

Research Article

Variation of blubber thickness of the Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*) in human care: Adaptation to environmental temperature

Bin Tang^a, Yujiang Hao^{a,b,*}, Chaoqun Wang^{a,b}, Zhengyu Deng^{a,b}, Guilin Shu^a, Kexiong Wang^{a,b}, Ding Wang^{a,b}

^a Key Laboratory of Aquatic Biodiversity and Conservation, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, 430072, China

^b National Aquatic Biological Resource Center, NABRC, Wuhan, 430072, China

ARTICLE INFO

Keywords:

Yangtze finless porpoises
Blubber thickness
Water temperature
Thermal adaptation
Food intake

ABSTRACT

Blubber thickness (BT) has a seasonal pattern in most small cetaceans in temperate and polar regions, which may be a crucial adaptive mechanism in response to environmental temperature changes. However, BT and environmental temperature correlations have never been tested experimentally in any cetacean species owing to logistical difficulties in the aquatic environment. The Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*, YFP) is one of the smallest cetacean species worldwide, which exclusively inhabits the middle and lower regions of the Yangtze River in China. Here, we investigated BT variation patterns in YFPs and their relationship to environmental temperature changes using ultrasound imaging technology by longitudinally monitoring four YFPs in human care. We found that blubber was not evenly distributed in the skin of YFPs. BT increased along the craniocaudal axis from the head to the umbilical girth, and decreased towards the fluke, with relatively thicker blubber in the dorsal region than in the ventral and lateral regions. Significant negative correlations between BT and seasonal water temperature changes were observed in YFPs. However, different body regions display different sensitivities to seasonal temperature changes. The BT in the anal girth region exhibited noticeable seasonal changes. In contrast, the umbilical lateral and ventral regions showed relatively blunt seasonal changes, indicating different adaptive functions of the blubber in different regions. BT in the dorsal region decreased linearly with increasing water temperature. In the lateral and ventral regions, BT significantly changed with water temperature at a threshold of 18 °C. The YFPs had relatively thinner BT than similar-sized harbor porpoises that inhabit relatively high latitudes with much lower water temperatures. This further demonstrates the adaptive function of BT in response to environmental temperatures in small cetaceans. This study elucidates the seasonal pattern of BT variation in small cetaceans and provides insight into adaptation mechanisms of small cetaceans to temperature changes.

1. Introduction

Marine mammals live in aquatic environments with high thermal conductivity (Nadel, 1984). Therefore, it is a greater challenge for them to maintain their core body temperature compared to terrestrial mammals (Davis, 2019). Blubber is the primary thermal barrier for marine mammals, especially cetaceans without fur or hair, and the blubber is considered the exclusive thermal barrier (Worthy and Edwards, 1990; Kanwisher and Sundnes, 1966; Dunkin et al., 2005). As such, cetaceans must maintain sufficiently thick blubber to adapt to aquatic

environments with high thermal conductivity (Parry, 1949; Favilla et al., 2021). The blubber thickness (BT) of large baleen whales can reach approximately 50 cm (Iverson, 2009), while small cetaceans generally have a BT of 2–5 cm (Meyer et al., 1995; Koopman, 1998; Koopman et al., 2002; Noren and Wells, 2009; Zeng et al., 2015).

Previous studies have speculated that blubbers in different body regions might be functionally specialized (Koopman, 1998; Koopman et al., 2002; Gómez-Campos et al., 2015; Zeng et al., 2015; Cornick et al., 2016). However, there is considerable speculation regarding the interpretation of blubber-specific regional functions. For example, the dorsal

* Corresponding author. Key Laboratory of Aquatic Biodiversity and Conservation, Institute of Hydrobiology, Chinese Academy of Sciences, Wuhan, 430072, China.
E-mail address: hao.yj@ihb.ac.cn (Y. Hao).

<https://doi.org/10.1016/j.watbs.2023.100200>

Received 29 November 2022; Received in revised form 20 April 2023; Accepted 13 June 2023

Available online xxx

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region with a thicker blubber may serve as energy storage (Zeng et al., 2015; Cornick et al., 2016). In contrast, several studies have suggested that the blubber in the ventral region, with a high number of adipocytes and lipid concentrations, mainly functions as energy storage (Ishaq et al., 2000; Tornero et al., 2006; Gómez-Campos et al., 2015). However, the blubber in the dorsal region with a lower adipocyte number and lipid content may help shape the body and regulate buoyancy (Koopman, 1998; Koopman et al., 2002; Hamilton et al., 2004; Tornero et al., 2006; Gómez-Campos et al., 2015).

Moreover, the blubber in marine mammals is unanimously stratified (Dunkin et al., 2005; Meagher et al., 2008; Montie et al., 2008; Bagge et al., 2012; Zeng et al., 2015; Ji et al., 2019; Tang et al., 2021). The outer layer mainly provides structural support and acts as a thermal barrier, whereas the inner layer is responsible for energy mobilization (Mellish et al., 2004; Struntz et al., 2004; Montie et al., 2008; Gómez-Campos et al., 2015; Zeng et al., 2015; Ji et al., 2019). For example, starved harbor porpoises (*Phocoena phocoena*) had fewer and smaller adipocytes in the inner layer than normal harbor porpoises. However, the outer blubber adipocytes were uniform among animals with different nutritional statuses (Koopman et al., 2002), suggesting that BT variation may occur primarily in the inner layer.

Additionally, blubber storage is affected by environmental temperature across cetacean species. Cetaceans inhabiting higher latitudes with lower mean annual temperatures usually have significantly higher blubber stores (23–43%) than those inhabiting lower latitudes with relatively higher mean annual temperatures (15–32%) (Miyazaki et al., 1981; Lockyer, 1991; McLellan et al., 2002). For example, the BT of harbor porpoises living in cold water was double that of similar-sized spotted dolphins (*Stenella attenuata*) inhabiting warm waters (Worthy and Edwards, 1990). Moreover, BT shows similar seasonal variations in most cetacean species but with contradictory interpretations. For instance, adult beluga whales (*Delphinapterus leucas*) in Bristol Bay had significantly higher BT in the fall than in the spring, which was assumed to be mobilized to compensate for energetic deficits in winter (Cornick et al., 2016). Both wild and captive harbor porpoises showed seasonal changes in their blubber thickness, which were considered to be related to energy storage and metabolism affected by ambient water temperatures (Siebert et al., 2022; Stepien et al., 2023). Similarly, wild and captive bottlenose dolphins (*Tursiops truncatus*) also showed significantly thicker blubbers in winter than in summer, which might be a direct adaptation associated with its insulative properties (Kanwisher and Sundnes, 1966; Meagher et al., 2008; Noren and Wells, 2009).

With accelerating global warming, extreme weather is becoming more frequent (Bindoff et al., 2019; Cheng et al., 2019), with potentially far-reaching implications for cetaceans, including changes in prey availability affecting distribution, abundance, migration patterns, community structure, susceptibility to disease, and biomagnification of contaminants (Albouy et al., 2020; Learmonth et al., 2006; Simmonds and Isaac, 2007). As water temperature changes, baleen whales are less affected than toothed whales in their mobility and thermoregulatory ability (Burns, 2002). However, physical limits may hinder the ability of several small cetaceans to change their geographic range, which may be particularly vulnerable and affected by changes in water temperature (Learmonth et al., 2006; Simmonds and Isaac, 2007). For example, Yangtze finless porpoises (*Neophocaena asiaorientalis asiaorientalis*, YFPs) are a small cetacean species that exclusively inhabit the middle and lower reaches of the Yangtze River (Jefferson and Wang, 2011). The body mass (mainly influenced by blubber thickness) and food intake of YFPs in human care change seasonally, which might be an indispensable adaptive mechanism to seasonal changes in water temperatures. Here, we explore the distribution and seasonal variation patterns of BT in Yangtze finless porpoises (YFPs) using longitudinal monitoring of the changes in BT of YFPs in human care and investigate correlations with environmental water temperature. This study will help elucidate the seasonal patterns of BT variation in small cetaceans as well as provide insights into the adaptive mechanisms of small cetaceans to temperature change. We

believe that predicting the consequences of global warming on the adaptive capacity of small cetaceans is crucial.

2. Materials and methods

2.1. Animals

The BT of four adult YFPs in human care, including two males (TT and DD) and two females (F7 and YY), housed in the Baiji Dolphinarium (Wuhan, China), was monitored for at least one calendar year, except for the pregnant animal (YY) (Table 1). TT and DD were monitored twice monthly for 12 consecutive months from April 2020 to March 2021. The data obtained from female animals were incomplete owing to unstable training and physiological conditions. F7 was monitored once or twice per month for 12 months from April 2020 to March 2021, and YY was monitored once or twice per month for 8 months from August 2019 to April 2020 (no data were available in February). During the study period, the animals were mainly fed crucian carp (*Carassius auratus*), common carp (*Cyprinus carpio*), and sharp belly (*Hemiculter leucisculus*), and the daily intake was adjusted based on body mass and appetite. Daily food intake was measured using an electronic scale with a precision of 0.001 kg and recorded throughout the study. As the species of dietary fish remain similar throughout the year, food intake was used as a proxy for energy intake. The daily water temperature of the breeding pool was monitored throughout the study.

The animals were housed in a kidney-shaped rearing pool and a connected round rearing pool. All the animals were in good health during the study period. The water temperature changed naturally from 11 °C to 28 °C except for the summer when the cooling system was started to keep the water temperature under 28 °C. The animals were cared for by skilled and experienced trainers to ensure their health and well-being under human care.

2.2. Ultrasonographic examinations

The animals were trained to lie on their side in a straight line on the water without restraint for ultrasonographic examination (Wu et al., 2010). All examinations were conducted using a LOGIQ Book XP ultrasound unit (General Electric Co., Schenectady, NY, USA) in conjunction with a broadband curvilinear array transducer (3–5 MHz). The ultrasound settings were standardized to a 4 MHz frequency, 48 overall gain, and 11 cm scanning depth. The settings for near and far gains were consistent throughout the study.

The blubber was divided into two or three layers, depending on the echo intensity. The outer layer was anechoic, and the middle and inner layers exhibited changing echoes that gradually increased towards the inner layer (Zeng et al., 2015). As the boundary between the middle and inner layers was difficult to distinguish, the outer layer and overall BT were measured on each ultrasound image using the built-in caliper (Fig. 1). The measured images were saved as a .jpg file for future review when necessary. Blubber thickness images were obtained from nine sites in the thoracoabdominal regions of the two male animals (Fig. 2). However, owing to inadequate training, only three sites (L1–3) were sampled from the two female animals (Fig. 2). Only the left side was sampled because the animals were bilaterally symmetric. Dorsal sites were sampled at the dorsal eminence at the left side of the dorsal ridge, and lateral and ventral sites were sampled along the midline.

Table 1
Information on the Yangtze finless porpoises investigated in this study.

Animal ID	Sex	Year of birth	Length (cm)	Reproductive status
TT	Male	2005	157	Normal
DD	Male	2008	156	Normal
F7	Female	2009	145	Normal
YY	Female	2007	144	Pregnant

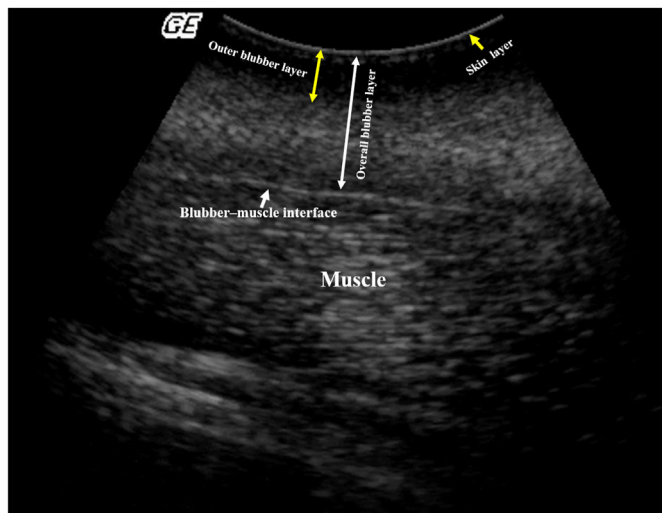


Fig. 1. Ultrasound image shows the measurement process for blubber thickness. The white line shows the measurement of the overall blubber thickness, and the yellow line shows the thickness of the outer layer. White arrows indicate the blubber-muscle interface, and yellow arrows indicate the skin layer.

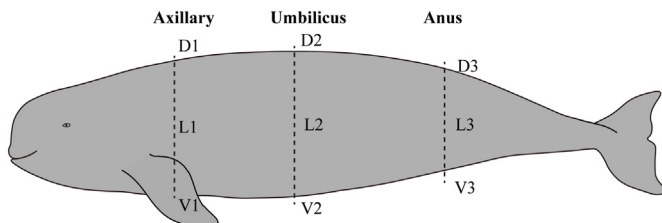


Fig. 2. Sampling sites of the Yangtze finless porpoises for blubber thickness ultrasound measurements. A total of nine sites were selected from the thoracic-abdominal region, including three dorsal (D1–D3), three lateral (L1–L3), and three ventral sites (V1–V3), respectively.

The study methods, including animal training and ultrasonographic examination, were approved by the Research Ethic Committee of the Institute of Hydrobiology, Chinese Academy of Sciences. The study strictly followed all Chinese laws and ethical guidelines for wildlife.

2.3. Data analysis

BT values are shown as the mean \pm standard deviation (SD) unless otherwise noted. The variation coefficient (CV) was calculated from BT data collected during the entire year at nine body sites. A higher CV value indicated a higher variation in BT. The ordinary kriging method was used to predict the distribution of CV (Zhu and Lin, 2010). One-way analysis of variance (ANOVA) was used to compare the differences in BT and CV among body sites and regions, followed by Tukey's honest significant difference (HSD) post hoc tests using the agricolae package in R. Equal variance was examined using Levene's test, and normality was assessed using the Shapiro–Wilk test. An independent-sample *t*-test was used to compare differences in BT between sexes, animal groups, and layers. Generalized additive models (GAM) in the mgcv package in R were used to predict variation in BT and food intake related to water temperature for each animal. These models included only water temperature as a predictor variable. Separate models were constructed using the response variables of BT of each blubber layer from each body region (dorsal, lateral, and ventral) and food intake (Table S1). All statistical tests were conducted using R (version 4.1.0), and the significance was set at $\alpha < 0.05$.

3. Results

3.1. Topographic changes of blubber thickness

Significant differences were not observed between sexes ($p > 0.05$) by the *t*-test; therefore, sex classes were not used as factors in the subsequent analysis. The overall BT of normal YFPs averaged 2.26 ± 0.26 cm, and the inner and outer BT averaged 1.23 ± 0.27 cm and 1.03 ± 0.10 cm, respectively. The thickest mean blubber (with overall BT 2.65 ± 0.19 cm, inner BT 1.28 ± 0.29 cm, and outer BT 1.37 ± 0.27 cm) appeared in winter (December and February) when the water temperature dropped to lower than 15°C . Conversely, the thinnest mean blubbers (with overall BT 1.80 ± 0.03 cm, inner BT 0.83 ± 0.11 cm, and outer BT 0.97 ± 0.09 cm) were observed in summer (June and August) when the water temperature increased above 25°C . Except for three dorsal sites (D1–D3) with significantly thicker inner BT ($p < 0.05$), there was no significant difference in BT between the inner and outer layers of other regions for normal (non-pregnant) YFPs. In contrast, the pregnant YFP had a significantly thinner inner layer at the three lateral sites (L1–L3) ($p < 0.05$). Overall (2.74 ± 0.39 cm) and outer (1.56 ± 0.43 cm) BT of the pregnant YFP were significantly higher than those of normal YFPs ($p < 0.01$). However, the inner BT (1.19 ± 0.09 cm) was similar to that of normal YFPs (Table 2).

There were significant differences in BT across body sites of normal YFPs ($p < 0.01$) (Fig. 3). Generally, D2 was the thickest, and V3 was the thinnest site. Along the craniocaudal axis, the blubber close to the caudal dorsal site (D3) was significantly thinner than that of the other two dorsal sites (D1 and D2) ($p < 0.01$), and D2 appeared slightly thicker than D1, although the difference was not statistically significant ($p > 0.05$). Similarly, the BT close to the caudal ventral site (V3) was significantly thinner than that of the other two ventral sites (V1 and V2) ($p < 0.01$), and V2 seemed slightly thicker than V1, but the difference was not statistically significant ($p > 0.05$). Laterally, the BT close to the head (L1) was thinner than that of the other two lateral sites (L2 and L3), but there was no significant difference between L1 and L3 (Fig. 3).

On the axillary and umbilical girths, the blubber at the dorsal sites (D1 and D2) was significantly thicker than the blubber at the lateral (L1 and L2) and ventral sites (V1 and V2), and there were no significant differences between the lateral and ventral sites. Similarly, the anal girth blubber was also thicker at the dorsal site (D3) than at the lateral (L3) and ventral sites (V3), but this difference was only significant for D3 versus V3 (Fig. 3).

3.2. Seasonal variation of blubber thickness

The coefficients of variation (CV) of BT throughout the year were calculated to assess the seasonal variation in BT. There were no significant differences in CVs among body sites in the overall, inner, and outer blubbers ($p < 0.05$). However, the anal girth and axillary lateral regions had higher CV values than other regions (Fig. 4A), whereas the axillary dorsal-ventral region and the lateral umbilical region had relatively lower CV values (Fig. 4A). The inner layer had significantly higher CVs than the outer layer ($p < 0.01$) (Fig. 4B). There was no significant difference in the CV of BT between normal animals and the pregnant female ($p > 0.05$).

3.3. The effect of water temperature

A generalized additive model (GAM) was used to explore the correlation between BT and water temperature in the dorsal (D1–D3), lateral (L1–L3), and ventral (V1–V3) regions. Owing to data limitations for female YFPs, only the lateral region was investigated in this analysis. The BT of all YFPs was negatively correlated with water temperature, and there were no significant differences between sexes in the lateral region (Fig. 5, Table S1). However, the BT variation trend with water temperature differed significantly across body regions. BT declined almost

Table 2
Blubber thickness across body sites of Yangtze finless porpoises in human care

Body sites	Groups	Min blubber thickness (cm)			Max blubber thickness (cm)			Mean blubber thickness (cm)		
		Overall	Inner	Outer	Overall	Inner	Outer	Overall	Inner	Outer
D1	Normal (n = 2)	2.07	0.91	0.82	3.25	2.09	1.43	2.53 ± 0.32	1.46 ± 0.29*	1.07 ± 0.13
D2	Normal (n = 2)	2.11	0.34	0.67	3.60	2.53	1.81	2.72 ± 0.39	1.71 ± 0.47*	1.01 ± 0.29
D3	Normal (n = 2)	1.70	0.86	0.50	2.89	2.05	1.35	2.29 ± 0.40	1.47 ± 0.39*	0.82 ± 0.17
L1	Normal (n = 3)	1.26	0.35	0.65	2.86	1.63	1.61	2.02 ± 0.32	0.94 ± 0.25	1.10 ± 0.25
L2	Normal (n = 3)	1.58	0.52	0.78	2.97	1.58	1.70	2.27 ± 0.32	1.14 ± 0.26	1.13 ± 0.26
L3	Normal (n = 3)	1.55	0.63	0.70	2.65	1.77	1.73	2.13 ± 0.31	1.12 ± 0.30	1.01 ± 0.26
V1	Normal (n = 2)	1.61	0.51	0.75	2.95	1.85	1.68	2.21 ± 0.37	1.14 ± 0.31	1.07 ± 0.16
V2	Normal (n = 2)	1.75	0.64	0.91	3.13	1.86	1.74	2.37 ± 0.41	1.24 ± 0.32	1.13 ± 0.17
V3	Normal (n = 2)	1.31	0.34	0.78	2.62	1.67	1.66	1.86 ± 0.36	0.85 ± 0.22	1.01 ± 0.22
L1	Pregnant (n = 1)	2.32	0.55	1.23	3.37	1.76	2.43	2.93 ± 0.36	1.14 ± 0.39	1.79 ± 0.26*
L2	Pregnant (n = 1)	2.34	0.52	1.35	3.49	1.78	2.33	3.02 ± 0.37	1.22 ± 0.38	1.80 ± 0.26*
L3	Pregnant (n = 1)	2.20	0.26	1.28	3.36	1.70	2.11	2.90 ± 0.38	1.09 ± 0.42	1.81 ± 0.25*
Mean lateral blubber thickness Mean ± SD	Normal	1.46 ± 0.18	0.50 ± 0.14	0.71 ± 0.66	2.83 ± 0.16	1.66 ± 0.10	1.68 ± 0.06	2.14 ± 0.13	1.07 ± 0.11	1.08 ± 0.11
	Pregnant	2.29 ± 0.08 [†]	0.44 ± 0.16	1.29 ± 0.06 [†]	3.41 ± 0.07 [†]	1.75 ± 0.04	2.29 ± 0.16 [†]	2.74 ± 0.39 [†]	1.19 ± 0.09	1.56 ± 0.43 [†]

* Nine sites were measured in the thoracic-abdominal region, including three dorsal (D1–D3), three lateral (L1–L3), and three ventral sites (V1–V3). An independent-sample *t*-test was used to compare differences in BT between the animal groups and layers. The values with an asterisk (*) indicate a significant difference between inner and outer layers in mean blubber thickness ($p < 0.05$). Values with a dagger (†) indicate a significant difference between normal and pregnant YFPs in mean lateral blubber thickness ($p < 0.05$).

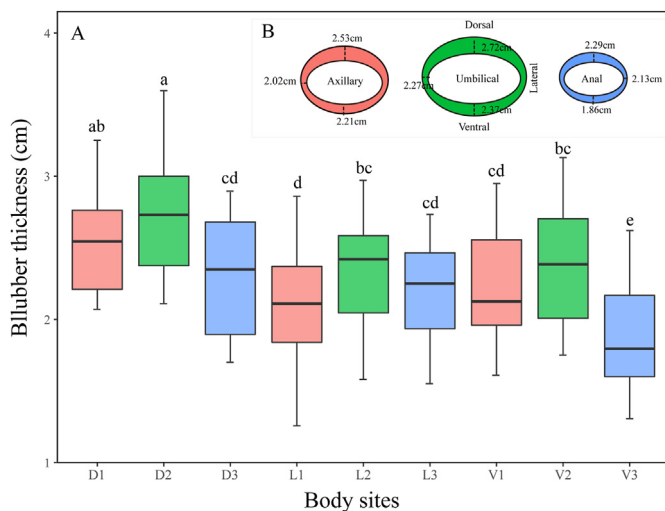


Fig. 3. Box plot of mean blubber thickness (BT) at nine body sites (A) and its distribution across body regions (B). Significant differences across body sites are noted by minuscule, and bars with different minuscules demonstrate significant differences ($p < 0.05$), while bars with the same minuscule are not significantly different ($p > 0.05$). The mean BT values for each body site are marked on the BT distribution schematic plot (B).

linearly in the dorsal region with increasing water temperature in the overall, inner, and outer blubber layers (Fig. 5 Dorsal-TT; DD, Table S1); however, the thickness of the inner layer dominated the changes in BT.

In contrast, in the lateral and ventral regions, the overall BT did not show a significant correlation with water temperature until it increased to approximately 18 °C (Fig. 5 Lateral-F7; TT; DD, Table S1), and the

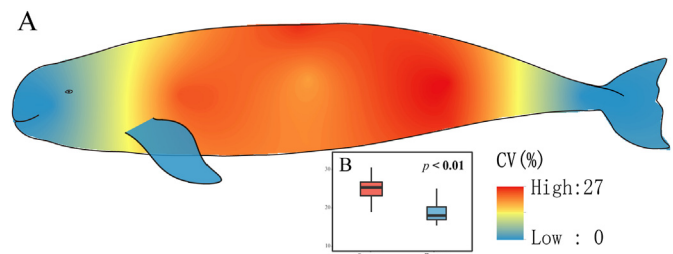


Fig. 4. Topographic changes of the coefficient of variation (CV) of BT across the thoracic-abdominal region (A). The ordinary kriging method was used to simulate the topographic changes of the CV of BT, where the head and flipper regions were assumed to be 0. The box plot shows the difference in CV values of BT between the inner and outer blubber layers ($p < 0.01$) (B).

variation trend did not show a significant difference between inner and outer blubber layers. The pregnant YFP showed a similar variation trend to normal YFPs in overall BT, whereas there was a significant difference between the inner and outer layers. The inner BT showed a similar variation trend to the overall BT, but the outer BT did not significantly correlate with water temperature (Fig. 5 Lateral-YY, Table S1).

Moreover, the animals' food intake was simultaneously affected by water temperature (Fig. 5, gray line, Table S1). The food intake of the three normal YFPs declined linearly with increasing water temperature (Fig. 5 TT, DD, and YY; Table S1). However, the food intake of the pregnant YFP showed a different pattern of variation. A positive correlation between food intake and water temperature was observed when the water temperature was lower than 19 °C. In comparison, when the water temperature was higher than 19 °C, the food intake and water temperature showed a negative correlation.

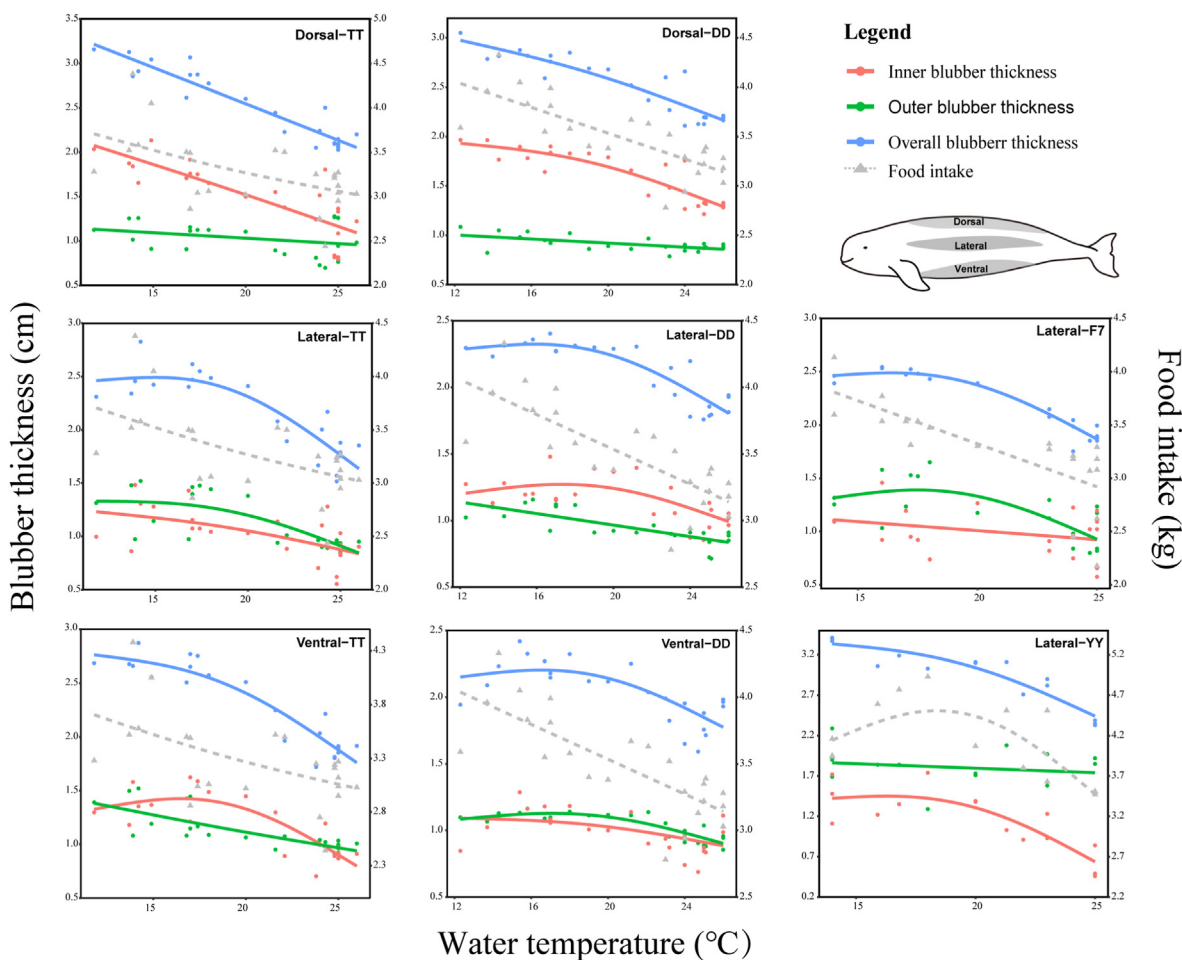


Fig. 5. Effect of water temperature on blubber thickness and food intake. The generalized additive model was used to fit the smooth curve. The blue, red, and green dashed curves represent the overall, inner, and outer blubber thickness. The gray dashed curve represents food intake. Each figure is numbered in the format of 'body regions-animal ID.'

4. Discussion

For marine animals, the primary function of blubber is insulation, which is particularly important for cetaceans that rely solely on blubber as a thermal barrier (Parry, 1949). The thermal conductivity of blubbers is primarily influenced by BT and biochemical composition (Dunkin et al., 2005; Bagge et al., 2012; Singleton et al., 2017; Guerrero and Rogers, 2019; Tang et al., 2021). Previous studies revealed that the lipid composition and fatty acid profile of marine mammals exhibit significant adaptable changes with environmental temperature (Samuel and Worthy, 2004; Guerrero and Rogers, 2019; Tang et al., 2021). Moreover, some studies also showed that BT exhibited apparent seasonal variations but with discrepant interpretations of its adaptation to environmental temperatures (Kanwisher and Sundnes, 1966; Meagher et al., 2008; Noren and Wells, 2009; Cornick et al., 2016).

Ultrasound imaging has been widely used to measure BT in marine mammals and evaluate body condition in cetaceans and pinnipeds because of its multiple advantages, such as portability, non-invasiveness, accuracy, and real-time measurements (Mellish et al., 2007; Noren et al., 2015, 2021; Cornick et al., 2016; Adamczak et al., 2021). In addition, the juncture between the blubber and muscle strongly reflects ultrasonic beams, and significant changes in blubber echo intensity show clear stratified images (Moore et al., 2001; Zeng et al., 2015; Cornick et al., 2016). Furthermore, ultrasound measurement of BT is accurate in marine mammals (Mellish et al., 2004; Cornick et al., 2016). Therefore, the ultrasound measurement of BT in YFPs presented in this study should reflect its blubber profiles.

The mean BT of normal YFPs ranged from 1.80 ± 0.03 cm to 2.65 ± 0.19 cm, which was significantly thinner than similar-sized harbor porpoises (the thickest blubber was 3.94 cm), which inhabit relatively low water temperature waters (Koopman, 1998). Cetaceans inhabiting colder waters usually have significantly thicker blubber stores (23–43%) than those inhabiting warmer waters (15–32%) (Miyazaki et al., 1981; Lockyer, 1991; McLellan et al., 2002), suggesting that the thickness of the blubber layer is a direct adaptive indicator of environmental temperatures.

In contrast to previous studies (Lockyer, 1987a; 1995; Pettis et al., 2004; Adamczak et al., 2021; Siebert et al., 2022), we did not detect significant differences in BT between males and females, which may be partly due to the limited sample size and differing reproductive statuses in the present study. However, the BT of the pregnant YFP was significantly higher than that of the non-pregnant female and mature male YFPs (Table 1), which is consistent across marine mammals (Kastelein et al., 2002; West et al., 2007; Hückstädt et al., 2018; Shero et al., 2018). A thicker blubber layer is assumed to provide better insulation (Parry, 1949; Struntz et al., 2004; Dunkin et al., 2005; Bagge et al., 2012), and, therefore, can provide a stable thermal environment for fetal development. Moreover, female marine mammals increased their blubber storage during gestation (West et al., 2007; Gulland et al., 2018; Hückstädt et al., 2018), which might store energy for future requirements to raise their calf (Lockyer, 1987b; Oftedal, 1997; Aguilar and Borrell, 1990; Aguilar et al., 1999; Ji et al., 2019).

Marine mammals share similar topographic blubber distributions, which is possibly vital for balancing the versatile functions of blubbers in

marine mammals, including thermal regulation, energy storage, buoyancy, and streamlining (Rosen and Renouf, 1997; Struntz et al., 2004; Mellish et al., 2007; Montie et al., 2008; Noren et al., 2021). The YFPs in the present study demonstrated a topographic pattern similar to that of blubber distribution with other marine mammals (Fig. 3), such as beluga whales, harbor porpoises, and East Asian finless porpoises (*Neophocaena asiaorientalis sunameri*) (Koopman, 1998; Zeng et al., 2015; Cornick et al., 2016). Generally, BT increased from the head to the umbilical girth along the craniocaudal axis and decreased towards the fluke. In addition, the dorsal region usually has a thicker blubber than the ventral and lateral regions (Doidge, 1990; Koopman, 1998; Zeng et al., 2015; Cornick et al., 2016). However, the interpretation of the specific topographic distribution of blubbers in marine mammals is highly controversial. Some studies have reported that the thick blubber in the dorsal region functions mainly for energy storage (Zeng et al., 2015; Cornick et al., 2016). However, other studies have suggested that the ventral region might be the preferred region for energy storage because it has more adipocytes and lipid content (Ishaq et al., 2000; Tormero et al., 2006; Gómez-Campos et al., 2015).

Comparing the variation in BT in different regions may shed light on the function of the blubber in different regions. For example, the lateral and ventral umbilical regions with lower CV values may indicate that these regions are vulnerable to blubber changes (Fig. 4), suggesting that the thickness of the blubber in these regions may be essential for maintaining a stable thermal environment for vital internal organs (Koopman, 1998). In contrast, the dorsal regions with prominently higher CVs may indicate their importance in energy storage and mobilization. The anal region also had a variable BT. It may be essential to shaping the streamlined body to reduce water resistance in swimming (Koopman, 1998; Cornick et al., 2016) (Fig. 4), or it may indicate an adaptive thermal sensitive mechanism of the reproductive organs inside this region (Rommel et al., 1993, 1998; Pabst et al., 1995).

In our study, we observed that the inner layer was more variable in BT than the outer layer (Fig. 4B), which is consistent with previous studies. This may indicate that the inner layer is mainly responsible for energy mobilization, while the outer layer serves as a structural support and thermal barrier in cetaceans (Struntz et al., 2004; Montie et al., 2008; Gómez-Campos et al., 2015; Zeng et al., 2015; Ji et al., 2019). Furthermore, the correlation between BT and water temperature further supported this assumption (Fig. 5). Particularly in the dorsal region, the BT of the outer layer was nearly identical across all seasons despite significant changes in water temperature. In contrast, the BT of the inner layer significantly declined with increasing water temperature, suggesting that the inner layer in the dorsal region may be more dynamic for thermoregulation (Fig. 5 Dorsal-TT; DD).

Previous research suggested that the blubber thickness was mainly affected by food resources and ambient temperature (Worthy and Edwards, 1990; Montie et al., 2008; Cornick et al., 2016; Adamczak et al., 2021; Noren et al., 2021). Water temperature change may be the first environmental factor triggering variations in blubber thickness in marine mammals (Meagher et al., 2008; Noren and Wells, 2009; Kastelein et al., 2018; Adamczak et al., 2021), consistent with our results. Furthermore, the BT in the YFP showed a general pattern of increase with decreasing water temperature, which might be an essential mechanism for small cetaceans to adapt to regular seasonal temperature changes (Kanwisher and Sundnes, 1966; Meagher et al., 2008; Noren and Wells, 2009). However, irregular water temperature changes might be detrimental to the animals during the climate change scenario, particularly for YFPs and other small cetaceans living in relatively limited geographic regions. For example, the mass mortality of bottlenose dolphins in the Gulf of Mexico has been linked to an unusual cold-water event in winter following a regular or warmer autumn (IWC, 1997).

Moreover, our results revealed that BT varied differently in different body regions with water temperature in YFPs (Fig. 5). The dorsal region was more sensitive to changes in water temperature. As it is an over-insulated region (Ryg et al., 1988; Rosen and Renouf, 1997) that

features many skeletal muscles that generate excessive heat, the heat must be disposed of after exercise, particularly in warmer waters (Gulland et al., 2018). However, in the lateral and ventral regions, the BT did not change significantly until the temperature increased above 18 °C (Fig. 5 Lateral; Ventral), implying that there is a threshold for BT to change with water temperature. Therefore, it can be concluded that BT was limited to thickening below this temperature. The animals may mobilize other physiological responses, for example, by changing the biochemical composition of the blubber (lipid, fatty acid, and water) (Dunkin et al., 2005; Bagge et al., 2012; Tang et al., 2021), increasing metabolic heat (Costa, 2002), and increasing blood perfusion (Gulland et al., 2018), to cope with water temperature changes.

It can be argued that food intake is the dominant factor in determining BT. The animals in human care were fed *ad libitum* during all seasons. Notably, food intake also varied significantly with water temperature, like BT. This implies that BT might be mainly regulated by changes in food intake in response to environmental cues such as water temperature. Understandably, the thicker blubber in winter contributes to energy storage (Lockyer et al., 2003; Cornick et al., 2016) and improves insulation in colder water (Meagher et al., 2008; Noren and Wells, 2009). However, the mechanism by which environmental temperature regulates the BT of YFPs by changing the appetite or food intake of animals warrants further investigation.

In contrast to the other three animals, the food intake of the pregnant animal did not show a typical linear correlation with water temperature (Fig. 5 YY, Table S1). Therefore, it seems that food intake of pregnant animals also has a temperature threshold, or it may be influenced by the fetus's development. Indeed, we are cautious about providing a detailed explanation owing to the limited data from a case study. Further investigations with more data from more cases are warranted in future studies.

5. Conclusion

By longitudinally monitoring changes in the blubber thickness of YFPs in human care, we evaluated the distribution and seasonal variation patterns in BT of YFPs. We aimed to elucidate the possible adaptive mechanism of small cetaceans to environmental temperature changes by changing their BT. We found that BT increases from the head to the umbilical girth along the craniocaudal axis and decreases towards the fluke with a relatively thicker dorsal blubber than in the ventral and lateral regions. Moreover, the BT in different regions had different sensitivities to seasonal changes in water temperature. The lateral and ventral umbilical regions had a relatively blunt BT, which may be essential for maintaining a stable thermal environment to protect vital internal organs.

In contrast, the back dorsal and anal girth regions showed noticeable seasonal changes in BT, possibly indicating the importance of this region in energy storage and mobilization. Significant negative correlations between BT and water temperature were observed in YFPs. However, different regions showed different sensitivity patterns to changes in water temperature. The dorsal BT decreased linearly with increasing water temperature, whereas the lateral and ventral BT demonstrated a threshold pattern of variation. This study sheds light on an essential mechanism by which small cetaceans adapt to water temperature changes and provides critical knowledge for predicting the viability of cetaceans experiencing climate change and corresponding irregular temperature changes.

Ethical statement

The animal study was reviewed and approved by the Ministry of Science and Technology of the People's Republic of China, with all animals procured and examination procedures strictly adhering to Chinese ethical guidelines and legal requirements.

Declaration of competing interest

Ding Wang is a Guest Editor for *Water Biology and Security* and was not involved in the editorial review or the decision to publish this article. All authors declare that there are no competing interests.

Funding

This study was financially supported by the National Key R&D Program of China, Grant No. 2021YFD1200304.

Author contributions

Bin Tang: Experiment design and conduct, Writing. Chaoqun Wang, Zhengyu Deng and Guillin Shu: Assistance with sampling. Yujiang Hao: Proofreading, Funding, Supervision, Reviewing and Editing. Kexiong Wang and Ding Wang: Supervision and Review. All authors read and approved the final manuscript.

Acknowledgments

We thank the animal trainers from the Baiji Dolphinarium (Wuhan, China), Hongbin Guo, Zhangbing Kou, and Yuanze Feng, for their assistance in the ultrasonographic examination.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.watbs.2023.100200>.

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