

Research



Cite this article: Muscutt LE, Dyke G, Weymouth GD, Naish D, Palmer C, Ganapathisubramani B. 2017 The four-flipper swimming method of plesiosaurs enabled efficient and effective locomotion. *Proc. R. Soc. B* **284**: 20170951.
<http://dx.doi.org/10.1098/rspb.2017.0951>

Received: 2 May 2017
 Accepted: 24 July 2017

Subject Category:

Morphology and biomechanics

Subject Areas:

biomechanics, evolution, palaeontology

Keywords:

Mesozoic, marine reptiles, flapping, wake, anatomy, hydrodynamics

Author for correspondence:

Luke E. Muscutt
 e-mail: luke@muscutt.org

Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.3846208>.

The four-flipper swimming method of plesiosaurs enabled efficient and effective locomotion

Luke E. Muscutt¹, Gareth Dyke², Gabriel D. Weymouth¹, Darren Naish³, Colin Palmer⁴ and Bharathram Ganapathisubramani¹

¹Engineering and the Environment, University of Southampton, Southampton SO17 1BJ, UK

²Evolutionary Zoology, University of Debrecen, 4032 Debrecen, Hungary

³Ocean and Earth Science, University of Southampton, Southampton SO14 3ZH, UK

⁴School of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK

GD, 0000-0002-8390-7817

The extinct ocean-going plesiosaurs were unique within vertebrates because they used two flipper pairs identical in morphology for propulsion. Although fossils of these Mesozoic marine reptiles have been known for more than two centuries, the function and dynamics of their tandem-flipper propulsion system has always been unclear and controversial. We address this question quantitatively for the first time in this study, reporting a series of precisely controlled water tank experiments that use reconstructed plesiosaur flippers scaled from well-preserved fossils. Our aim was to determine which limb movements would have resulted in the most efficient and effective propulsion. We show that plesiosaur hind flippers generated up to 60% more thrust and 40% higher efficiency when operating in harmony with their forward counterparts, when compared with operating alone, and the spacing and relative motion between the flippers was critical in governing these increases. The results of our analyses show that this phenomenon was probably present across the whole range of plesiosaur flipper motion and resolves the centuries-old debate about the propulsion style of these marine reptiles, as well as indicating why they retained two pairs of flippers for more than 100 million years.

1. Introduction

Plesiosaurs were a diverse lineage of secondarily aquatic marine reptiles that attained a near global distribution in the world's oceans during the Mesozoic, 220–66 million years ago. Plesiosaurs were unique because they evolved four large wing-like flippers almost always identical in size and form; all other animals that swim using lateral flapping appendages (e.g. turtles and sea lions) use their forward pair primarily for propulsion and the hind pair for manoeuvring, and this results in markedly different morphologies [1–3]. Thus, the almost identical morphology of the fore and hind flippers of plesiosaurs poses the question of *why* they adopted such a different approach to all other living and extinct vertebrates and maintained it for such a long time.

There has been a great deal of speculation over how plesiosaurs swam, dating back to the 1950s. Early work [4] suggested that these reptiles used a single forward-and-backward antero-posterior rowing stroke, while subsequent studies [1,5,6] have argued that a dorso-ventral 'underwater flight' flapping movement was more likely, at least for the fore flippers, although a rowing movement for the hind pair has also been proposed. Some combination of these two patterns (i.e. antero-posterior 'rowing' versus dorso-ventral 'underwater flight') remains the general consensus [2,6–11], but this has never been tested quantitatively, either via numerical modelling or physical experiments.

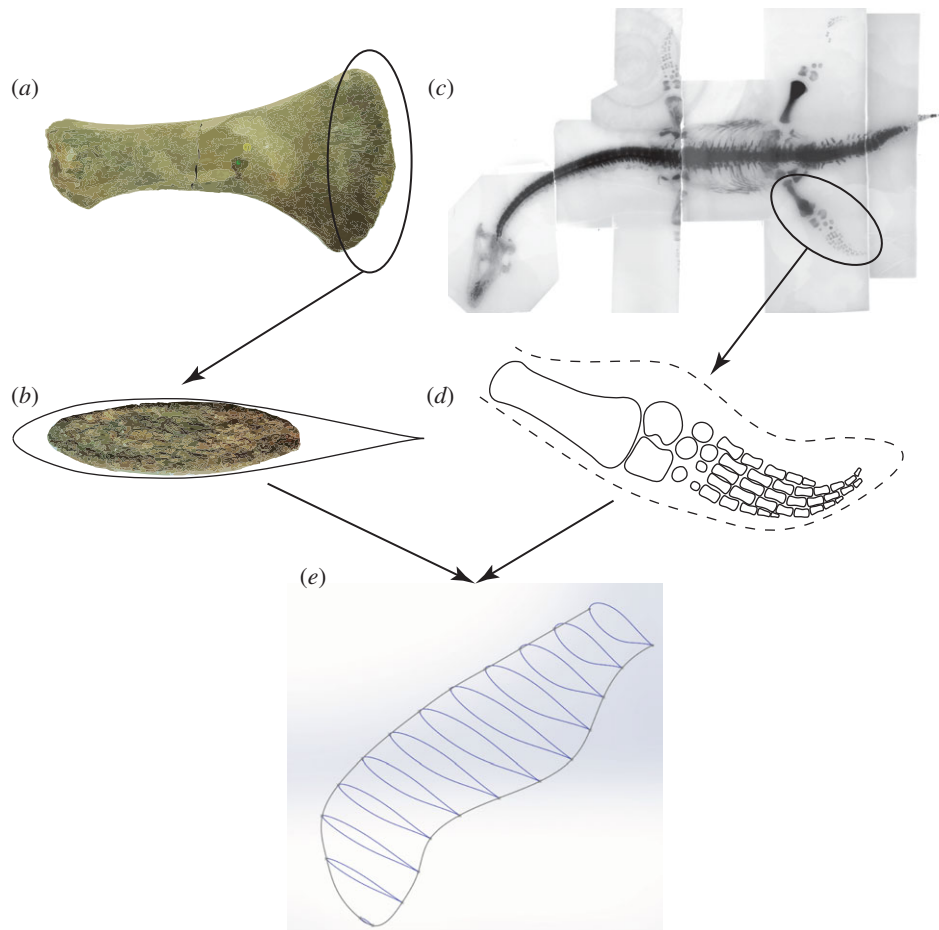


Figure 1. Methodology used to obtain flipper geometry. (a) X-ray of the Collard plesiosaur full fossil. (b) Drawing of the planform of the hind flipper of the Collard plesiosaur showing estimated soft tissue outline. (c) Femur of *Muraenosaurus leedsii* NHMUK R2428. (d) Distal end of the femur of *M. leedsii*, with surrounding Eppler E387 profile. (e) Final flipper geometry in isometric view. (Online version in colour.)

Apart from speculations about individual flipper movement patterns, previous work has also focused on the problem of how plesiosaurs used their *two pairs* of flippers in relation to each other (i.e. the phase difference, ϕ , between the fore and hind flippers). This has been referred to as the ‘four-wing problem’, and in the absence of living analogues has necessarily been speculative, leading to various hypotheses: plesiosaurs moved their flipper pairs out-of-phase with one another [7] (i.e. one pair moved up while the other moved down, $\phi = 180^\circ$ to maintain continuous locomotion); they moved the two pairs in-phase $\phi = 0^\circ$ (i.e. up and down together [10]); they employed a phase difference that was neither in-phase or out-of-phase, leading to a ‘porpoising’ motion [12] $\phi \approx 90^\circ$ or 270° ; or they flapped their hind flippers with a small amplitude, or held them stationary and used them just for steering [13].

It is possible that a mixture of the above locomotory gaits was used by plesiosaurs: living animals use different gaits at different times, as one propulsion strategy may not provide optimum performance in all circumstances [14,15]. For example, sometimes an animal requires a high-speed ‘sprint’ gait for catching prey or evading predators, while at other times it will employ a high-efficiency ‘cruising’ gait.

The hypothesis tested in this study is that the thrust and efficiency of the hind flippers should be influenced by the phase and spacing between the fore and hind flippers because of the way the hind flippers interact with the wake of the fore flippers. This is because a flapping flipper, or

wing, creates a vortex on its leading edge when moving up, and another vortex of opposite rotation when moving down. At the top and bottom of the flapping stroke, these vortices separate from the wing and are shed downstream to create two lines of vortices of alternating sign behind the wing, known as a ‘vortex street’ [16–18]. Thus, if another wing is present behind the first, these vortices and induced velocities will affect the performance (thrust and efficiency) of the hind wing [19–27]; this effect is known as performance (or thrust or efficiency) augmentation, and is strongest for certain spacing and phase differences between the wings, shown by a variety of studies [19–30], including on dragonfly flight [28,29] and the flocking of migrating birds [30].

In this study, we examine the performance augmentation mechanism in plesiosaur propulsion, and quantify the conditions when these reptiles would have benefitted from this mechanism along with the magnitude of the resultant hydrodynamic advantages. We examine the performance and utility of the four-flipper propulsion system across a wide range of conditions to establish the most efficient and effective ways to use four flippers, as well as the extent of the possible benefits under different circumstances. In the absence of other evidence, we must assume that natural selection acted on plesiosaur locomotion to enable the most efficient, or close to the most efficient, movement pattern. If this were otherwise then it is unlikely that the four-flipper system would have been maintained over such a long evolutionary time-span.

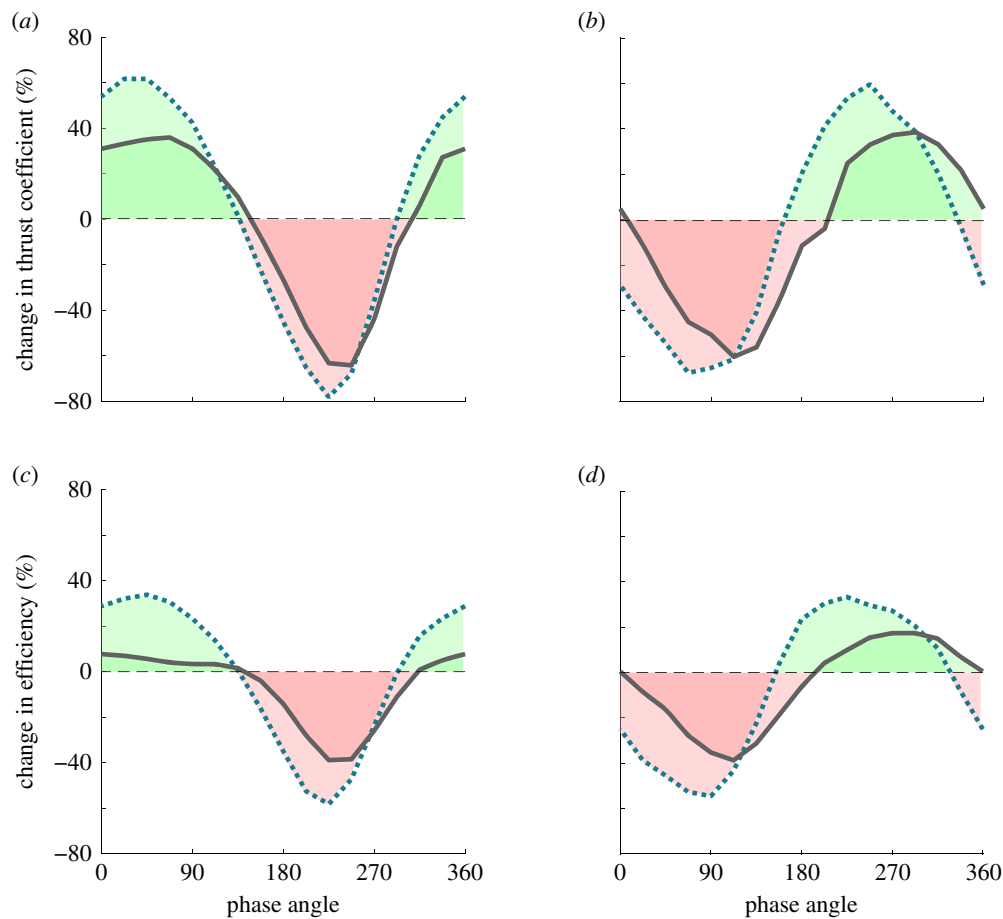


Figure 2. Modification of hydrodynamic performance of hind flipper owing to interaction with the fore flipper. Percentage changes in thrust coefficient of the hind flipper (C_T^*) for (a) low flapping frequency ($St = 0.18$) and (b) high flapping frequency ($St = 0.36$). Percentage changes in efficiency of the hind flipper (η^*) for (c) low flapping frequency ($St = 0.18$) and (d) high flapping frequency ($St = 0.36$). These results are at a flipper-spacing of three chord lengths, and show the augmentation for 16 phases between the fore and hind flippers, and for two maximum angles of attack (α_{\max}). Solid grey curves are $\alpha_{\max} = 20^\circ$ and dotted green curves are $\alpha_{\max} = 10^\circ$. Each curve is normalized by the corresponding value of a single flipper, and the dashed lines at 0% represent the single-flipper values. Green and red shaded areas show the parameter combinations that yield improved or degraded hind flipper performance, respectively. The curves show that both the thrust and efficiency of the hind flipper are strongly dependent on the phasing between the flippers, and can be up to as much as 60% larger than the single flipper. The augmentation is largest for the case with the lowest maximum angle of attack. The phases that increase/decrease the thrust are minimally affected by the maximum angle of attack. (Online version in colour.)

Our results provide the first clear answer to the long-running debate about *how* and *why* plesiosaurs used their unique tandem flippers and, more generally, advance our knowledge of plesiosaur locomotion and propulsion effectiveness.

2. Material and methods

We adopted a multi-stage approach in this study combining fossil evidence, anatomical observations of a number of extant flipper-propelled analogue species and engineering principles to (1) determine the likely kinematics of the flippers of a representative plesiosaur; (2) reconstruct plesiosaur flipper geometry; and (3) construct a ‘robotic plesiosaur’ that flapped two plesiosaur flippers over a range of parameter combinations including phase differences between fore and hind flippers, flapping frequencies, flapping amplitudes and flow speeds, to identify the hydrodynamic characteristics of the four-flipper system across the parameter space available to plesiosaurs. To enable development of the robotic plesiosaur used in our experiment, the kinematics and geometry of each flipper were determined. The kinematics are dependent on the range of motion, likely stroke pattern, and limitations of the

mechanical system, while geometry is dependent on the shape of the fossilized bones, plus estimated soft tissue. Two different fossils were used to obtain the range of motion and the flipper geometry.

The specimen used to obtain the range of motion was the cryptoclidid *Muraenosaurus leedsii* held in the collections of the Natural History Museum, UK (NHMUK R2428), from the Middle Jurassic Oxford Clay Formation, Leicestershire, UK [31]. This specimen was selected because of its three-dimensionally preserved girdles and propodials, from which the approximate ranges of motion of the flippers were determined. These were compared with and averaged with the ranges estimated by previous researchers [1,10,13]. Through this method the dorso-ventral range was observed to be far greater than the antero-posterior range. Through comparison with extant analogue species, the stroke pattern of the plesiosaur was determined to be a lift-based motion similar to a turtle, penguin or sea lion, and we assume that the plesiosaur would be capable of implementing the same kinematics to both flippers.

Constructing a wing or flipper requires two geometries: the *profile* and the *planform*. The *profile* is the cross-section of the flipper, and the distal end of the propodial of the *Muraenosaurus* specimen was used as a basis for this (figure 1a). An Eppler E387 hydrofoil profile was found to match this satisfactorily (figure 1b).

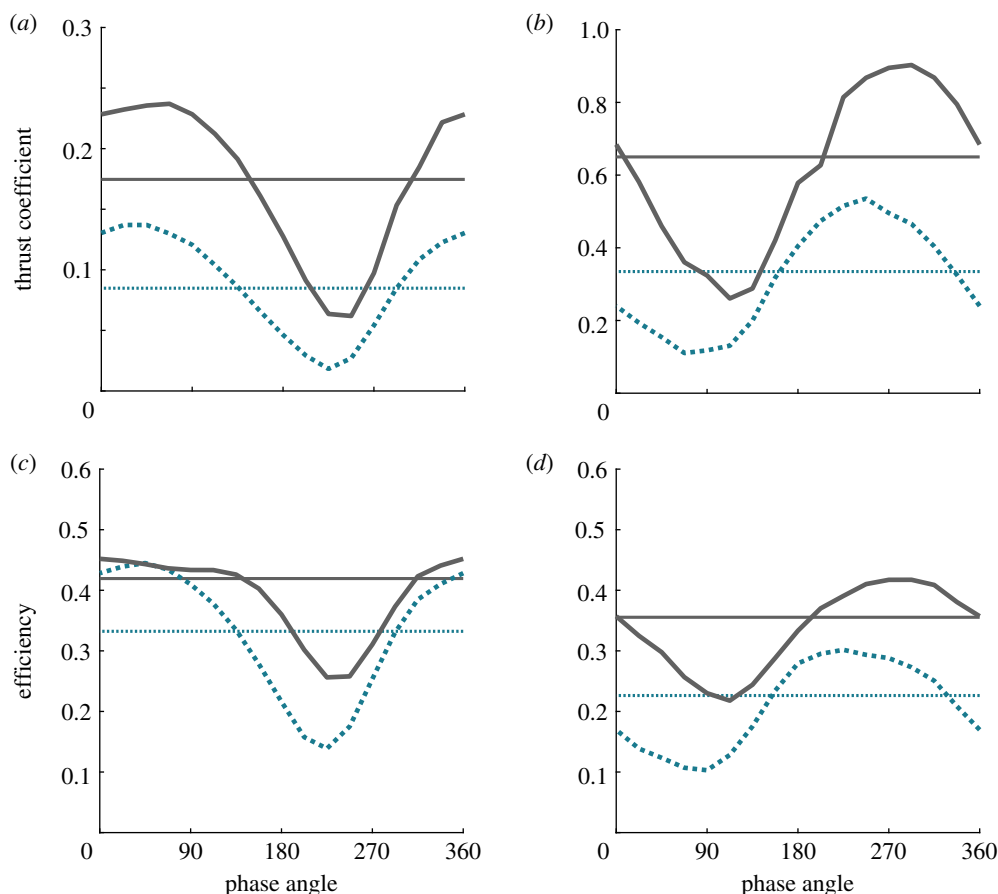


Figure 3. Modification of hydrodynamic performance of hind flipper owing to interaction with the fore flipper. Absolute thrust coefficient of the hind flipper (C_T) for (a) low flapping frequency ($St = 0.18$) and (b) high flapping frequency ($St = 0.36$). Efficiency of the hind flipper (η) for (c) low flapping frequency $St = 0.18$ and (d) high flapping frequency $St = 0.36$. These results are at a flipper-spacing of three chord lengths, and show the augmentation for 16 phases between the fore and hind flippers, and for two maximum angles of attack. Solid grey curves are $\alpha_{\max} = 20^\circ$ and dotted green curves are $\alpha_{\max} = 10^\circ$. (Online version in colour.)

The *planform* was based on the Collard plesiosaur from the Lower Liassic Kilve shales of Somerset, UK, Somerset County Museum (TTNCM) 146/2003, an as-yet-undescribed member of Rhomaleosauridae [32]. This specimen was selected because one of the hind flippers has all of its osteological elements preserved (figure 1c), along with the fact that we can be certain that it has not been tampered with during preparation, unlike many of the Victorian specimens from NHMUK, for example. The flipper planform geometry was found by combining the geometry of the bones in the flipper of the Collard plesiosaur with an estimation of the amount of soft tissue on the leading and trailing edges, derived using a novel method involving medical X-rays of extant analogue species (fully described in the electronic supplementary material). This yielded the flipper planform shown in figure 1d.

Once both the profile and the planform were determined they were combined to give the final flipper geometry (figure 1e). The flippers were 3D printed in rigid plastic, with internal cavities to allow the injection of dye for flow visualization. The flippers each had a span of 400 mm, a maximum chord length of 130 mm and an average chord length of around 100 mm, and were larger than the flippers of the Collard specimen at a scale of approximately 1.3. This size ensured that the forces on the flippers were as large as possible to reduce force measurement error, while not being so large as to cause undesired blockage effects in the flume tank.

Certain simplifications of the stroke pattern were necessary to enable reproduction of the motion. Symmetrical simple harmonic motion in both heave (dorso-ventral) and pitch (pronation-supination) was used, and antero-posterior motion was neglected. The body, neck and tail of the plesiosaur were not

modelled and only two flippers were used (one fore and one hind) because we were only concerned with straight line swimming during which the left and right flippers flap synchronously, and because plesiosaurs were symmetric about their sagittal plane.

The flapping frequency was varied to give Strouhal numbers ($St = fA/U$, where f = flapping frequency, A = flapping amplitude and U = swimming speed) of 0.18 and 0.36, which are around the upper and lower bounds of the range reported for the great majority of extant animals that use flapping propulsion [14,33,34]. Two maximum angles of attack $\alpha_{\max} = 10^\circ, 20^\circ$ were used at each of the Strouhal numbers, as the maximum efficiency of flapping foils occurs between these values [17]. The flapping phase angle between the flippers was independently varied. All experiments were conducted in a flume tank in the Aerodynamics and Flight Mechanics Department at the University of Southampton, UK. The working section of the tank had a cross-section of 0.8 m by 1.2 m. A motion control 'robotic plesiosaur' system was constructed on the top of the tank which provided two degrees of motion to each flipper: heave and pitch. The motion of the axes was provided by stepper and servo motors, with gearboxes to match the required angular velocity and torque. Motion control and data acquisition was achieved using a National Instruments cRIO system and a PC running LabView. The forces were measured using a custom-made load-cell assembly which measured forward force (thrust), side force and pitching moment at an acquisition frequency of 200 Hz. The flow visualization images were taken with a 16 megapixel FujiFilm X-T1 camera at a focal length of 18 mm. Most data were collected at a flow speed of 0.22 m s^{-1} giving a Reynolds number (Re) of 22 000, although some

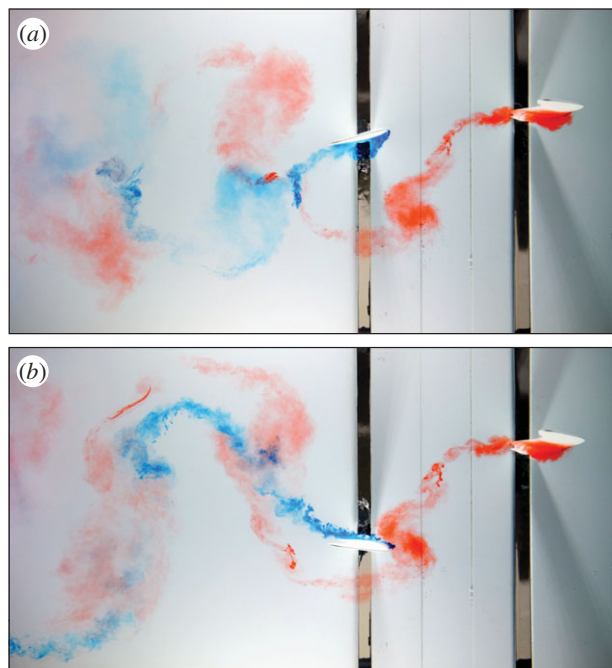


Figure 4. Flow visualization of flippers. (a) High-thrust interaction. (b) Low-thrust interaction. The water is moving from right to left, and the fore foil is near the top of its flapping cycle, commencing the down-stroke in both images. Red dye is injected from the fore flipper, blue dye from the hind flipper. In the high-thrust interaction (a), the hind flipper weaves in between the vortices that have been shed from the fore flipper, and the red and blue vortices merge to create a strong and thin jet behind both flippers. In the low-thrust interaction (b), the hind flipper intercepts the vortices that have been shed from the fore flipper, which inhibits the formation of the hind-flipper (blue) vortices and creates a lower velocity, diffuse spread-out wake behind both flippers. Videos of these flow visualizations are given in the electronic supplementary material.

tests were performed at a flow speed of 0.44 m s^{-1} , giving a Re of 44 000. This was based on the average chord length of the flipper of 0.1 m. ($Re = \rho U c \mu^{-1}$, where ρ is fluid density, U is flow speed, c is average chord length and μ is dynamic viscosity of the fluid.)

Together the two plesiosaur specimens enabled the design of the experimental apparatus, although we recognize that they may not be representative of anatomical diversity across Plesiosauria as a whole, and that further tests are required in order to generalize the findings across the entire clade. The geometry of the fore and hind flippers of the Collard plesiosaur are the same (fore/hind flipper area ratio = 1), so identical geometry for both flippers was used in the experiment. Although some plesiosaurs have larger fore flippers than hind flippers (or vice versa), the case of identical flippers is representative of the clade as a whole. Furthermore, while we endeavoured to reconstruct flippers with the greatest fidelity, it is important to note that the fundamental flow phenomena that result in the propulsive performance reported herein are relatively insensitive to either the details of the outline or the flexibility of the flippers. The vortex shedding and the interaction between the leading and trailing flippers are apparent in two-dimensional simulations [27], which demonstrate their independence from planform shape. Flexibility has been shown to affect the details of flapping foil propulsion, but not the basic flow patterns [35]. Therefore, the primary source of performance augmentation is expected to be the spacing between flippers and the phase difference between the motion of the flippers. Other details such as flipper planform, shape and flexibility are expected to be secondary factors that can attenuate or amplify the primary effect.

3. Results and discussion

The results of this study show that hind-flipper thrust performance is strongly affected by the phase ϕ between the flippers at both values of Strouhal number and maximum angle of attack (figure 2a,b). At the optimum phase the thrust was increased by 60% and the efficiency by 40% compared with an isolated single flipper (that had the same kinematics). Large decreases in performance were also observed for other phases. These results suggest that plesiosaurs would have experienced substantial thrust and efficiency augmentation by using all their limbs during locomotion, but would have needed to alter the phasing to achieve the highest thrust and/or efficiency for different swimming conditions.

Considering the absolute values of thrust and efficiency (figure 3), further insights can be gained regarding the likely kinematics of plesiosaur locomotion. For both values of the maximum angle of attack the efficiency is greatest for $St = 0.18$, while the thrust coefficient is greatest for $St = 0.36$. This implies that plesiosaurs would have used a lower Strouhal number for a slow, efficient ‘cruising’ gait, but a higher Strouhal number for a fast ‘sprint’ gait.

This discussion shows that the performance of the flippers is dependent on the phase. The fluid–mechanical interactions that facilitate this result are examined through flow visualization using dye. This reveals that when improved performance is achieved, the hind flippers weave in between the vortices shed by the fore flippers (figure 4a). At the high Strouhal number the highest performance augmentation occurs at a phase difference between the two flippers of 270° , meaning that the hind flipper was lagging behind the fore flipper slightly. This phase difference would have been necessary to ensure that the hind flipper was able to take advantage of the wake shed from the fore flipper. At the lower Strouhal number the peak performance augmentation occurs at a phase difference of around 45° which means that the hind flipper was leading the motion. These different phases that are required to produce maximum thrust and efficiency at different Strouhal numbers show that plesiosaurs would have needed to adjust their phase depending on the swimming speed and frequency, and thus there is not one phase that would be optimum for all swimming conditions.

When the phase difference was 180° different from the peak augmentation, the thrust and efficiency were greatly reduced. At this phase difference, the hind flipper intercepts the vortices from the leading flipper (figure 4b), thereby negating any hydrodynamic advantage. This clearly demonstrates the overriding importance of flapping phase on the effectiveness of propulsion by tandem flippers, and the necessity of the plesiosaur to accurately control the relative motion of the fore and hind flipper pairs.

The flipper spacing of the above experiments was based on the Collard specimen, as was the flipper geometry. However, different flipper morphologies and spacings are present in different plesiosaur lineages [36–38]. Experiments were, therefore, conducted at a spacing of seven flipper chord lengths, which is much larger than any plesiosaur in NHMUK from personal measurements. At a flipper spacing of seven chord lengths the maximum thrust augmentation is unchanged at 40% (figure 5a,b) although as would be expected, the phase difference that yields the optimum

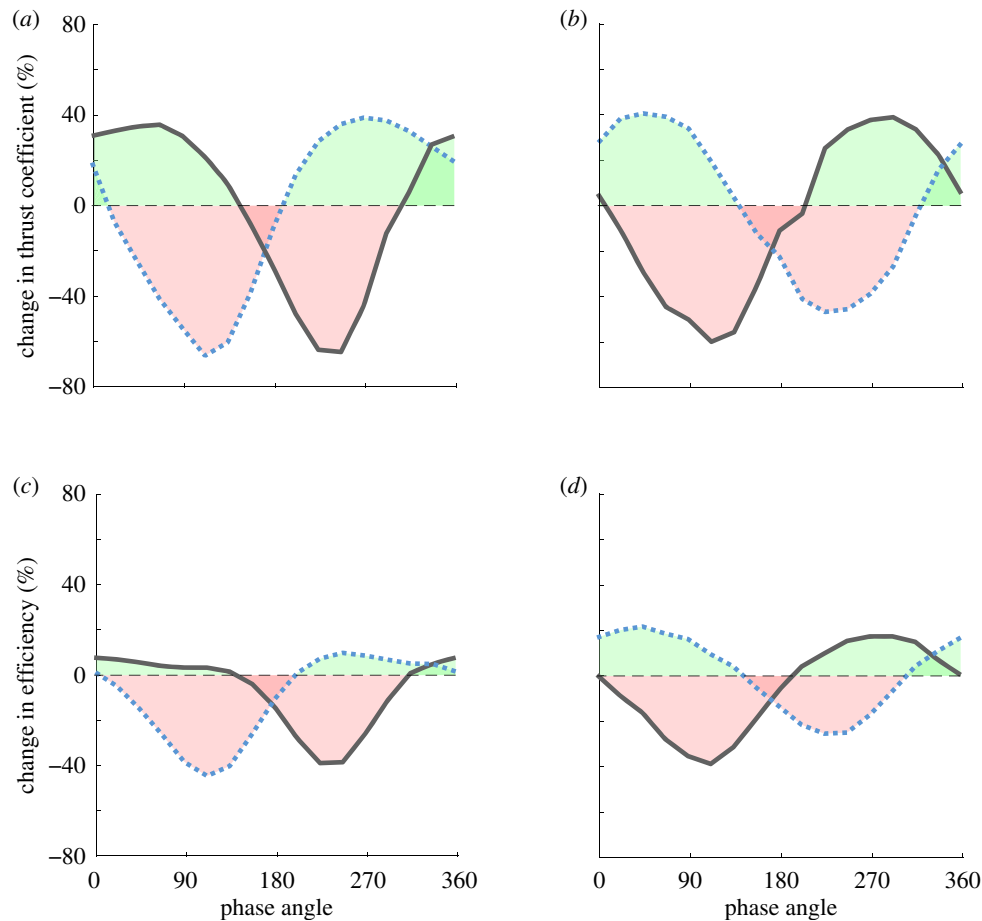


Figure 5. Effect of spacing on hydrodynamic performance of hind flipper owing to interaction with the fore flipper. Percentage changes in thrust coefficient of the hind flipper (C_T^*) for (a) low flapping frequency ($St = 0.18$) and (b) high flapping frequency ($St = 0.36$). Percentage changes in efficiency of the hind flipper (η^*) for (c) low flapping frequency ($St = 0.18$) and (d) high flapping frequency ($St = 0.36$). All curves have a maximum angle of attack of $\alpha_{\max} = 20^\circ$. Solid grey curves are data at three chord lengths, the same data as the black curves in figure 2, and dotted blue curves are data at seven chord lengths. Red/green colour coding same as before. The amount of augmentation is similar for both spacings. This implies that all plesiosaurs would have been able to benefit from the increased performance of the hind flipper. Note that the phase that gives the best performance is different for each spacing, showing that there is not one motion that is best for all conditions, and that plesiosaurs with different flipper spacings would have different optimum motions. (Online version in colour.)

thrust changes. The maximum efficiency is also little changed (figure 5b,c). As the flipper spacing increases, a reduction in the augmentation is to be expected because the vortices shed from the fore flippers lose strength due to viscous diffusion as they advect downstream, so the further back the hind flippers are, the weaker the interaction is between the flippers and the wake. However, our results show that the magnitude of the augmentation at both seven and three chord lengths spacing is almost indistinguishable, showing that most—if not all—plesiosaurs would have experienced marked increases in thrust and/or efficiency from tandem-flipper interactions, provided they had the appropriate phase difference in their kinematics.

Previous estimates of plesiosaur swimming speeds [39,40] are higher than the speed at which our experiments were conducted, so some cases were run at twice that flow velocity, 0.44 m s^{-1} , to determine the sensitivity of the augmentation levels to flow speed. Data show (figure 6a,b) that thrust and efficiency augmentation is similar for both speeds, demonstrating that our results can be generalized to cover the likely range of plesiosaur swimming speeds.

The performance of the hind flipper when held stationary at a zero angle of attack behind a flapping fore flipper was also investigated as previous studies have claimed that the hind flippers may have only been used as ‘rudders’. These experiments show that when the fore flipper is flapping

with a high Strouhal number and large amplitude $St = 0.36$, $A = 4$, the hind flipper can produce a small amount of thrust, owing to a favourable interaction of the flipper with the vortices shed from the fore flipper (figure 6c). Although it appears that thrust can be produced with no hind flipper energy input, for forces to be produced in this way it must be held in a fixed position, which would require muscle power. Furthermore, all the other stationary hind flipper cases we tested produced drag or zero net force, so it is unlikely that the plesiosaur would use this strategy, as their hind flippers would be a hindrance if used in this way.

For the first time we illustrate the most efficient and effective way for plesiosaurs to move their flippers. In the absence of other evidence, we assume that natural selection acted on plesiosaur locomotion to enable the most efficient, or close to the most efficient, movement pattern or this four-flipper system would have not have been maintained over such a long evolutionary time-span. Our experiments show that (1) plesiosaurs likely used both pairs of flippers for continuous forward propulsion; (2) the hind flippers could produce up to 60% more thrust and were up to 40% more efficient than in the absence of the fore flippers; (3) this strong performance augmentation effect was present over the entire range of likely plesiosaur swimming conditions and morphologies; (4) given a particular spacing and flapping frequency, these large increases in thrust and efficiency

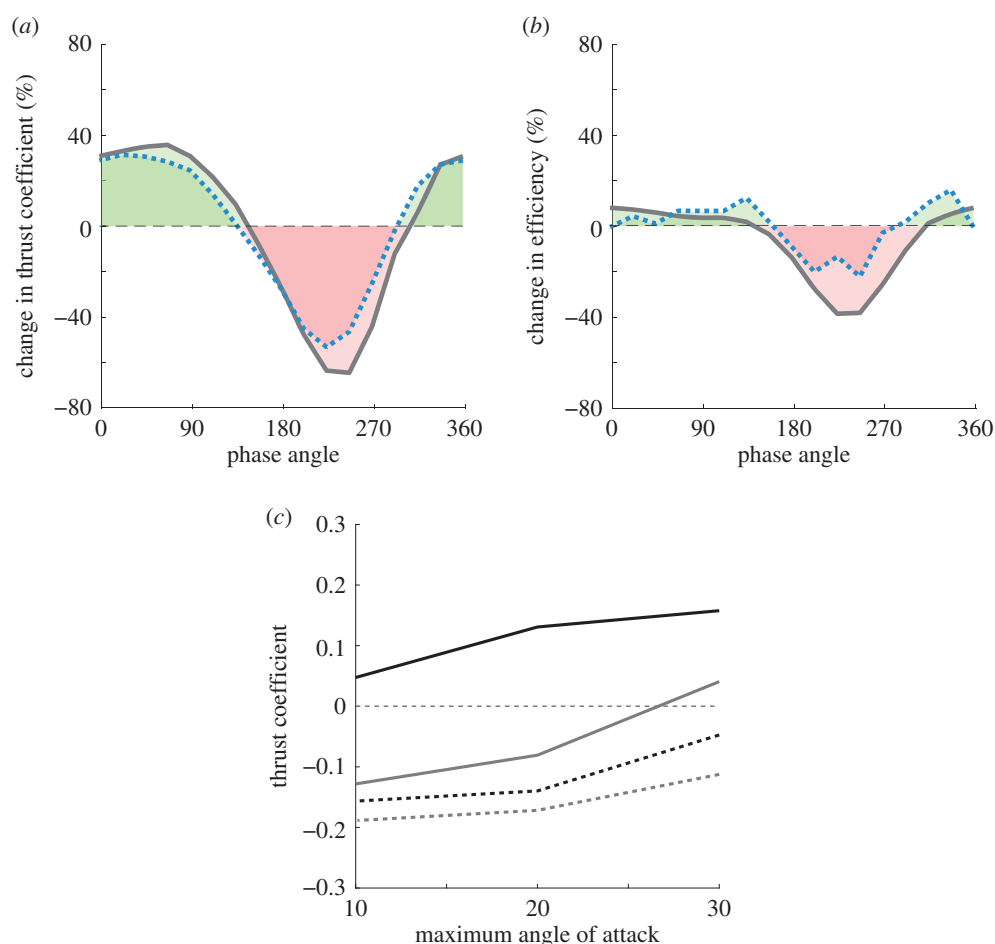


Figure 6. Effects of swimming speed on hydrodynamic properties of hind flipper owing to interaction with the fore flipper. (a) Percentage change in thrust coefficient (C_T^*). (b) Percentage change in efficiency (η^*). Solid grey curve is hind-flipper value at a flow speed of 0.22 m s^{-1} and dotted blue curve is hind-flipper value at flow speed of 0.44 m s^{-1} . The solid and dotted lines are the corresponding single-flipper values. All are at low frequency ($St = 0.18$). The percentage change in both thrust coefficient and efficiency are unaffected by a change in the swimming speed. (c) Thrust of stationary hind flipper while only fore flipper is flapping. Grey lines are low St of 0.18, black lines are high St of 0.36. Solid lines are high flapping amplitude and corresponding low frequency, dotted lines are low flapping amplitude and corresponding high frequency. This shows that it is possible for the hind flipper to generate a small amount of thrust, but this only occurs when the fore flipper is flapping at a high frequency and large amplitude, i.e. producing a lot of thrust and a strong wake. (Online version in colour.)

were observed for a limited range of phases; (5) as spacing between flippers would vary between plesiosaurs, and Strouhal number would vary during acceleration, the optimum phase would be different for each plesiosaur species, and vary with swimming speed and behaviour. There is no single 'optimum' phasing for flipper motion.

Experiments also show that increases in thrust are generally concurrent with increases in efficiency and are of comparable magnitude, a desirable property of an effective propulsion system. This strongly suggests that plesiosaurs used all four flippers for propulsion, because in doing so they produced more thrust at a higher efficiency than if they had used just one set for propulsion and the other for manoeuvring. Further work could include investigations into how differences in planform shape, flexibility and fore–hind flipper area ratios affect the details of these findings.

Data accessibility. All the data relevant to this study are presented in the electronic supplementary material and further information is available on request via e-mail: luke@muscutt.org.

Authors' contributions. This study was designed by B.G., C.P. and G.D. with considerable subsequent input from L.M. and G.W. L.M. carried out all experiments with support from B.G., C.P. and G.W. All authors contributed to writing the paper.

Competing interests. The authors declare no competing interests.

Funding. This study was supported by EPSRC and Ginko Investments Ltd.

Acknowledgements. We thank P. Oxborrow and S. Klitz for help building the experimental facilities, D. Parson and S. Chapman for granting access to plesiosaur specimens, and R. Forrest, M. Evans and D.J. Unwin for advice and comments on this manuscript. We thank the New England Aquarium, Central Warf, Boston, MA, USA, and the Marine Mammal Centre, 2000 Bunker Road, Fort Cronkhite, Sausalito, CA, USA for providing flipper X-rays. We are grateful to the associate editor Devi Stuart-Fox, Valentin Fischer and a second anonymous reviewer for their comments on this manuscript.

References

1. Robinson JA. 1975 The locomotion of plesiosaurs. *Neues Jahrb. Geol. Paläontol. Abh.* **149**, 286–332.
2. Godfrey SJ. 1984 Plesiosaur subaqueous locomotion: a reappraisal. *Neues Jahrb. Geol. Paläontol. Abh.* **11**, 661–672.
3. Robinson JA. 1977 Intracorporal force transmission in plesiosaurs. *Neues Jahrb. Geol. Paläontol. Abh.* **153**, 86–128.

4. Watson DMS. 1924 The elasmosaurid shoulder-girdle and fore-limb. *Proc. Zool. Soc. Lond.* **2**, 885–917.
5. Tarlo LB. 1958 The scapula of *Pliosaurus macrormerus* Phillips. *Palaeontology* **1**, 193–199.
6. Tarsitano S, Riess J. 1982 Plesiosaur locomotion; underwater flight versus rowing. *Neues Jahrb. Geol. Paläontol. Abh.* **164**, 188–192.
7. Frey E, Riess J. 1982 Consideration concerning plesiosaur locomotion. *Neues Jahrb. Geol. Paläontol. Abh.* **164**, 193–194.
8. Nicholls EL, Russell AP. 1991 The plesiosaur pectoral girdle: the case for a sternum. *Neues Jahrb. Geol. Paläontol. Abh.* **182**, 161–185.
9. Lingham-Soliar T. 2000 Plesiosaur locomotion; is the four-wing problem real or merely a theoretical exercise? *Neues Jahrb. Geol. Paläontol. Abh.* **217**, 45–87.
10. Carpenter K, Sanders F, Reed B, Reed J, Larson P. 2010 Plesiosaur swimming as interpreted from skeletal analysis and experimental results. *Trans. Kans. Acad. Sci.* **113/2**, 1–34. (doi:10.1660/062.113.0201)
11. Halstead LB. 1989 Plesiosaur locomotion. *J. Geol. Soc. Lond.* **146**, 37–40. (doi:10.1144/gsjgs.146.1.0037)
12. Newman B, Tarlo LB. 1967 A giant marine reptile from Bedfordshire. *Animals* **10**, 61–63.
13. Liu S, Smith AS, Gu Y, Tan J, Liu CK, Turk G. 2015 Computer simulations imply forelimb-dominated underwater flight in plesiosaurs. *PLoS Comput. Biol.* **11**, e1004605. (doi:10.1371/journal.pcbi.1004605)
14. Taylor GK, Nudds RL, Thomas ALR. 2003 Flying and swimming animals cruise at a Strouhal number tuned for high power efficiency. *Nature* **425**, 707–711. (doi:10.1038/nature02000)
15. Azuma A. 2006 *The biokinetics of flying and swimming*, 2nd edn. AIAA Education Series. Reston, VA: American Institute of Aeronautics and Astronautics.
16. Anderson JM, Streitlien K, Barrett DS, Triantafyllou MS. 1998 Oscillating foils of high propulsive efficiency. *J. Fluid Mech.* **360**, 41–72. (doi:10.1017/S0022112097008392)
17. Read DA, Hover FS, Triantafyllou MS. 2003 Forces on oscillating foils for propulsion and manoeuvring. *J. Fluids Struct.* **17**, 163–183. (doi:10.1016/S0889-9746(02)00115-9)
18. Schouveiler L, Hover FS, Triantafyllou MS. 2005 Performance of flapping foil propulsion. *J. Fluids Struct.* **207**, 949–959. (doi:10.1016/j.jfluidstructs.2005.05.009)
19. Warkentin J, DeLaurier J. 2007 Experimental aerodynamic study of tandem flapping membrane wings. *J. Aircr.* **44**, 1653–1661. (doi:10.2514/1.28160)
20. Kumar AG, Hu H. 2011 An experimental investigation on the wake flow characteristics of tandem flapping wings. In *6th AIAA Theoretical Fluid Mechanics Conference, Honolulu, Hawaii, 27–30 June 2011*.
21. Rival D, Hass G, Tropea C. 2011 Recovery of energy from leading- and trailing-edge vortices in tandem airfoil configurations. *J. Aircr.* **48**, 203–211. (doi:10.2514/1.C031062)
22. Broering TM, Lian Y. 2012 The effect of phase angle and wing spacing on tandem flapping wings. *Acta Mech. Sin.* **28**, 1557–1571. (doi:10.1007/s10409-012-0210-8)
23. Lian Y, Broering T, Hord K, Prater R. 2014 The characterisation of tandem and corrugated wings. *Prog. Aerosp. Sci.* **65**, 41–69. (doi:10.1016/j.paerosci.2013.08.001)
24. Boschitsch BM, Dewey PA, Smits AJ. 2014 Propulsive performance of unsteady tandem hydrofoils in an in-line configuration. *Phys. Fluids* **26**, 131–139. (doi:10.1063/1.4872308)
25. Gong WQ, Jia BB, Xi G. 2015 Experimental study on mean thrust of two plunging wings in tandem. *AIAA Journal* **536**, 1693–1705. (doi:10.2514/1.J053452)
26. Gong WQ, Jia BB, Xi G. 2016 Experimental study on instantaneous thrust and lift of two plunging wings in tandem. *Exp. Fluids* **57**, 1.
27. Muscutt LE, Weymouth GD, Ganapathisubramani B. 2017 Performance augmentation mechanism of in-line tandem flapping foils. *J. Fluid Mech* (accepted June 2017).
28. Lehmann FO. 2009 Wing-wake interaction reduces power consumption in insect tandem wings. *Exp. Fluids* **46**, 765–775. (doi:10.1007/s00348-008-0595-0)
29. Usherwood JR, Lehmann FO. 2008 Phasing of dragonfly wings can improve aerodynamic efficiency by removing swirl. *J. R. Soc. Interface* **5**, 1303–1307. (doi:10.1098/rsif.2008.0124)
30. Portugal SJ, Hubel TY, Fritz J, Heese S, Trobe D, Voelkl B, Hailes S, Wilson AM, Usherwood JR. 2014 Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature* **505**, 399–402. (doi:10.1038/nature12939)
31. Andrews CW. 1910 *A descriptive catalogue of the marine reptiles of the Oxford Clay, part 1*, 215 pp. London, UK: British Natural History Museum.
32. Larkin N, O'Connor S, Parsons D. 2010 The virtual and physical preparation of the Collard plesiosaur from Bridgwater Bay, Somerset, UK. *Geol. Curator* **93**, 107–116.
33. Nudds RL, Taylor GK, Thomas ALR. 2004 Tuning of Strouhal number for high propulsive efficiency accurately predicts how wingbeat frequency and stroke amplitude relate and scale with size and flight speed in birds. *Proc. R. Soc. Lond. B* **271**, 2071–2076. (doi:10.1098/rspb.2004.2838)
34. Rohr JJ, Fish FE. 2004 St and optimization of swimming by odontocete cetaceans. *J. Exp. Biol.* **207**, 1633–1642. (doi:10.1242/jeb.00948)
35. Heathcote S, Wang Z, Gursul I. 2008 Effect of spanwise flexibility on flapping wing propulsion. *J. Fluids Struct.* **24**, 183–199. (doi:10.1016/j.jfluidstructs.2007.08.003)
36. O'Keefe FR. 2001 Ecomorphology of plesiosaur flipper geometry. *J. Evol. Biol.* **146**, 987–991. (doi:10.1046/j.1420-9101.2001.00347.x)
37. O'Keefe FR. 2002 The evolution of plesiosaur and pliosaur morphotypes in the Plesiosauroidea Reptilia: Sauropterygia. *Paleobiology* **281**, 101–112. (doi:10.1666/0094-8373(2002)028<0101:TEOPAP>2.0.CO;2)
38. O'Keefe FR, Carrano MT. 2005 Correlated trends in the evolution of the plesiosaur locomotor system. *Paleobiology* **314**, 656–675. (doi:10.1666/04021.1)
39. Massare JA. 1988 Swimming capabilities of Mesozoic marine reptiles - implications for method of predation. *Paleobiology* **14**, 187–205. (doi:10.1017/S009483730001191X)
40. Motani R. 2002 Swimming speed estimation of extinct marine reptiles: energetic approach revisited. *Paleobiology* **282**, 251–262. (doi:10.1666/0094-8373(2002)028<0251:SSEOEM>2.0.CO;2)