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# The variability of muscle–blubber interface temperature with activity level in a captive Risso's dolphin (*Grampus griseus*)

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## Abstract

**Background** To reduce heat loss underwater, marine mammals cover their bodies with insulation. Cetaceans in particular rely solely on blubber for insulation which has low conductivity. Blubber establishes a great thermal gradient between the warmer body core and cooler body surface, reducing heat transfer to the environment. A temperature gradient within the blubber determines the conductive heat transfer from the body trunk, where conduction and convection are the primary heat transfer mechanisms in cetaceans. Therefore, measuring the temperature at the innermost part of the blubber, i.e., the temperature at the muscle–blubber interface (Tmbi), can enhance our understanding of thermoregulatory mechanisms in cetaceans. In thermoregulation, activity-induced heat produced by increased muscle metabolism is another factor that plays an important role, however, the effects of activity on Tmbi have not been investigated in cetaceans. To assess this relationship in free-swimming cetaceans, we measured Tmbi and activity levels in a captive Risso's dolphin (*Grampus griseus*) using an implantable biologging device.

**Results** Tmbi and activity data were analyzed for 11 days. The average Tmbi was  $35.1 \pm 0.6$  °C and the temperature gradient between Tmbi and the water temperature was  $13.0 \pm 0.7$  °C. Tmbi was higher during the daytime and lower in the early morning. The variation in Tmbi was best explained by both the activity levels and time of day. Tmbi did not simply increase with activity levels; it appeared to remain relatively constant at most activity levels. However, Tmbi appeared to decrease when the animal was inactive and increase when it was intensely active.

**Conclusion** Our results provide important insights into how a dolphin regulates its body temperature underwater. Thermal insulation by blubber and heat production by activity were suggested to play important roles in thermoregulation. Whole-body heat dissipation might be used to regulate temperature increases when heat production is excessive due to intense activity. During inactive periods, decreasing temperature gradient may help reduce heat loss from the body.

**Keywords** Body temperature, Cetacea, Insulation, Marine mammal, Thermoregulation

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## Introduction

The body temperature of animals is determined by the balance between internal thermogenesis and heat loss to their surroundings [1]. Mammals inhabit a wide variety of environments and have developed thermoregulatory strategies to maintain relatively constant body temperatures, adapting to their surroundings [2]. Marine mammals have unique thermoregulatory adaptations, because they live in physiologically stressful environments where the water has high thermal conductivity and heat loss is approximately 25 times faster than in air at the same temperature [3, 4]. One way marine mammals prevent excessive heat loss is by covering the body with insulating materials, such as fur and blubber. Blubber is a thick layer of subcutaneous adipose tissue [5–8] with a relatively low thermal conductance, less than 1/10th that of water (blubber:  $0.0001 \text{ cal s}^{-1} \text{ cm}^{-1} \text{ }^{\circ}\text{C}^{-1}$ ; water:  $0.0013 \text{ cal s}^{-1} \text{ cm}^{-1} \text{ }^{\circ}\text{C}^{-1}$ ) [9] and it is used as an insulator by many marine mammals, particularly those that are fully aquatic and/or deep diving [10–13]. Notably, all cetaceans rely solely on blubber, not fur, as an insulation material [14, 15], and the dynamic nature of blubber has allowed cetaceans to survive in diverse thermal habitats and oceanographic environments [16].

To control heat loss and the thermal balance in the body, heat is transmitted by the blood from the metabolically active core to other parts of the body, and toward the surface where most heat exchange occurs. Consequently, the internal temperature is not uniform throughout the body, but there is a temperature gradient from the warmer core to the cooler surface. In cetaceans, blubber which has low conductivity restricts heat transfer and it is primarily responsible for this temperature gradient [17]. This keeps the body surface at a low temperature and helps reduce heat transfer to the environment [18]. According to the Fourier equation, conductive heat transfer through the surface is proportional to the temperature gradient and thermal conductivity within the object [3, 19]. Therefore, the temperature gradient within the blubber determines the conductive heat transfer from the body trunk. In cetaceans, conduction and convection appear to be the main mechanisms of heat transfer during diving [4]. Decreasing the temperature gradient reduces conductive heat transfer through the blubber, which may reduce heat loss in the water. Studies measuring core, blubber, and skin temperatures in elephant seals (*Mirounga angustirostris*) reported that animals maintained relatively stable core temperatures during routine diving by adjusting the temperature gradient in the blubber [20, 21]. As well as seals, cetaceans routinely may experience changes in temperature gradients, which contributes to the maintenance of body temperature. Thus, direct measurement of the innermost part of the blubber,

that is, the temperature at the muscle–blubber interface (Tm<sub>bi</sub>), could provide information on the temperature gradient within the blubber and also heat loss. Furthermore, Tm<sub>bi</sub> is a preferred parameter in several heat loss models to estimate metabolic rates and critical temperatures for marine mammals [22, 23]. Taken all, the change in Tm<sub>bi</sub> represents the amount of conductive heat loss and provides a better understanding of cetacean thermoregulation in dynamic environments.

In thermoregulation, activity-induced heat which is generated through increased muscle metabolism is another factor that plays an important role. Hence, Tm<sub>bi</sub> should be measured when the animal is actively moving, but this might be challenging because thermometers need to be placed in between the muscle and the blubber; Tm<sub>bi</sub> in cetaceans has only been measured in limited situations, such as the dead carcasses of bowhead whales (*Balaena mysticetus*) [17], humpback whales (*Megaptera novaeangliae*) [24], minke whales (*Balaenoptera acutorostrata*) [25], fin whales (*Balaenoptera physalus*) and sei whales (*Balaenoptera borealis*) [26]. Therefore, it is unclear how Tm<sub>bi</sub> in cetaceans varies in response to activity.

Animal-borne sensor technology, known as biologging, has advanced considerably in recent years, making it easier to collect activity data from free-living animals in inaccessible areas [27, 28]. Furthermore, various physiological parameters can be measured, including the heart rate, body temperature, and blood pressure [29–32]. Recently, implantable data loggers have been developed that enable long-term measurements of behavior and physiological functions in various animal groups [e.g., [33–38]]. In cetaceans, sensors can only be attached for a limited time [39, 40], so physiological data such as heart rate are not recorded for long periods. Implantable loggers can also be a viable option for long-term measurements in cetaceans and are expected to provide new insights into ecology and physiology in response to environmental changes [41].

The objectives of this study were to measure Tm<sub>bi</sub> in a free-swimming dolphin and to investigate the effect of daily activity on Tm<sub>bi</sub>. To achieve this objective, we measured the Tm<sub>bi</sub> and activity of a captive Risso's dolphin (Odontoceti: Delphinidae: *Grampus griseus*), a medium-sized cetacean, using an implantable biologging device. Risso's dolphins are widely distributed in all major ocean basins between at least 64 °N to 46 °S [42] and have been sighted at surface water temperatures between 4.8–28 °C [43], which means that plastic heat dissipation and retention responses are necessary. In addition, the heart rate was measured as a basic physiological index related to both activity and body temperature. Understanding the relationship between

Tmbi and daily activities could help us understand the plasticity of their thermoregulatory responses.

## Materials and methods

### Ethics statement

The experiment was conducted from October to November 2021 at the Whale Museum and Aquarium (Wakayama, Japan). Animal husbandry and management were performed by aquarium staff under the careful supervision of aquarium veterinarians, with a strong emphasis on animal welfare. Veterinarians were responsible for providing medical care during the experiments. All experimental procedures were approved by the Animal Ethics Committee of Atmosphere and Ocean Research Institute of the University of Tokyo (permission number: P21-1).

### Animal's daily routine and environment

A female Risso's dolphin reared in the aquarium for more than 3 years (estimated age: 7 years, body length: 271 cm, body mass: 228.5 kg) was used in our study. The dolphin was housed under the professional care of that aquarium. It could swim freely during the daytime (from approximately 10:00 to 16:00 daily) in Moriura Bay (33° 35' 47.6" N 135° 56' 01.9" E, max depth: 14 m, approximate area: 25.8 ha), whose entrance was partitioned with a net. Hills and natural forests surrounding the bay created a shady environment. At other times, the animal was temporarily housed in a net pen (12 × 12 × 3–4 m, length × width × depth) located in the middle of the bay as a second housing facility, because careful monitoring by staff was difficult in the dark. The animal could swim around in circles in the pen. On the 3rd day of the measurement, there was heavy rain and strong winds. Therefore, it spent the entire day inside the pen, where it could be easily monitored by staff for more direct management. The animal spent a mean of 5.7 ± 0.6 h during the daytime in the bay, excluding this day. The water temperature ( $T_w$ ) was measured every 5 min using a Compact-CTD (JFE Advantech Co., Japan), which was set near the net pen at a depth of approximately 0.5 m. The dolphin was fed atka mackerel (*Pleurogrammus monopterygius*) and squid (*Todarodes pacificus*) daily at approximately 09:00 and 16:00 during the measurement, and consumed 8.5–12 kg of food each day. As part of a health check, rectal temperature ( $T_r$ ) was measured daily during the morning feeding time with a soft-wire style temperature probe inserted approximately 30–40 cm. During this study, the dolphin did not appear in front of aquarium visitors or participate in any kind of show or event.

### Physiological bilogger

In this study, we used a DST milli-HRT ACT tag (39.5 × 13 mm, length × diameter, 12 g, Star-Oddi Co., Iceland, Fig. S1). It was inserted into a tag–computer interface Communication Box and set up using the Mercury software (Star-Oddi Co., Iceland). The tag was programmed to record temperature every 15 min, raw 3-axis acceleration at 1 Hz for 60 s every 15 min, and raw electrocardiograms (ECGs) at 100 Hz for 6 s every 30 min. ECGs were detected using two electrodes aligned along the long axis of the tag surface. These settings allowed a recording time of approximately 30 days.

The tag was implanted in October 2021. Surgery was conducted by veterinarians, and the dolphin was monitored carefully by skilled veterinary nurses during all procedures. A few days before the surgery, the animal was moved 1.5 km from the bay to the aquarium, a journey that took 30 min. The dolphin was fasted for 14 h before surgery. At first, the animal was caught in the net pen by staff and sedated by a combination of midazolam (0.1 mg/kg, i.v.) and butorphanol (0.1 mg/kg, i.v.). After ensuring sufficient sedation, the dolphin was moved indoors to a soft mat on a bed for surgery. The heart rate, respiratory rate, and core body temperature were continuously monitored from sedation to recovery. Bupivacaine (0.25 mg/kg, i.m.) was injected for local anesthesia near the left axillary space, after which a small incision (approximately 7 cm) was made. During surgery, enrofloxacin (5 mg/kg, i.m.) and meloxicam (0.1 mg/kg, i.m.) were administered as antibiotic and anti-inflammatory drugs, respectively. The tag, sterilized with chlorhexidine gluconate solution before surgery, was placed between the muscle and blubber layer to measure Tmbi. To ensure the measurement of the ECGs, the tag electrode was oriented toward the body trunk and fixed at the same inclination as that of the heart using self-absorbing sutures. The blubber layer (ca. 3 cm.) was closed in a continuous pattern using self-absorbing sutures. The skin incision was closed twice with simple patterns and tension-relieving sutures using rubber catheters [44, 45]. In addition, surgical adhesive was applied to the incision. After these procedures, the animal was returned to the water, being held in the stretcher for post-surgical monitoring. To recover from sedation and prevent postoperative gastrointestinal deterioration, flumazenil (0.01 mg/kg, i.v.) was administered along with metoclopramide (0.1 mg/kg, i. v.). The dolphin recovered without incident and was released from the stretcher after its consciousness was deemed to be clear. Meloxicam tablets (0.1 mg/kg) were mixed with the fish fed to the dolphin only on the morning following the surgery. After surgery, the dolphin was administered tablets of ampicillin/sulbactam (12.5 mg/kg) and levofloxacin (8.3 mg/kg) three times daily for 3 weeks as an antibiotic

treatment. The surgical wound was treated with povidone-iodine for approximately 3 weeks, and gentamicin was applied once every few days. Blood examinations were conducted every 5 days to evaluate the dolphin's health condition and any postoperative infections, and we confirmed that it was recovering well.

Two weeks after the surgery, we confirmed the incision site had healed enough to enable suture removal, then the animal was moved from the aquarium to the bay. For 4 more days of acclimation to the bay environment, the dolphin was taken care of in a net pen. After that, it was allowed to swim in the bay during the daytime to measure Tmbi, activity levels, and heart rate.

One month after implantation, the tag was extracted from the animal using the same procedure as described above. Following extraction, the tag was inserted into the Communication Box and the data were downloaded using the Mercury software. The retrieved data were visualized and processed using Igor Pro ver. 9.0.5.1 (Wave-Matrices Inc., USA) using the package “ethographer” [46]. The tag successfully recorded a total of 29 days of data, as it had been set up, but 11 days were used for analysis, which excluded the treatment period in the aquarium and the acclimation period in Moriura Bay.

#### Data processing

Mercury software calculates the vectorial sum of the dynamic body acceleration in each of the three axes every second and defines it as the external acceleration (EA, mG;  $1000 \text{ mG} = 1 \text{ g}$ ;  $9.8 \text{ m s}^{-2}$ ). In this study, we used EA as an index of gross motor activity. The activity levels were calculated every 15 min by averaging the EA over 60 s in order to match the temperature measurement interval, defined as EA<sub>60</sub>. Similarly, to align with the ECG measurement period, the average value of the EA for 6 s was calculated every 30 min and defined as EA<sub>6</sub>.

To calculate heart rate, QRS waves were manually detected from the raw ECG data for 6 s. The instantaneous heart rate (HR, bpm; beats per minute) was calculated by dividing 60 s by the average time interval between the two R waves. If there was too much noise to detect the QRS waves, or if there was only one QRS wave during the recording period, the heart rate could not be calculated. The 126 instantaneous heart rates were successfully calculated from 528 sections of raw ECGs over 11 days.

#### Statistical analysis

All statistical analyses were performed using R4.2.2 [47]. Unless otherwise noted, means  $\pm$  SD are shown, and statistical significance for all tests was set at  $P < 0.05$ . To compare Tmbi with Tr measured every morning for 11 days, the Tmbi recorded at the time point nearest to

the Tr measurement was used. Both Tmbi and Tr for 11 days passed the Shapiro–Wilk test for normality, so a paired *t*-test was used for comparison.

To examine 24-h variations in Tmbi and EA<sub>60</sub>, all data for 11 days were pooled and averaged every 15 min. The HR data were also pooled, and hourly averages were obtained because the number of data points per measurement time was uneven. Three characteristic periods of 6 h were established based on sunrise, sunset, and bay swimming time, i.e., the period just before sunrise was defined as before sunrise (00:00–06:00), the period just after sunset was defined as after sunset (17:15–23:15), and the period including the bay swimming was defined as during the daytime (10:00–16:00). During the measurement period, sunrise ranged between 06:03–06:15 and sunset ranged between 17:03–17:13. In addition, EA<sub>60</sub> during the day was compared by the weather conditions (usual days or heavy rain day) and time (10:00–16:00 or other daytime). For group comparisons, the Kruskal–Wallis test was used followed by the Steel–Dwass test as a post hoc test.

To examine the effects of time of day, Tw, and EA<sub>60</sub> on Tmbi, generalized additive models (GAMs) implemented in the package “mgcv” [48] in R were used to construct the best-fit model that explains the variation in Tmbi. GAMs reveal nonlinear relationships between explanatory and response variables by fitting a smooth function for each explanatory variable. Furthermore, “*gam*” function can incorporate a first-order autoregressive (AR (1)) structure to avoid overestimating the model because of autocorrelation. The first step in data processing was to summarize Tw over 15 min to match the same recording interval as the Tmbi measurement. Second, considering the possibility that Tmbi did not immediately reflect the effect of environmental temperature and activity, a time lag analysis was performed, in which Tw or EA<sub>60</sub> was shifted backward every 15 min with respect to Tmbi for four hours and Spearman's rank correlation coefficients were calculated for each time shift. The time lag analysis (Fig. S2) showed that Tw without a time shift and Tw shifted by 15 min had the same correlation coefficient with Tmbi ( $\rho = 0.27$ ), and EA<sub>60</sub> shifted by 30 min had the strongest correlation with Tmbi ( $\rho = 0.34$  compared to  $\rho = 0.18$  without time shift). Therefore, Tw without a time shift and EA<sub>60</sub> 30 min prior were incorporated into the GAMs as explanatory variables together with the time of day. We used gamma distribution structures and applied cubic splines (bs = “cs”) to Tw and EA<sub>60</sub>, and cyclic cubic regression spline (bs = “cc”) to the time of day. Finally, models with varying combinations of the three explanatory variables were compared, and the optimal



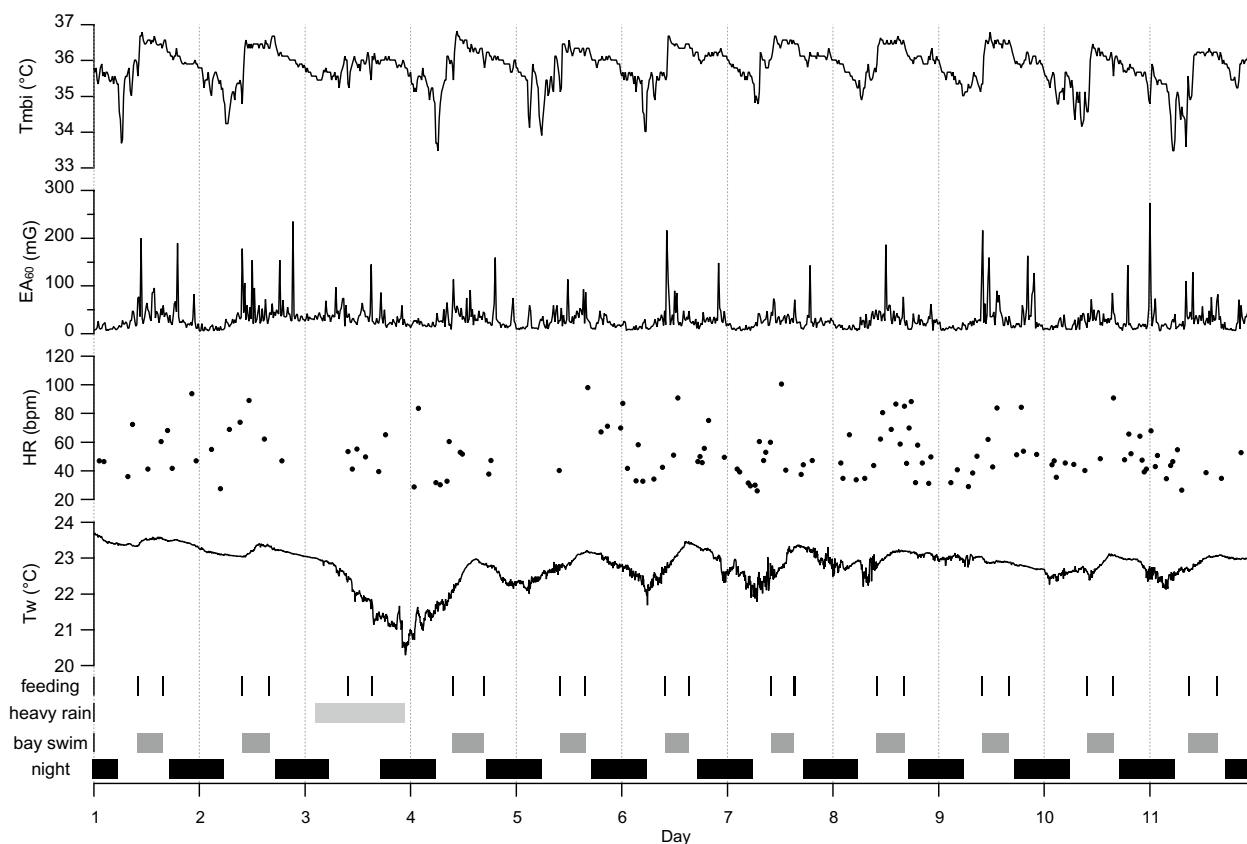
model that minimized the value of the Akaike Information Criterion (AIC) was selected. The autocorrelation function (ACF) of the model residuals was also checked to ensure that the autocorrelation at lag 1 was reduced to a non-significant level. We evaluated concavity to check multicollinearity and confirmed there were no strong correlations among the explanatory variables [49].

GAMs with a gamma distribution using the "gam" function were used to construct the model that best explained the variation in HR. The HR was no longer continuous because some could not be calculated from 6 s of ECG measurements. Therefore, time lags and autocorrelations were not considered; the time of day, Tw, and EA<sub>60</sub> when HR was measured were used as explanatory variables in the GAMs. Cubic splines (bs="cs") were also applied to Tw and EA<sub>60</sub>, and cyclic cubic regression spline (bs="cc") was applied to the time of day. Concavity was also checked and we ensured no strong correlation among explanatory variables.

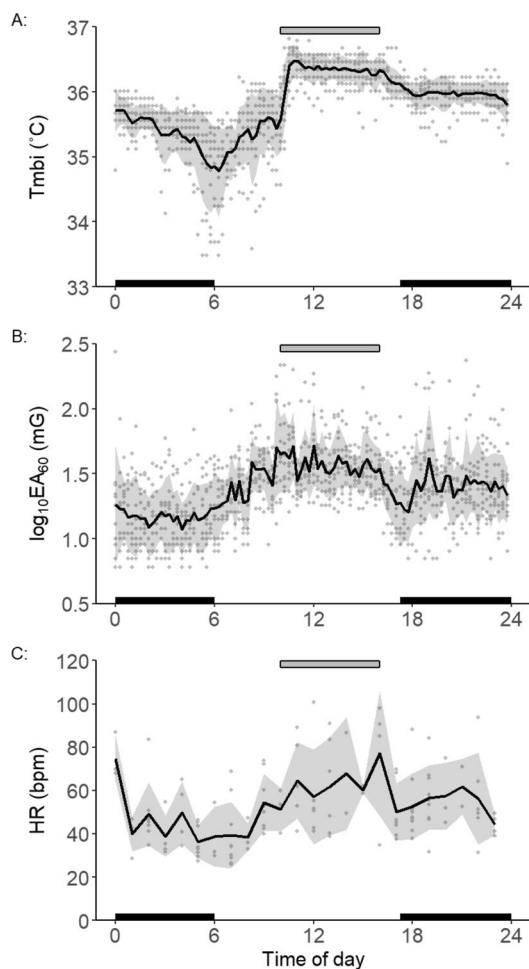
## Results

Tm<sub>bi</sub> averaged  $35.1 \pm 0.6$  °C over the 11 post-recovery days, varying from a minimum of 33.5 °C to a maximum of 36.8 °C. Tw in this study ranged from 20.4–23.7 °C (mean  $22.8 \pm 0.5$  °C, Fig. 1). The temperature difference between Tm<sub>bi</sub> and Tw averaged  $13.0 \pm 0.7$  °C. The mean Tr measured every day in the morning was  $36.5 \pm 0.4$  °C, while Tm<sub>bi</sub> recorded at the nearest timing with Tr measurement was  $35.5 \pm 0.4$  °C. Each Tm<sub>bi</sub> value was always lower than the corresponding Tr value ( $n=11$ ,  $P<0.05$ ).

The lowest Tm<sub>bi</sub> recorded throughout the day was  $34.3 \pm 0.6$  °C, at around 06:00, and the mean temperature before sunrise was  $35.4 \pm 0.5$  °C. Tm<sub>bi</sub> rose quickly in the first hour following the start of the bay swim and maintained at around  $36.3 \pm 0.3$  °C during the daytime. After sunset, it was maintained at approximately  $36.0 \pm 0.2$  °C (Fig. 2A). EA<sub>60</sub> was at a low level ( $18.2 \pm 19.1$  mG) before sunrise and gradually increased after sunrise. The dolphin had a higher level of activity ( $43.2 \pm 30.0$  mG) during the daytime. Except for the 3rd day when it rained heavily, EA<sub>60</sub> when swimming in the bay (the median



**Fig. 1** Profiles of measurement parameters in a free-swimming Risso's dolphin over 11 days. The temperature of the muscle–blubber interface (Tm<sub>bi</sub>) and external acceleration averaged over 60 s (EA<sub>60</sub>) were recorded every 15 min. Heart rate (HR) was recorded every 30 min, and the water temperature (Tw) was recorded every 5 min. The black short lines on the bottom indicate feeding time. The bars on the bottom indicate the time of heavy rain (light gray), the bay swimming time (dark gray), and the night phase (black)



**Fig. 2** Diurnal pattern of measurement parameters in a free-swimming Risso's dolphin. Temperature of the muscle-blubber interface (Tmbi, **A**) and external acceleration averaged over 60 s ( $EA_{60}$ , **B**) were plotted every 15 min.  $EA_{60}$  data are shown in the figure as log-transformed data to make it easier to visualize the variation. Heart rate (HR, **C**) was plotted hourly. The black lines indicate the mean across the 11 days at each time point, and the gray ribbons indicate the standard deviation. The gray points show the individual data. The bars on the top indicate the bay swimming time (gray: 10:00–16:00), and those on the bottom indicate the night phase (black: 0:00–6:00 and 17:15–24:00), which approximately correspond to three characteristic periods of “during the daytime”, “before sunrise”, and “after sunset”

35.0 mG) was significantly higher than when in the pen during the day (the median 25.0 mG,  $P < 0.05$ , Fig. S3). Then, the animal remained moderately active after sunset ( $31.5 \pm 29.0$  mG, Fig. 2B). On the 3rd day, the water temperature decreased by approximately 3 °C during the heavy rain and strong winds (Fig. 1). Tmbi did not drop at around 06:00, as observed other days, and Tmbi during the daytime was lower ( $35.9 \pm 0.2$  °C) than on the other days. The animal swam almost constantly on this day

**Table 1** Result of the best-fit model to explain the variation of temperature of muscle-blubber interface (Tmbi)

	Estimate	SE	T	P
Intercept	3.578	0.001	4087	< 0.05
		EDF	F	P
s (time of day)		6.436	25.24	< 0.05
s ( $EA_{60}$ 30 min prior)		2.451	2.292	< 0.05

AIC of the generalized additive models (GAMs) explaining the variation of Tmbi was lowest when the time of day and external acceleration averaged over 60 s ( $EA_{60}$ ) 30 min prior were included. The effective degree of freedom (EDF) is a proxy for the degree of non-linearity of the term effect. The adjusted  $R^2$  of the model was 0.634

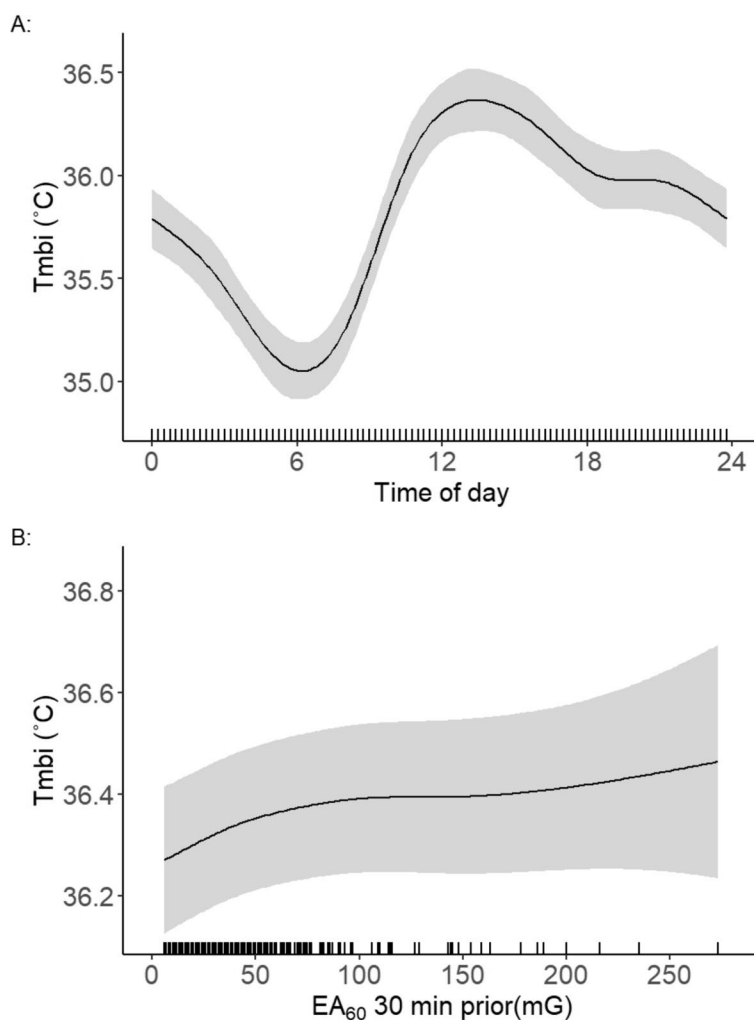
in the pen, and the median  $EA_{60}$  between 10:00–16:00 and other daytime were 35 mG and 36 mG, respectively (Fig. 1 and S3).

According to the best-fit model of the GAMs, the variation of Tmbi was best explained by the time of day and  $EA_{60}$  30 min prior. The time of day had a stronger effect as shown by the F-values (Table 1). Tmbi exhibited a diurnal pattern, as the 95% confidence intervals (CIs) of predicted Tmbi did not overlap between early morning and daytime values (Fig. 3A, e.g., 34.9–35.2 °C at 06:15 vs 36.2–36.5 °C at 13:30). The effect of  $EA_{60}$  on Tmbi was constant at most activity levels (approximately 50–180 mG). However, Tmbi appeared to decrease when the activity was lower than 30 mG, and conversely, it increased when the activity was over 200 mG (Fig. 3B).

HR varied considerably from a minimum of 26.0 bpm to a maximum of 100.7 bpm (Fig. 2C). HR was also usually lower before sunrise ( $44.5 \pm 14.4$  bpm) and higher during the daytime ( $62.9 \pm 18.6$  bpm), being intermediate after sunset ( $54.3 \pm 14.6$  bpm). The variation in HR was explained only by the time of day according to the GAM result (Table 2). The 95% CIs for the predicted HR in the morning (e.g., 36.8–46.2 bpm at 05:15) did not overlap with that during the daytime (e.g., 53.4–68.4 bpm at 13:45), which showed that HR also showed diurnal pattern (Fig. S4). Although Tw and  $EA_6$  were not significant predictors, they were included in the model with the lowest AIC values (Table 2).

## Discussion

In this study, the use of an implantable tag allowed us to simultaneously measure the blubber temperature, activity, and heart rate in a Risso's dolphin, which enabled us to uncover the factors contributing to blubber temperature variations. To the best of our knowledge, this is the first report of the continuous measurement of body temperature in a free-swimming cetacean for weeks.



**Fig. 3** Partial effects of selected explanatory variables on the temperature of the muscle–blubber interface (Tmbi). The variation of Tmbi was best explained by **A** the time of day and **B** external acceleration averaged over 60 s ( $EA_{60}$ ) 30 min prior according to the best-fit model of generalized additive models (GAMs). The y-axis represents the partial effect of each variable. The tick symbols on the x-axis are the data points observed in this study. The shaded areas indicate the 95% confidence intervals

**Table 2** Result of the best-fit model to explain the variation of heart rate (HR)

	Estimate	SE	T	P
Intercept	3.937	0.026	149.6	< 0.05
	EDF	F	P	
s (time of day)	3.459	2.801	< 0.05	
s (Tw)	0.632	0.169	0.105	
s ( $EA_{60}$ )	0.628	0.386	0.064	

AIC of the generalized additive models (GAMs) explaining the variation of HR was lowest when all variables of the time of day, water temperature (Tw), and external acceleration averaged over 6 s ( $EA_6$ ) were included. The effective degree of freedom (EDF) is a proxy for the degree of non-linearity of the term effect. The adjusted  $R^2$  of the model was 0.206

Furthermore, this may also be the first study to report the heart rate of a cetacean over a period of several consecutive days.

**Tmbi in a Risso’s dolphin**

In this study, the Tmbi of a Risso’s dolphin was higher during the daytime and lower in the early morning (Figs. 2A, 3A, and Table 1). This variation is similar to that reported for core body temperatures in Delphinidae dolphins [50–52]. In addition, the  $EA_{60}$  activity levels also decreased in the morning and increased during the day (Fig. 2B), similar to the activity patterns reported for captive bottlenose dolphins (*Tursiops truncatus*) [53]. However, it must be considered that these diurnal variations

might be affected by aquarium management like swimming schedules and place. The animal swimming in the bay was more active than that swimming in the pen during usual days, although the same level of movement was possible in the pen as in the bay (Fig. S3). In addition, the effects of feeding should also be considered because the heat increment of feeding (HIF) which is produced by food digestion seems to be an essential thermoregulation mechanism for some marine mammals and birds [54, 55]. It is not yet known whether HIF contributes to thermoregulation in cetaceans, but the metabolic rate in some dolphins has been reported to increase after feeding [56, 57]. In this study, Tmbi was highest during the day, followed by after sunset (Fig. 2A). Both times were after feeding, so Tmbi may have been affected by HIF.

The Tmbi recorded at the nearest time point to the Tr measurement was always lower than the corresponding Tr. In other marine animals, Tmbi has been reported to be several degrees lower than the core body temperature (in fin and sei whales [22], harp seals, *Phoca groenlandica* [58], and minke whales [59]), consistent with the present results. Given the temperature difference between Tmbi and Tw of  $13.0 \pm 0.7$  °C, our results highlight that the blubber of a Risso's dolphin also contributes greatly to the temperature gradient. Large thermal gradients within the blubber can contribute to a small difference between the surroundings and the body surface.

### Factors influencing Tmbi

Body temperature does not always quickly reflect the effects of activity; indeed, time lags of a few minutes have been reported for terrestrial mammals [60–62]. In the present study, Tmbi had the highest correlation with EA<sub>60</sub>, which was measured 30 min prior. It has been reported that dolphins can postpone the dissipation of heat through their activities until they reach the surface after diving [63, 64]. This delay in heat dissipation is a result of a decrease in heart rate and peripheral blood flow known as the diving response [65], which limits heat loss during diving. Once the dolphin returns to the surface, the re-established blood flow releases the heat rapidly. In the present study, dive responses may affect Tmbi by peripheral vasoconstriction and heart rate by bradycardia, however, the relationship between them was unclear due to the challenges of continuously attaching depth recorders to the animal. Further studies on finer time scales with depth recorders are required for a more detailed evaluation of these relationships.

Considering the effect of activity levels on Tmbi (Fig. 3B), the rate of increase in Tmbi was not simply proportional to the activity levels, but rather, the effect was constant for most activity levels. During activity, the process of muscle contraction increases metabolism

and generates much heat due to inefficient energy conversion [66]. Nevertheless, the reason for the weak effect of EA<sub>60</sub> on Tmbi may be due to the thermoregulatory mechanisms of blood circulation that buffer excessive body temperature increases. The blubber of cetaceans is perfused by capillaries [67] and its conductivity can be regulated by the degree of perfusion [68]. Thus, increased blood perfusion of the blubber during animal exercise may have enhanced the conductivity, resulting in greater heat dissipation via blubber. Additionally, it has also been reported that peripheral blood flow through appendages like their fins and flippers, which have minimal insulation, is important for thermoregulation in cetaceans to regulate heat loss to the environment [63, 69–71]. Vasoconstriction of the skin and appendages reduces heat loss by decreasing heat flow to the periphery in cold water, whereas these vessels expand and contribute to a large portion of whole-body heat dissipation during heat stress such as increased activity or high-water temperature. The active regulation of blood flow described above may conduct thermal balancing throughout the body with little change in the temperature gradient within the blubber. In the current study, body temperature was measured from only one location, but measurements at multiple sites including muscles and appendages would provide a more detailed understanding of how heat dissipation occurs from the entire body.

The effect of conductive heat transfer on body temperature may be more powerful when activity is higher or lower. At higher activity levels (over 200 mG), Tmbi was shown to potentially increase (Fig. 3B). This may facilitate heat dissipation via conductive heat transfer, along with sophisticated blood regulation. Furthermore, Tmbi tended to decrease during periods of low activity (Fig. 3B); this smaller blubber temperature gradient reduces heat loss and may help maintain balance with less heat production during low activity. Indeed, the body temperature decreased sharply in the morning when the dolphin was inactive (Fig. 2A, B).

The animal body sizes significantly impact heat generation and loss via volume and surface area, respectively. The relationship between them is quantified by the surface area-to-volume ratio as a parameter for the heat balances of animals [16]. In general, small animals have high surface area-to-volume ratios, which results in high heat loss and cost to maintain their body temperature. It has been suggested that small dolphins and calves may need to continuously swim for thermoregulation because of their larger surface area-to-volume ratios than large-sized dolphins or adults [50, 72]. In this study, the dolphin continued to swim on a heavy rain day when the water temperature decreased rapidly (Fig. 1 and S3).



This suggests that the dolphin may require thermogenic behavior by maintaining a moderate level of activity, even though Risso's dolphin is a medium-sized cetacean.

In this study, Tmbi was not influenced by Tw according to the GAM results. Tw did not have a significant effect on Tmbi in this study because its range was very narrow (20.4–23.7 °C). The Tmbi values of cetaceans measured immediately after death at ambient temperatures of 0–13.6 °C were lower than those in the present study (e.g., 25 ± 5 °C in bowhead whales [17]; 24 °C in minke whales [25]; and 30–33 °C in fin and sei whales [26]). The blubber properties (e.g., physical thickness and lipids composition) are different among species, seasons, prey, and nutrition states [10, 73–75]. For instance, blubber thickens in colder waters to improve insulation while dietary variations affect its lipid composition and thermal conductivity [76]. During nutrition stress, cetaceans need to use stored blubber lipids as energy, which has a trade-off effect on the thermoregulatory and buoyancy functions [16]. Therefore, it is difficult to directly compare Tmbi of the current study with that of previous studies, but Tmbi may vary in response to various water temperatures affected by season, latitude, and depth to maintain high core body temperature [20, 21, 58].

### Changes in heart rate

The heart rate of cetaceans has been reported to be significantly altered by bradycardia during dives and respiratory sinus arrhythmia [e.g., [77]], which is observed in most vertebrates. It refers to a change in the heart rate synchronized with respiration, such as tachycardia with inspiration, which decreases with expiration until the next breath. A previous study has shown that the heart rate of a Risso's dolphin temporarily increased to a maximum of 74 ± 8 bpm after respiration and gradually decreased by approximately half to 35 ± 5 bpm 40 to 50 s later [78]. Despite the effect of diving and respiratory sinus arrhythmia, which could mask changes in heart rate, we found that HR also exhibited patterns under this experimental condition (Fig. 2C, S4, and Table 2). Diurnal heart rate variations in cetaceans have not been investigated because of the challenges in measuring the heart rate of marine mammals [79, 80]. Heart rate is one of the basic vital signs of animals and is an important indicator for health checkups and stress assessment. This study thus provides a basic insight into the heart rate of captive Risso's dolphins and may contribute to their improved management in both the captive and free-ranging situation [81, 82].

While EA<sub>6</sub> and Tw were included in the lowest AIC model, they did not demonstrate significant impacts on HR. In general, exercise increases cardiac output by increasing the heart rate and providing more oxygen to

the active muscles. Previous studies have reported that an increase in heart rate during a dive is associated with activity indices such as stroke frequency, swim speed, and acceleration in cetaceans [83–85]. In contrast, a contradictory report indicated that harbor porpoises (*Phocoena phocoena*) diving in shallow waters did not exhibit an increase in heart rate during activity [86]. The authors suggested that if the muscles were supplied with sufficient oxygen, dolphins might not need to increase their heart rate. A shorter measurement interval than that used in this study may reveal a finer-scale relationship between these factors in free-swimming dolphins.

### Conclusion

Thermoregulation is an important factor enabling cetaceans to survive in thermally challenging environments. Our study successfully measured for the first time both blubber temperature and activity in a free-swimming dolphin for 11 days. Our results suggest that thermal insulation by blubber and heat production by activity maintain the body temperature of dolphins by regulating heat loss to the water, which may reflect the plasticity of thermoregulation in cetaceans. Simultaneous measurements of the core temperature and blood flow, in addition to the temperature of the blubber and its activity, could reveal further details of the thermoregulatory mechanisms of cetaceans.

### Abbreviations

EA	External acceleration
ECG	Electrocardiogram
HIF	Heat increment of feeding
HR	Instantaneous heart rate
Tmbi	Temperature of the muscle–blubber interface
Tr	Rectal temperature
Tw	Water temperature

### Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40317-024-00375-0>.

Supplementary Material 1.

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### Author contributions

K.S., D.F., D.I., N.F., K.A., and K.Q.S. designed the experiment. All the authors conducted the experiments. K.S. analyzed the data. K.S. and K.Q.S. wrote the first draft. K.Q.S. supervised the experiments. All authors contributed to the study and approved the final version of the manuscript.

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### Availability of data and materials

The datasets used and/or analyzed in the current study are available from the corresponding author upon reasonable request.

### Declarations

#### Ethics approval and consent to participate

All experimental procedures were approved by the Animal Ethics Committee of Atmosphere and Ocean Research Institute of the University of Tokyo (permission number: P21-1). This study complied with the recommendations of the Life Science Research Ethics and Safety of the University of Tokyo for Experiments on Animals.

#### Consent for publication

Not applicable.

#### Competing interests

We declare we have no competing interests.

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