pattern presented in Figure 4. In Late\textsubscript{ABP} cycles, the positive $\Delta T_{PM}$ found during the descent phase and until the bird reached the bottom of the dive was +0.40 ± 0.67°C. This increase was no different from the typical temperature pattern of the muscle during diving (Fig. 4).

Regarding the dive characteristics, dive duration and maximal depth were significantly shorter and shallower for Early\textsubscript{ABP} cycles in comparison with Late\textsubscript{ABP} cycles (279 ± 52s vs. 321 ± 73s, p<0.001, and 153 ± 44m vs. 182 ± 60m, p<0.001, respectively). No difference was found in the post-dive duration in Early\textsubscript{ABP} and Late\textsubscript{ABP} cycles, and dive cycles following
these negative $\Delta T_{BP}$ selections showed no difference with the average temperature and dive profile (Fig. 4).

**Discussion**

The findings of this study contrast with the classical model of thermoregulation proposed for diving endothermic homeotherms (32). Firstly, because of the lowered temperature of deep and active tissue during diving activity, and secondly, because of normothermic peripheral tissues during inactivity at sea. The discussions we provide concerning temperature changes are based on the change of thermal conductance. At the level of peripheral tissues, changes in thermal conductance will then be discussed with regards to Fourier’s heat flux law. When measuring tissue temperature, we have the direct result of environmental and physiological cumulative effects. Thus, when taking into account 1) environmental features (water temperature, pressure), 2) the intrinsic characteristics of the tissue (being constant over the course of the temperature events we observed: e.g. fat deposit or utilization), 3) the relative rate of heat production, then, the remaining factors that could possibly influence tissue temperature is the rate of blood flow and blood temperature. Accordingly, even if blood flow or blood temperature were not directly measured in this study, temperature events discussed below can confidently be related to vascular adjustments.

1. **Body temperatures during diving.**

   a. **Pectoral muscle temperature.**

   The pectoral muscle is the largest muscle in the king penguin (25% of total body mass at the beginning of the reproductive period, (14). In many bird species, the pectoral muscle
plays a major role in thermoregulation (10). Due to low mechanical efficiency, intensive muscular work generally implies increased muscle temperature (31, 48). Therefore, we initially expected the pectoral muscle to warm up during swimming activity. However, despite the thermogenic property of muscular contraction, averaged $T_{PM}$ was found to be normothermic over the whole dive bout, and on some occasions, $T_{PM}$ even decreased by up to 5.5°C below inactivity values at sea.

This degree of cooling was not immediate at the onset of the dive bout. $T_{PM}$ first increased at the beginning of each dive bout (GI phases) and then decreased systematically after several deep dives. This progressive cooling of the pectoral tissue could be attributed to the inability of the bird to repress heat loss through the periphery and to a cooling effect linked with the ingestion of prey. In this context, cooling of internal tissues would be irrepressible and passive. However, $T_{PM}$ always stabilized before the end of the dive bouts, and even exhibited episodes of warming inside the bouts. The stabilization of $T_{PE}$ and the occurrence of warming episodes during the dive bout are illustrated by the typical $T_{PE}$ profile during the dive cycle (Fig. 4) which shows, on average, no trend of pectoral cooling during the course of the dive bout. These episodes of warming were not correlated with less challenging dives or environmental characteristics. Furthermore, these warming episodes did not start either when attaining a given $T_{PM}$ threshold or a minimal temperature difference between the pectoral and the brood patch or ambient. Thus, if variation of heat production/loss alone does not explicate $T_{PM}$ changes inside the bout, variation of heat exchange via modification of heat conduction could provide an explanation.

Pectoral temperature always showed a fast drop during the pre-dive period. $T_{PM}$ then continued to decrease in the first seconds of submersion (2.5 s on average). With regards to diving behavior and muscular activity, the pre-dive period is very similar to the ascent and the post-dive period. However, the speed of $T_{PM}$ change ($\Delta T_{PM}/dt$) during the 12 to 14 s prior to
immersion was much greater than during the post-dive and the passive ascent phase underwater (-0.50 ± 1.15°C/min Vs -0.08 ± 0.14°C/min and -0.03 ± 0.12°C/min respectively). We hypothesized that blood perfusion was maximal in the pectoral muscle during this short period preparing the dive. This enhancement of blood flow prior to the dive may be in accordance with the anticipatory tachycardia found to occur before each dive (22).

In king and emperor penguins, measurement of acceleration data has revealed the flipper stroking pattern, and thus the locomotory effort, during the different phases of the dive (47, 51). The beginning of the descent to depth, and to a lesser extent the bottom phase, are characterized by considerable flipper beating whereas during the last part of the ascent, king penguins stop beating their flippers and use their buoyancy to return passively to the surface. In addition, blood flow through the skeletal muscles is supposed to cease (ischemia) during submergence in order to preserve the circulating oxygen for strictly oxygen dependent tissue (32). This particular perfusion characteristic may presumably also occur in free-diving birds such as the king penguin (32). Assuming such muscle perfusion, it was expected that the heat produced by muscular activity remains stored in the surrounding tissues and thus that the pectoral muscle temperature will reflect the pattern of flipper activity during submergence. Our data seem to verify the hypotheses of a low perfusion rate in the pectoral muscle during diving since $T_{PM}$ profiles agree with the trends anticipated according to the variations in mechanical work (see Fig. 4): $T_{PM}$ increases during the descent phase, then stays stationary until the end of the dive, and finally, progressively decreases during the post-dive period. An additional argument for pectoral ischemia during diving is provided by the comparison of the speed of $T_{PM}$ change ($\Delta T_{PM}/dt$) in two phases where animals have no locomotory activity; the ascent and the post-dive period. During the post-dive period $\Delta T_{PM}/dt$ was three-fold higher than during the ascent phase of the dive (-0.08 ± 0.14°C/min vs. -0.03 ± 0.12°C/min, respectively). This suggests that blood flow through the muscle increases considerably during
this recovery period, and/or that blood at a lower temperature perfused the pectoral while surfacing. An increasing blood flow after the extended breath hold is coherent with the replenishment of the oxygen stores and related to a general vasodilatation as already observed in captive seals (32). Following the reasoning on speed of temperature change at known muscular activity and insulation properties, our results call attention to the fact that even at 5.5°C below inactivity temperature levels at sea, the pectoral muscle may still be warmer than the blood flowing into them. This in turn supports the hypothesis that the temperature of mixed blood is greatly influenced by blood returning from cold tissues and organs (e.g. limbs, skin, and digestive tracts) (17, 25). Moreover, despite the negative $\Delta T_{PM}$ during dive bouts, this organ may still be one of the warmest tissues during sustained exercise (swimming and diving). Thus, our results suggest an accurate regulation of the rate of blood perfusion through the pectoral muscle in order to set the muscle temperature to an optimal value for a given period of diving activity.

A number of studies proposed that reduction in body temperature may allow marine species to lower their diving metabolic rate (via the Q10 effect) (3, 5, 6, 25, 27, 38), and thus increase their breath hold duration. Even though our results describe reductions in temperature reduction within one of the most energetically demanding tissues during swimming activity, the benefits of a lower functional temperature for muscle are still debated and necessitate further investigation. However, counter to the possible energetic benefits, a lowered temperature may impair muscle functional properties (2, 21, 48) and thus hunting efficiency. Pectoral cooling should then be adjusted and stay within the range of normothermic temperatures in order to avoid declining beyond a minimal and mechanically disadvantageous value. From this point of view, variations of $T_{PM}$ in diving king penguins may be a trade-off between an energy sparing strategy and the maintenance of efficient locomotion.
Pectoral muscle temperature has already been studied in emperor penguins diving from an isolated ice hole (44). In this study, authors reported the preservation of pectoral and core temperatures. However, trends in body temperatures in relation with diving activity reported in (38) are similar to those observed in free ranging king penguins at the beginning of each dive bout. In both studies, the trend in $T_{PM}$ was firstly an increase during the first 20 min of the diving activity and then a slight $T_{PM}$ decrease (see Figure 5 in ref. 38, and Figure 4 in the present study), after which emperor penguins stopped diving and rested on ice, while king penguins continued sustained diving for several hours. As subcutaneous temperature was also found to decrease (see Figure 9 in ref. 38), we believe that emperor penguins practicing extended durations of diving activity without leaving the water would extend the $T_{PM}$ cooling already in progress. At the level of the dive cycle, in both studies $\Delta T_{PM}$ was initially negative prior to the dive and was then positive through to the bottom phase of the dive (Figure 5, ref. 38). However, emperor penguins also showed a positive $\Delta T_{PM}$ during the ascent phase, which we attribute to the fact that this species does not stop flipper beats at any point when returning to the ice hole (51). Thus heat production in relation with locomotory effort may not diminish as it was assumed to do in the king penguin. Finally, conclusions proposed in both studies may not be contradictory if we consider, in the present study, that birds start diving activity with normothermic body temperatures. Indeed, the present study revealed that several consecutive deep dives were necessary to lower pectoral temperatures.

b. The brood patch

The speed of swimming enhances peripheral convective heat loss (28, 32). However, the swimming speed in shallow and deep dives is equivalent (45), yet it did not influence $T_{BP}$ in the same way. Therefore, this parameter is insufficient to explain peripheral body cooling at sea, and pressure must also be considered. Indeed, when pressure increases, the thickness of
the air layer trapped in the feathers is reduced, and thermal conductivity increases. Thus, with progression to depth, the decrease of body insulation and water temperature (1-5°C depending on distance to the polar front, (11) favor a decrease in body temperatures (36, 53). This assumption was confirmed since $\Delta T_{BP}$ at the end of a dive bout correlated well with the time spent at depths greater than 50 m during the dive bout (Fig. 3). This trend was also shown in diving macaroni penguins with abdominal temperature being correlated with duration and average depth of the dive bout (23). The systematic decrease of $T_{BP}$ in the course of the dive bout is illustrated in Fig. 4, which shows an average $T_{BP}$ drop of -0.40°C during each dive cycle.

During diving, the brood patch is protected by a fold of adjacent feathered tissue. When swimming back to the surface, the remaining air layer in the feathers, which has not been expelled under the effect of speed and pressure, expands and water temperature increases. Consequently, the plumage recovers, at least partly, its insulation property. Nevertheless, $T_{BP}$ was found to decrease at the same rate during the descent and ascent phases (see Fig. 4). This observation supports the reduction of peripheral thermal conductance through limited skin perfusion (vasoconstriction) when diving, in order to limit peripheral heat loss, as expected (32). Warm blood bypassing the skin avoids cooling and enhances the temperature reduction of the periphery, and thereby, minimizes heat loss to ambient. However, a positive $\Delta T_{BP}$ was observed during the last 32 s on average before surfacing. Near the surface, the air sacs expand and gas exchange may carry on, making available a certain quantity of oxygen. This positive $\Delta T_{BP}$ might then be an anticipatory vasodilatation, commonly occurring at the surface, to supply tissues with oxygen (32). However, because of these latter factors (perfusion rate and ambient parameters), as long as birds are under water, it is impossible to define the influence of each phenomenon on $T_{BP}$. 
Efficient mechanisms of heat conservation and the requirement for such would imply a strong decrease of peripheral thermal conductance from the onset of a dive bout. Consequently, the brood patch should first cool rapidly to the minimum values observed and remain at this level until the end of the dive bout. Nevertheless, since $T_{BP}$ was found to undergo different ranges of temperature drops, from a few degrees up to $>20^\circ C$, we hypothesize that the reduction of blood perfusion through the brood patch was not maximal at the beginning of the dive bout, and that an adjusted rate of perfusion still occurred at any time during the dive bout. The perfusion of peripheral tissues permits the evacuation of heat and may contribute to the reduction of body temperatures. However, to avoid body tissues from dropping beyond a vital range of temperatures, effective heat conservation mechanisms have to take place throughout the dive bout to maintain tolerable core temperatures. With increasing vasoconstriction, the temperature difference between the skin and the water is reduced, and heat transfer is minimized. This change in perfusion rate was observed in the course of each dive bout. The hypothesis of adjusted peripheral heat loss as a response to variations in heat production is illustrated in Figure 2, where at a given moment (annotated 'peripheral perfusion adjustment'), $T_{BP}$ abruptly decreased while the progressive decline of $T_{PM}$ was interrupted.

If the brood patch is used to regulate peripheral heat loss, the mechanisms involved should also fit as precisely as possible to the level of internal heat production. Therefore, we should observe dive cycles representative of periods of heat conservation or heat loss. Following the classic model of heat conservation, we have showed that a large proportion of $\Delta T_{BP}$ corresponds to a decrease in peripheral thermal conductivity. In 79% of dive cycles, $T_{BP}$ decreased while the bird was under water. In contrast with this modal scenario, 21% of dive cycles revealed significant positive $\Delta T_{BP}$ during the descent phase (Early$_{ABP}$ and Late$_{ABP}$ cycles). In Early$_{ABP}$ cycles, positive $\Delta T_{BP}$ occurred in the first part of the descent, while
muscular effort was maximal. Related maximal heat production and possible warmer blood perfusing the brood patch could explain the temperature increase at this moment. However, the fact that this event occurred in only 12.3% of dives casts doubt on the possibility that it is a passive consequence of muscular activity, and is rather an argument for vascular adjustments. Moreover, in 8.3% of the dive cycles, positive $\Delta T_{BP}$ occurs in the second part of the descent to depth (Late $\Delta BP$ cycles), when penguins progress with lowered stroking frequency but maintain a constant swimming speed (47, 54), and where peripheral thermal conductance is maximal. The positive $\Delta T_{BP}$ occurring at depth is unlikely to be related to an elevation of blood temperature. During Late $\Delta BP$ cycles, $T_{PM}$ was found to increase in a fashion similar to the typical temperature trend (+0.4°C, Fig. 4), thereby rejecting the possibility of increased muscular heat release during submergence. Thus, the positive $\Delta T_{BP}$ occurring at depth most probably takes place if blood perfuses the brood patch at a higher rate, i.e. after vasodilation. In this particular situation, where heat loss is enhanced, birds clearly carry out an active and adjusted thermolytic process, in contradiction to the principle of heat conservation.

2. **Body temperatures during prolonged inactivity**

King penguins at sea spent time resting at the surface between dive bouts (12). At that time, muscular activity was minimal and maximum feather insulation minimized the chill effect of the ambient temperature. When staying inactive in cold water, penguins showed a homogenization of body temperatures between deep and peripheral tissues, all stabilized at their highest level. Even supposing effective insulation at the sea surface, the energy expenditure (resting metabolic rate, RMR) needed to maintain this high temperature difference between the skin and water is presumed to be important. This assumption is supported by the fact that average heart rate (indicative of MR, (8, 41) measured during resting periods in the king penguin is significantly higher than average heart rate during dive
bouts (22). Heat increment of feeding (HIF) has often been suggested as the explanation of high energy expenditure and elevated body temperature during the inter-bout phases. However, the duration of inter-bout phases largely exceeds common duration of HIF (26, 30). This paradox in energetics (diving MR < RMR) may also explain why $T_{PM}$ when inactive at sea was higher than average $T_{PM}$ brooding on shore. If energy demand for temperature maintenance was higher, the major organ of shivering thermogenesis would require a higher metabolic rate.

Brooding king penguins have to return to sea in order to replenish energy stores depleted by the previous fasting period in the colony (15). Our hypothesis is that the paradoxically high temperatures and energy expenditure observed in king penguins when inactive at sea may be the counterpart for the low temperature and/or insufficient blood perfusion the subcutaneous adipose tissues undergo during diving activity (19). Indeed, the most important tissue for accumulation of energy stores in penguins is the subcutaneous fat layer (14). Our hypothesis is that extremely low temperatures or poor oxygen supply during diving activity make the use of metabolic pathways for energy storage (fatty acids) impossible. Consequently, high blood perfusion of the periphery would be the thermoregulatory cost a post-absorptive penguin has to face for the restoration of its body reserves (20).

To Conclude

Our aim was to examine body temperatures and underlying physiological adjustments, as a probable trade-off between foraging behavior and environmental constraints in relation with the acquisition/assimilation of body fuel. This study highlighted thermoregulatory strategies and revealed possible vascular adjustments that may occur in king penguins at sea. We found that temperature decreases occur in deep hyperactive and in peripheral tissue only
after a succession of deep dives. The fact that the thermogenic pectoral muscle also undergoes temperature reductions raises the question as to what extent the volume of the body and the organs are involved in temperature reductions (24). Importantly, this study suggests that the progressive cooling of the pectoral muscle and the brood patch is not the result of the single and passive effect of a constraining environment. Indeed, we hypothesize accurate regulation of body temperatures via adjusted peripheral heat loss through alternating episodes of heat conservation and thermolysis. Finally, our results give new insight into thermoregulatory strategies that may be encountered in other endotherms when facing the opposite constraints of high energetic costs while foraging and the replenishment of body stores.
Acknowledgements:

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References


Table 1. *Summary of trip, dive bout and dive cycle duration.*

<table>
<thead>
<tr>
<th>Bird</th>
<th>Trip (day)</th>
<th>Bout (h)</th>
<th>Dive cycle (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>duration</td>
<td>range</td>
<td>dive</td>
</tr>
<tr>
<td>1</td>
<td>12</td>
<td>12.4 ± 5.8 1.8 to 23.5</td>
<td>310 ± 73</td>
</tr>
<tr>
<td>2</td>
<td>23</td>
<td>8.2 ± 7.2 0.6 to 19.3</td>
<td>289 ± 54</td>
</tr>
<tr>
<td>3</td>
<td>22</td>
<td>7.6 ± 4.0 1.2 to 16.3</td>
<td>262 ± 69</td>
</tr>
<tr>
<td>4</td>
<td>23</td>
<td>7.8 ± 4.4 0.9 to 18.0</td>
<td>295 ± 41</td>
</tr>
<tr>
<td>5</td>
<td>21</td>
<td>4.8 ± 3.4 0.5 to 17.5</td>
<td>/</td>
</tr>
<tr>
<td>6</td>
<td>25</td>
<td>9.2 ± 4.9 0.8 to 18.6</td>
<td>/</td>
</tr>
<tr>
<td>Average</td>
<td>21.0 ± 4.6</td>
<td>8.3 ± 2.5 1.0 to 18.9</td>
<td>286 ± 64</td>
</tr>
</tbody>
</table>

Values are means ± SD; values for bird 5 and 6 are not reported because of inappropriate sampling interval (see method).
Table 2. Summary of pectoral and brood patch temperature during different activities, and maximal temperature drop for each tissue during dive bouts.

<table>
<thead>
<tr>
<th>Bird</th>
<th>Pectoral muscle</th>
<th>Brood patch</th>
<th>Pectoral muscle</th>
<th>Brood patch</th>
<th>Pectoral muscle</th>
<th>Brood patch</th>
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<th>Brood patch</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Body temperatures (°C)</td>
<td>Max. temp. drop / bout (°C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td></td>
<td>Brooding</td>
<td>Resting at sea</td>
<td>Diving</td>
<td>mean</td>
<td>n</td>
<td>max.</td>
<td>Brooding</td>
<td>Resting at sea</td>
<td>Diving</td>
<td>mean</td>
<td>n</td>
<td>max.</td>
</tr>
<tr>
<td>1</td>
<td>36.9 ± 0.2 a,†,‡</td>
<td>37.4 ± 0.4 a,†</td>
<td>36.5 ± 0.8 a,‡</td>
<td>1.7 ± 1.3</td>
<td>16</td>
<td>3.3</td>
<td>38.0 ± 0.2 b,†</td>
<td>37.0 ± 0.5 b,‡</td>
<td>27.3 ± 4.1 b,•</td>
<td>17.0 ± 3.1</td>
<td>12</td>
<td>21.6</td>
</tr>
<tr>
<td>2</td>
<td>37.8 ± 0.4 a,†</td>
<td>40.0 ± 0.1 a,‡</td>
<td>39.7 ± 0.4 a,‡</td>
<td>0.5 ± 0.6</td>
<td>17</td>
<td>1.2</td>
<td>38.0 ± 0.4 a,†</td>
<td>38.3 ± 0.6 b,†</td>
<td>32.5 ± 4.5 b,‡</td>
<td>9.2 ± 6.9</td>
<td>17</td>
<td>18.9</td>
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<tr>
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<td>39.1 ± 0.2 a,‡</td>
<td>38.5 ± 0.2 a,†</td>
<td>1.1 ± 0.4</td>
<td>26</td>
<td>1.7</td>
<td>38.3 ± 0.2 a,†</td>
<td>37.7 ± 0.6 b,†</td>
<td>33.1 ± 2.6 b,‡</td>
<td>15.1 ± 5.9</td>
<td>22</td>
<td>20.8</td>
</tr>
<tr>
<td>4</td>
<td>38.7 ± 0.2 a,†</td>
<td>39.0 ± 0.2 a,‡</td>
<td>38.5 ± 0.4 a,†</td>
<td>1.8 ± 0.9</td>
<td>22</td>
<td>3.3</td>
<td>38.7 ± 0.2 a,†</td>
<td>37.6 ± 0.4 b,‡</td>
<td>28.0 ± 3.0 b,•</td>
<td>15.8 ± 3.9</td>
<td>22</td>
<td>20.5</td>
</tr>
<tr>
<td>5</td>
<td>37.0 ± 0.3 a,‡</td>
<td>38.0 ± 0.3 a,•</td>
<td>35.9 ± 0.5 a,†</td>
<td>2.9 ± 0.5</td>
<td>40</td>
<td>4</td>
<td>37.8 ± 0.2 b,‡</td>
<td>36.6 ± 0.7 b,‡</td>
<td>28.8 ± 2.6 b,•</td>
<td>9.7 ± 3.0</td>
<td>40</td>
<td>16.1</td>
</tr>
<tr>
<td>6</td>
<td>37.4 ± 0.3 a,‡</td>
<td>38.3 ± 0.2 a,•</td>
<td>36.2 ± 0.7 a,†</td>
<td>4.0 ± 1.0</td>
<td>34</td>
<td>5.5</td>
<td>36.9 ± 0.3 b,‡</td>
<td>36.6 ± 0.6 b,‡</td>
<td>27.9 ± 2.9 b,•</td>
<td>13.2 ± 4.2</td>
<td>34</td>
<td>18.6</td>
</tr>
<tr>
<td>Average</td>
<td>37.7 ± 0.7</td>
<td>38.6 ± 0.9</td>
<td>37.6 ± 1.6</td>
<td>2.0 ± 1.3</td>
<td>6</td>
<td>3.2 ± 1.6</td>
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<td>37.3 ± 0.7</td>
<td>29.6 ± 2.5</td>
<td>13.3 ± 3.3</td>
<td>6</td>
<td>19.4 ± 2.0</td>
</tr>
</tbody>
</table>

Values are means ± SD. Comparison between tissues (different letters - a, b - indicate a significant difference, p<0.05); comparison between activities (different symbol - †, ‡ and • - indicate a significant difference, p<0.05).
Fig. 1A. Visualization of one dive cycle with description of the 5 phases (pre-dive, descent, bottom, ascent and post-dive).

Fig. 1B. Example of data analysis during one of the dive phases; the bottom phase. Analyzed temperatures are initial and final temperatures and also minimum and maximum temperatures during each of the dive phase. Each temperature is associated with the time of occurrence in the dive cycle.
Fig. 2. The pectoral and the brood patch temperatures (time vs. T°) are superimposed on a diving activity chart (dive profile, time vs. depth), e.g. bird I, 06/03/2001. The dive bout is split according to the speed of brood patch temperature change \( \Delta T_{BP}/dt \) (°C/min). The dashed line at the interface between sequence 2 and 3 is the illustration of peripheral perfusion adjustment (see Discussion).
Fig. 3. Illustration on Bird #4 (lowest significance found among all birds) of the brood patch temperature (°C) at the end of each dive bout as a function of time spent at depth > 50m per dive bout (h).
Average temperature profiles at the scale of the dive cycle, n=2389

Fig. 4. Typical body temperature profile over pooled dive cycles (average on four penguins, n=2389). The vertical dashed lines separate the dive cycle into its different phases. Horizontal dotted lines are indicative of the initial temperature of each tissue.
Fig. 5. Selection of dive cycles showing: 5A: final negative $\Delta T_{PM}$ (Dec$_{APE}$, $n=407$) or 5B: a final positive $\Delta T_{PM}$ (Inc$_{APE}$, $n=252$) of the pectoral temperature. The vertical dashed lines separate the dive cycle into its different phases. Horizontal dotted lines are indicative of the initial temperature of each tissue.
6A Positive $\Delta T_{BP}$ at the beginning of the dive

6B Positive $\Delta T_{BP}$ at depth

Fig. 6. Selection of dive cycles showing brood patch warming up events. Fig. 6A shows positive $\Delta T_{BP}$ occurring during the beginning of the dive (Early$_{ABP}$, $n=293$). Fig. 6B shows positive $\Delta T_{BP}$ occurring during the second half of the descent to depth (Late$_{ABP}$, $n=199$). The vertical dashed lines separate the dive cycle into its different phases. Horizontal dotted lines are indicative of the initial temperature of each tissue.