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CFD MODELLING OF THE THERMO- AND HYDRODYNAMIC CAPABILITIES OF LONG-NECKED PLESIOSAURS (REPTILIA, SAUROPTERYGIA)

Miguel MARX[2], Róbert-Zoltán SZÁSZ[1], Johan LINDGREN[3]

[1] Corresponding Author. Department of Energy Sciences, Lund University. PO.Box 118, S-22100, Lund, Sweden. Tel.: +46 46 222 0480, E-mail: robert-zoltan.szasz@energy.lth.se
[2] Department of Geology, Lund University. E-mail: miguel.marx@geol.lu.se
[3] Department of Geology, Lund University. E-mail: johan.lindgren@geol.lu.se

ABSTRACT

Plesiosaurs are secondarily aquatic reptiles with a fossil record that extends for over 140 million years, and their remains have been found in localities representing both warm, equatorial waters and cold, high-latitude environments. They are usually portrayed as a snake threaded through the body of a sea turtle. However, due to a general absence of preserved soft tissues, reconstructing the life appearance of particularly long-necked forms is anything but a straightforward task. Moreover, animals with such an oddly-shaped body are unlikely to survive in cold-water environments. To investigate the ability of these ancient marine reptiles to inhabit high-latitude waters, we examined the heat transfer in two virtually reconstructed plesiosaurs: one built according to conventional wisdom (i.e., with a long and narrow neck) and one equipped with a peripheral layer of insulating blubber. We compared several modelling approaches (gradually increasing the complexity of our approach) to assess their pros and cons. We also investigated the temperature distribution within the two body types and tested their hydrodynamic performance by simulating a cruising plesiosaur at a steady velocity. The results of our endeavours show that an insulating blubber layer must have been present to assure a suitable temperature distribution within the plesiosaur body when it inhabited cold water regions.

Keywords: blubber, heat transfer, plesiosaurs, temperature distribution

NOMENCLATURE

c_p	$[J/(kg\,K)]$	specific heat at constant pressure
L	$[m]$	length
MR	$[W/kg]$	metabolic rate
R	$[m]$	radius
T	$[K]$	temperature
t	$[s]$	time
q	$[W/m^3]$	heat source
α	$[m^2/s]$	thermal diffusivity
κ	$[W/(m\,K)]$	heat conductivity
ϕ	$[W/m^2]$	heat flux per unit area
ρ	$[kg/m^3]$	density

1. INTRODUCTION

Palaeontology is an interdisciplinary science that incorporates methods from various fields, including Computational Fluid Dynamics (CFD) [1]. Plesiosaurs (an iconic group of Mesozoic marine reptiles) have garnered some attention in recent years due to their peculiar body shape (long neck, turtle-like body, and four flippers), making them interesting subjects for CFD analyses [2, 3]. While some experiments have been conducted on their swimming performance [2, 3], little is known about their thermodynamic capabilities. Notably though, plesiosaur fossils have been recovered from high-latitude environments [4, 5], to suggest that they were capable of surviving in cold water regimes, something that likely would have necessitated some sort of insulation. Modern whales and even a species of sea turtle (*Dermochelys coriacea*; the Leatherback turtle) utilize a combination of high metabolism, large body size and blubber (a peripheral insulating tissue) to resist the effects of cold water. Blubber was apparently also present in at least some derived ichthyosaurs, another group of extinct marine reptiles [6]. Thus, we hypothesize that plesiosaurs, in which endothermy (warm-bloodedness) has been proposed [7, 8, 9], likewise employed some sort of peripheral tissue layer to enable life in cold water environments.

Modelling heat transfer in an animal poses a number of challenges. To start with, there are several body regions (e.g., muscles, the brain) with heat production that are hard to assess. The heat conductivity of tissues is also difficult to measure accurately, and the circulatory system that regulates heat transfer between different body parts is challenging to model [10]. Furthermore, if a species is extinct, then the required parameters have to be estimated from analogies in living animals.

Several models are available that replicate physical phenomena involved in heat transferring processes. However, by adding more details, the complexity of the models is amplified, in turn increasing both the required computing resources and human efforts to set-up and analyse the cases. Furthermore, when there are several unknown parameters, a model with increased complexity does not necessarily yield better results.

The purpose of this study is to compare modelling approaches at different levels of complexity to simulate a plesiosaur living in a cold water environment. We also test the effects of an added blubber layer on hydrodynamic drag.

2. METHODS

2.1. One-dimensional analysis

The simplest model assumes that the blubber layer thickness is small relative to the surface area of the skin. For such a condition, the heat transfer through the blubber can be presumed to be one-dimensional and thus assessable by Fourier's law of heat conduction (Eq. 1). Fourier's law can be used, e.g., to estimate the heat flux if the heat conductivity, blubber thickness and temperature difference between the surrounding environment and inner body temperature are known.

$$\phi = -\kappa \frac{\Delta T}{\Delta x} \tag{1}$$

For this initial model, blubber thicknesses and thermal conductivity values for various whale species were adapted from [10, 11] and references therein. Leatherback turtle blubber thickness was obtained from [12], and the thermal conductivity value was assumed to be 0.24 $W/(m\,K)$. The thermal conductivity value for human fat was acquired from [11].

2.2. Cylindrical model

Due to their overall elongate body form, the heat transfer characteristics of several marine animals were investigated by assuming a cylindrical shape. For example, Hokkanen [10] studied the temperature regulation of marine mammals using such a model. By neglecting end-effects, heat transfer can be evaluated in one (radial) direction. This model has the advantage of considering volume and surface area effects compared to the one-dimensional model presented in the previous sub-section.

Here, we estimated the heat flux transferred across a blubber layer with an inner radius R_{in} and outer radius R_{out} for an animal of length L using Eq. 2[13].

$$Q = 2\pi\kappa L \frac{\Delta T}{ln(R_{out}/R_{in})} \tag{2}$$

The heat flux was calculated using body dimensions of the modern Right whale [10, 14], Harbour porpoise [10, 15], Leatherback turtle [12, 16], and two plesiosaur models: one with a thin (1 cm) layer of blubber and a second geometry with a thicker (7 cm) layer of blubber; the required parameters being adopted from [10, 12, 14]. The total length of the plesiosaur cylinder model was set to 11.7 meters based on a reconstruction of the extremely long-necked elasmosaurid, *Albertonectes vanderveldei* (TMP 2007.011.0001).

2.3. 3D heat conduction

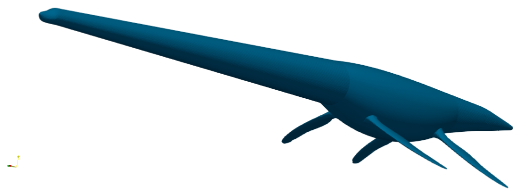
Heat conduction in an arbitrary three-dimensional geometry, which can include heat sources, can be investigated by solving the Poisson equation (Eq. 3). For this purpose, the laplacianFoam solver implemented in OpenFOAM v.2306 [17] was used.

$$\frac{\partial T}{\partial t} = \nabla \cdot (\alpha \nabla T) + \frac{q}{\rho\, c_p} \tag{3}$$

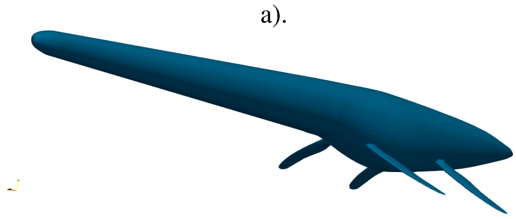
Two plesiosaur geometries were constructed using FreeCAD [18]: one without blubber and a second one coated in an insulating layer (based on actual blubber thicknesses of the Leatherback turtle [12]). The total length of the geometry was set to 11.7 meters. The thickness of the muscle tissues encasing the skeleton was approximated from comparisons with modern reptiles [19, 20, 21]. In the blubber-coated model, this peripheral tissue was added to all parts of the body except the flippers. Figure 1 shows a perspective view of the reconstructed geometry without (top) and with blubber (bottom).

The heat conductivity of blubber ($\approx$ 0.30 $W/(m\,K)$) is significantly lower than that of muscles ($\approx$ 0.57 $W/(m\,K)$) [10]; therefore, it is important to investigate the impact of regions with different heat conductivity on the resulting thermal balance. Furthermore, the heat source in the present case is due to metabolism, which depends on the activity level of the animal [22].

As a result, a third geometry was created to include simplified viscera (internal organs), arteries and a brain (which, for simplicity, hereafter is referred to as the 'organ region'). This simplified region is located inside the reconstructed plesiosaur body as shown in Figure 2. The division of the geometry into multiple regions primarily affects the mesh generation process. At the interfaces separating the regions, internal boundaries (referred to as 'baffles' in OpenFOAM terminology) are introduced. Additionally, the mesh is refined in these regions to better capture temperature gradients. From the solver's perspective, the entire mesh remains as a single computational domain; the purpose of the various regions is solely to assign different material properties.



a).



b).

Figure 1. Perspective view of the adopted plesiosaur geometry a) without and b) with blubber.

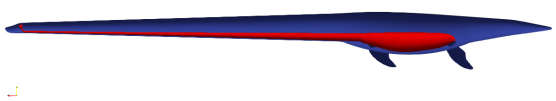


Figure 2. Side view of the adopted plesiosaur geometry with the internal region marked in red.

Tissues in the geometries were assigned thermal conductivity values reported for extant marine animals: muscle and organ region (0.57 $W/(m\,K)$) [10], and blubber (0.30 $W/(m\,K)$) [10, 11, 22]. In certain cases, the thermal conductivity of the blubber was adjusted to 0.57 $W/(m\,K)$ to replicate vasodilation of the circulatory system in the blubber tissue [23], since this is a known physiological adaptation of marine animals [10, 24]. A specific heat of 3.75 $kJ/(kg\,K)$ was applied to all tissues [22]. Two different metabolic rates were assigned to the models: a lower rate ($MR = 0.083\ W/kg$) corresponding to an inactive cold blooded animal, and an elevated value ($MR = 1.51\ W/kg$) typical of a Leatherback turtle exercising [24]. The heat-generating regions were either assigned to the entire body or only to the organ region. A metabolic rate was not, however, assigned to the blubber as this is not a heat generating tissue. A water temperature of $12\,^oC$ ($285.15\,K$) was chosen because it is comparable to what *A. vanderveldei* would have experienced [4]. Prescribing the water temperature directly on the skin neglects the thermal boundary layer formed in the water in the immediate vicinity of the body. As a consequence, the cooling effect of the water is over predicted. Nevertheless, according to the analysis in [10], the associated error likely is small.

2.4. Hydrodynamic force computations

In addition to heat balance, an added blubber layer affects the hydrodynamic forces acting on the body. In order to estimate this impact, two additional computations were performed. The flow around the two plesiosaur geometries was solved using the simpleFoam solver included in OpenFOAM v.2306. The pressure-velocity coupling is based on the SIMPLE algorithm (see, e.g., [25]). The computational domain extended from (-40 m, -25 m, -25 m) to (100 m, 25 m, 25 m) (Figure 3), the model being located at (0,0,0). The k-omega SST turbulence model developed by Menter [26, 27] was employed. The velocity magnitude was set to 1.5 m/s; i.e., close to the estimated cruising speed of other extinct marine reptiles [28]. A sensitivity study involving grids with 1.2, 3.0, 9.1, and 31.4 million cells indicated that 9.1 million cells were sufficient for our purposes.

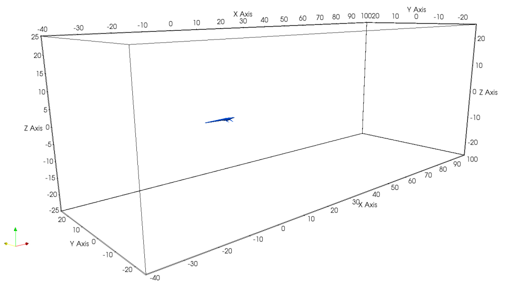


Figure 3. The computational domain used in our flow computations.

3. RESULTS

3.1. One-dimensional analysis

The effects of blubber thickness and the thermal conductivity of this tissue can be clearly seen in Figure 4. The proportionally thin layer of fat in a human allows for a larger heat flux relative to fluxes predicted for cetaceans that have both thicker blubber and lower thermal conductivity values. Notably, a plesiosaur inhabiting cold water environments would benefit from possessing a peripheral layer of insulating blubber.

3.2. Cylindrical model

Using Eq. 2, the total heat flux was estimated for two versions of the modelled plesiosaur (one with and one without blubber), as well as for a number of comparative extant tetrapods. The adopted parameters and the estimated heat fluxes for an assumed temperature difference of $\Delta T = 20\,K$ are summarized in Table 1.

A Northern right whale (a species that is well-adapted for life in cold waters) at approximately the same length as our modelled plesiosaur (~12 meters), but with a greater volume and blubber thickness, has a significantly lower heat flux compared to the plesiosaur version without blubber. An addition of seven

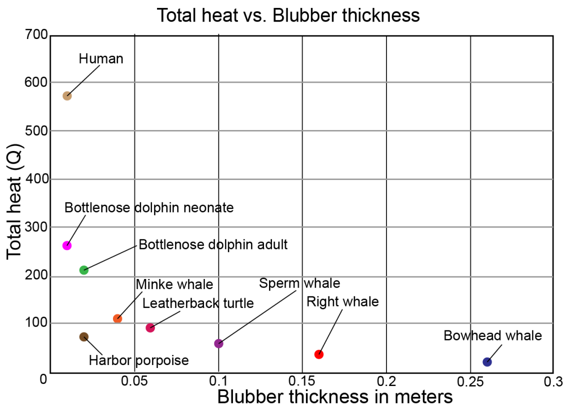


Figure 4. Predicted heat flux values for select extant tetrapods.

Table 1. Heat flux predicted for plesiosaurs and select modern animals.

Animal	R_{out} $[m]$	R_{in} $[m]$	L $[m]$	κ $[\frac{W}{mK}]$	Q $[W]$
Harbour porpoise	0.08	0.06	1.6	0.1	70
Right whale	1.45	1.29	12	0.3	3867
Leatherback Turtle	0.52	0.45	2	0.3	1093
Plesiosaur (no blubber)	0.43	0.42	11.7	0.3	18736
Plesiosaur (blubber)	0.49	0.42	11.7	0.3	2860

centimetres of blubber (which is similar to the blubber layer covering an adult Leatherback turtle) to the plesiosaur model significantly reduces the heat flux to an order of magnitude that is comparable to that of the other considered species. This reduction suggests that plesiosaurs would have benefited from an insulating blubber layer.

3.3. Three-dimensional heat transfer calculations

The purpose of these computations was to investigate the temperature within the plesiosaur body in a variety of scenarios. In all simulations, the water temperature was set to 12^oC. Moreover, based on experiments conducted on hatchling sea turtles [29], the lowest temperature that a plesiosaur probably could comfortably tolerate is 15^oC, whereas the highest temperature is 40^oC. Hence, the color scales used in the figures that follow span the 12–40^oC interval (i.e., 285.15–313.15 K) (Optimal temperatures are considered to be regions coloured either dark-blue or red).

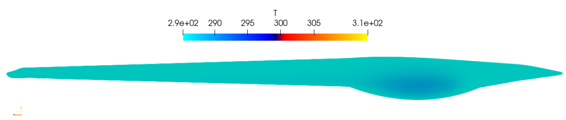
There are two important regions to consider. Firstly, due to the long and narrow neck, the water might cool the brain to dangerously low temperatures. Secondly, the torso has a low surface area-to-volume ratio, and thereby may be prone to overheating.

We investigated the impact of the main parameters (such as the metabolic rate, heat conductivity and presence of a peripheral blubber layer) on the temperature distribution in the body. Additionally, a case with three regions was set-up, where the effect(s) of enhanced heat transfer due to an introduced circulatory system was modelled, albeit in a simplified manner.

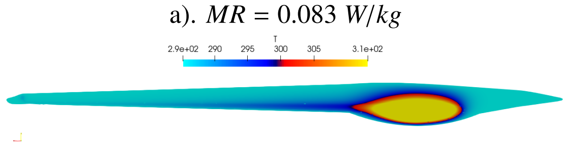
3.3.1. Influence of metabolic rate

The impact of metabolic rate on the temperature distribution was evaluated for a model without blubber. Two extreme cases were considered: one corresponding to an inactive individual ($MR = 0.083\ W/kg$) and one to a highly active animal ($MR = 1.585\ W/kg$). In both cases, the heat conductivity was set to $0.57\ W/(m\,K)$.

In the low activity case (Fig. 5), the temperatures across the body are suboptimal, the head and neck essentially being of the same temperature as the surrounding water. It is exceedingly unlikely that a plesiosaur would have survived under such conditions over an extended period of time. Conversely, in the high-activity case, the temperatures are closer to optimal in the brain region; however, in the torso they are too high for comfort.



a). $MR = 0.083\ W/kg$



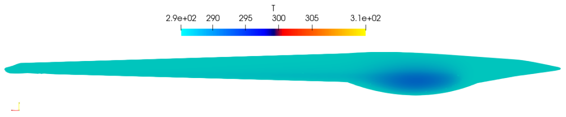
b). $MR = 1.585\ W/kg$

Figure 5. Temperature distribution in a plesiosaur model without blubber at low a) and high b) metabolic rates, respectively ($\kappa = 0.57\ W/(m\,K)$).

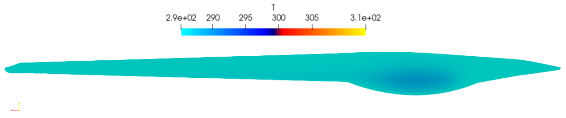
3.3.2. Influence of heat conductivity

The heat conductivity can vary not only between tissues, but also for the same tissue depending, e.g., on the influence of the circulatory system. Three values were considered. The lowest one ($\kappa = 0.30\,W/(m\,K)$) is typical for blubber [10], whereas the second one ($\kappa = 0.57\,W/(m\,K)$) is representative of muscles. The third considered value ($\kappa = 2.0\,W/(m\,K)$) was adopted to mimic improved heat transfer by convection effects caused by the circulatory system.

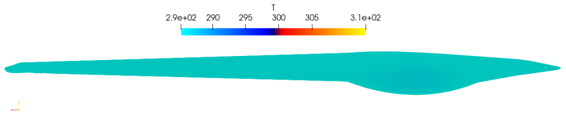
Figure 6 shows the temperature distribution for the low metabolic rate case. As expected, higher heat conductivity values lead to a more uniform heat distribution, but also to a stronger cooling effect in the torso region.



a). $\kappa = 0.30\ W/(m\,K)$



b). $\kappa = 0.57\ W/(m\,K)$



c). $\kappa = 2.00\ W/(m\,K)$

Figure 6. The impact of heat conductivity on the temperature distribution in the plesiosaur without blubber. $MR = 0.083\ W/kg$

3.3.3. Influence of blubber

The temperature distribution of a plesiosaur model covered by an external blubber layer was evaluated for a number of metabolic rates and heat conductivity values. In Figure 7, three parameter combinations are depicted.

Figure 7a shows the temperature distribution in a low metabolic rate case. Here, the heat conductivities are typical of muscle and blubber tissues. Compared to the corresponding setup of the case without blubber (Fig. 6a), it is noticeable that there are more favourable temperatures in most parts of the body. Nevertheless, in the brain region, the predicted temperatures are still very low.

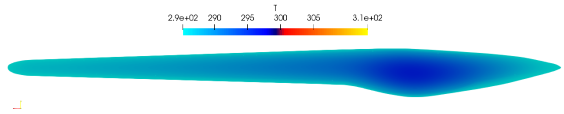
In the second case (Fig. 7b), the blubber heat conductivity is increased to $0.57\ W/(m\,K)$. Such a condition could mimic, e.g., improved heat transfer due to vessel dilatation. As expected, there is a stronger cooling effect in the body, but the temperatures are still more viable than in the case without blubber (Fig. 6b).

The third case is characterised by a high metabolic rate (Fig. 7c). Even if the blubber heat conductivity is set to higher values (typical of muscles), and therefore a more intense cooling is assumed, the predicted temperatures for most parts of the body remain too elevated, suggesting that the analysed metabolic rate is too high for the adopted blubber layer thickness.

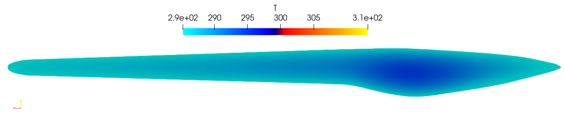
3.3.4. Three-region model

Heat transfer due to convection by blood is an important phenomenon that is difficult to account for. Due to the range of the involved scales, an explicit computation, even if restricted to the larger diameter parts of the vascular system would still be too demanding from a computational point of view. Accordingly, here we employed a simplified approach where the convective heat transfer by the vascular system is accounted for by an increased heat conductivity coefficient. According to Hokkanen [10], realistic blood flow rates are in the range of 1–4 $kg/(m^3\,s)$ which cause a heat transfer of approximately 4000–16000 $W/(m^3\,K)$. By dimensional analysis, the adopted heat conductivity coefficient ($\kappa = 2\ W/(m\,K)$) results in cross sectional area magnitudes of 125–500 mm^2, which are reasonable, given the size of the animal (the largest diameter of the torso is approximately 1 m).

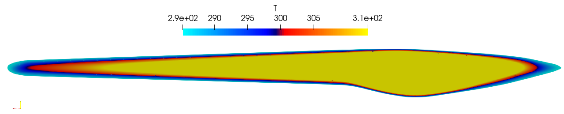
In the three-region set-up, the outermost region corresponded to blubber ($\kappa = 0.30\,W/(m\,K)$), the middle region muscle ($\kappa = 0.57\ W/(m\,K)$) and the inner region was adjusted for higher heat transfer rates ($\kappa = 2\,W/(m\,K)$). The metabolic rate was set to a high level ($MR = 1.51$); however, heat was generated only in the core region of the body. The resulting temperature distribution is shown in Figure 8. One may notice the relatively strong heat transfer in the inner region (compare, e.g., with Fig. 5b), which results in more favourable temperatures in the brain region. In the torso, the temperatures remain elevated, to suggests that an added blubber layer likely is unnecessary in this region.



a). $MR = 0.083\ W/kg$, $\kappa_{muscle} = 0.57\ W/(m\,K)$, $\kappa_{blubber} = 0.30\ W/(m\,K)$



b). $MR = 0.083\ W/kg$, $\kappa_{muscle} = 0.57\ W/(m\,K)$, $\kappa_{blubber} = 0.57\ W/(m\,K)$



c). $MR = 1.51\ W/kg$, $\kappa_{muscle} = 0.57\ W/(m\,K)$, $\kappa_{blubber} = 0.57\ W/(m\,K)$

Figure 7. Impact of blubber layer on the temperature distribution.

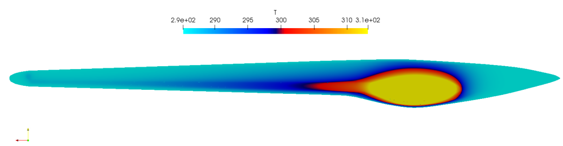


Figure 8. Temperature distribution in the three-region model.

3.3.5. Summary of the three-dimensional cases

A quantitative summary of the three-dimensional cases is shown in Figure 9, where the recorded temperatures are plotted at two monitoring points: the first one located near the brain and the second one located close to the centre of the torso. For reference, the inferred minimum and maximum viable temperatures are also plotted. There are several cases where the torso temperature is within viable limits. Conversely, there is only one case where the brain temperature is suitable for survival. However, in that particular case the torso temperature significantly exceeds the upper allowable limit. Nevertheless, there are other cases where the brain temperature is close to the lower limit. With slightly higher metabolic rates than the minimum value and with less insulation in the torso region, both the brain and torso temperatures should be within viable limits.

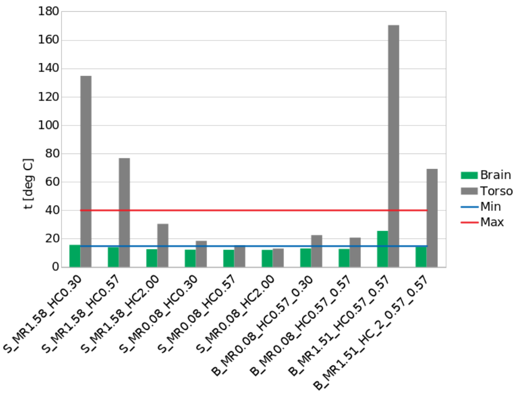


Figure 9. Summary of the observed temperatures in monitoring points located in the brain and torso areas. The labels along the horizontal axis indicate each case. 'S' stands for cases without blubber, 'B' for the ones with an extra blubber layer. The number after 'MR' shows the metabolic rate, while the numbers after 'HC' indicate the heat conductivities.

Models with increased complexity lead to longer computation times. Table 2 summarizes the typical execution times to convergence when running 16 parallel processes on an AMD Ryzen 9 7950X3D 16-core processor. As expected, execution time increases significantly with higher mesh resolution. Moreover, higher thermal conductivity values result in faster convergence, suggesting that longer timesteps could have been used for the lower conductivity cases. Nevertheless, the required computing times are relatively short compared to the more complex CFD simulations, and the impact of sub-optimal timestep selection is considered to be negligible.

Table 2. Typical CPU times.

Case type	MR $[\frac{W}{kg}]$	κ $[\frac{W}{mK}]$	N_{cells} $[\cdot 10^6]$	t_{conv} $[s]$
No blubber	1.58	0.30	1.9	509
No blubber	1.58	0.57	1.9	314
No blubber	1.58	2.00	1.9	134
No blubber	0.083	0.30	1.9	430
No blubber	0.083	0.57	1.9	307
No blubber	0.083	0.30	1.9	137
With blubber	1.51	0.57 0.57	3.8	5260
With blubber	0.83	0.57 0.30	3.8	6434
With blubber	0.83	0.57 0.57	3.8	5496
Three regions	1.51	2.0 0.57 0.25	16.2	35036

3.4. Flow computations

These computations were performed to evaluate the impact of the added blubber layer on hydrodynamic drag. Figure 10 shows the pressure distribution along the surface of both the original (top) and blubber-coated (bottom) geometries. No significant difference can be seen in the pressure distributions, which is quantitatively reflected in a tiny (1%) increase of the drag force from 100.92 (original geometry) to 101.93 N (with blubber). This minor rise indicates that the addition of blubber did not lead to any significant penalty in hydrodynamic performance of the selected body shapes.

4. DISCUSSION AND SUMMARY

The impact of an added blubber layer on the heat balance of a plesiosaur (marine reptile) was investigated using numerical models of varying complexity. The simple one-dimensional and cylindrical models predicted a need for an extra insulating layer to reduce the simulated heat fluxes to levels observed in modern animals living in cold-water environments.

The three-dimensional computations further showed that a peripheral insulatory layer was a necessity to achieve a viable internal body temperature. Without an extra blubber layer, the predicted internal temperatures were lethally low for animals at low metabolic rates. Conversely, when a high metabolic rate was introduced, the predicted core temperatures were abnormally high. Nevertheless, as a consequence of the long and slender neck, the temperatures in the brain region remained too low for a real animal.

The addition of a layer of blubber significantly improved the viability chances for individuals with low metabolic rates. For a highly active animal, the added insulation turned out to be too much; the predicted temperature levels exceeded the viable limits in the majority of the body. This suggests that,

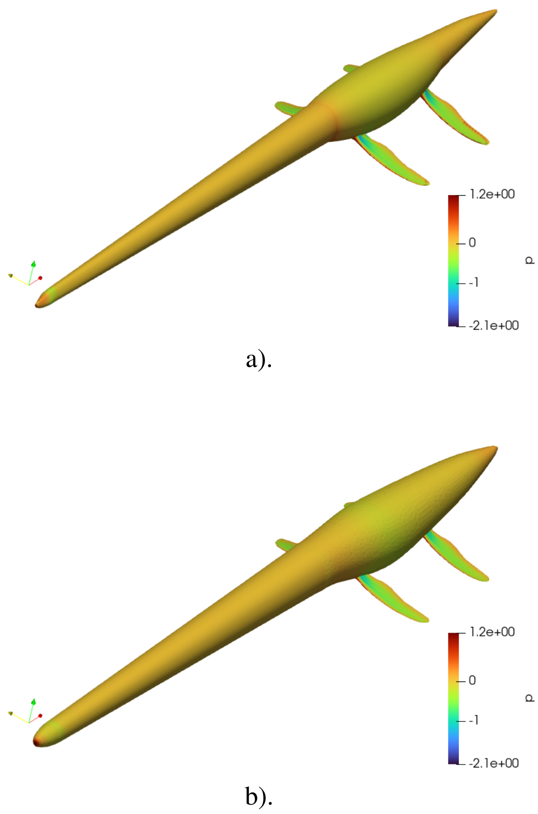


Figure 10. Pressure distribution along the body for a case a) without and b) with blubber

in reality, the thickness of the blubber was probably rather thin in certain regions of the body.

There are several inherent uncertainties in the presented predictions. First of all, there is no widely accepted overall body shape for a plesiosaur; our geometry is a simplification of the general body design, based on a real specimen [30]. The thermodynamic properties of tissues were further approximated based on data from modern animals. Most of these vary between organs and tissues, and sometimes even for the same tissue. Nevertheless, our sensitivity study adopted realistic extreme values. Thus, real-case scenarios are expected to occur within the predicted limits.

The predictions also significantly simplified the heat generation within the body. For better accuracy, several heat generation zones of different magnitudes would be needed. Unfortunately, the information required to set up such simulations is, at present, scarce.

Another limiting factor in the accuracy of our predictions is the difficulty to account for heat convection by the vascular system. A simple model was adopted to account for this phenomenon, but more advanced modelling approaches are expected to substantially improve the accuracy of this parameter.

The adoption of a constant temperature boundary condition implies that the cooling effect of the surrounding water is overpredicted by our models. Although the published literature suggests that this effect is small, it will be verified in the future by a conjugate heat transfer simulation.

We conclude that even if there are unavoidable sources of error in the predictions presented in this paper, our results nonetheless suggest that the currently widely accepted plesiosaur body shape needs to be refined by the addition of a peripheral blubber layer.

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