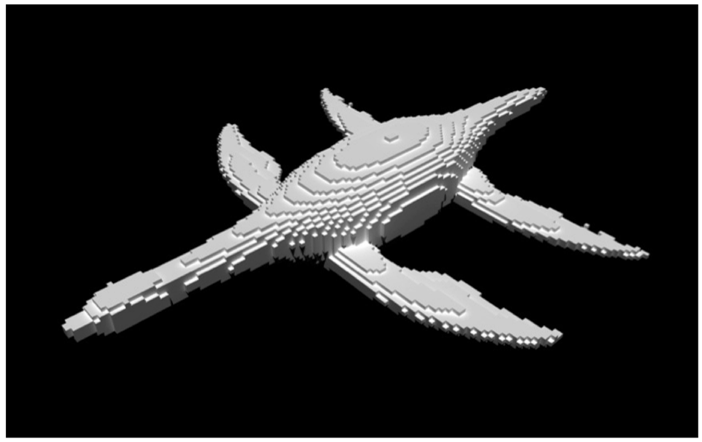

Fig 8. Model voxelization. The voxelized version of the plesiosaur mesh, using 3x3x3 sub-grid voxelization. The model is re-voxelized at each simulated time-step, which further minimizes the effects of voxelization.

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We calculate the swimming distance as the displacement of the plesiosaur's center of mass (COM) in one swimming cycle projected onto its initial heading direction. The deviation from straight swimming is decomposed into two components: Directional deviation is measured by the displacement of COM that is perpendicular to the initial heading direction. Orientation deviation is measured simply as the orientation change in one swimming cycle. Since the simulation starts with a static plesiosaur submerged in motionless water, we evaluate the objective function only after the first stroke cycle is completed, when the plesiosaur has reached a steady speed. Forelimb-only and all limb optimizations were initiated with the front limbs in the fully abducted position and the hindlimbs in the neutral position. Hindlimb-only optimizations were initiated with the hindlimbs in the fully abducted position and the forelimbs in the neutral position. This forced all of the gait samples to begin with a downstroke, so that no gait was penalized for a slow start that is mid-way through a stroke.

We used Covariance Matrix Adaptation (CMA) [34, 45] to search for the sample s that gives us the highest quality. CMA is a sample-based approach to optimization that uses a Gaussian distribution to guide its selection of motion samples to test. Each iteration of the CMA draws a new set of samples based on the current distribution, and evaluates the quality of these samples using $q(s)$. The mean and the covariance matrix of the Gaussian are then updated according to a subset of sample with higher quality. As more iterations are taken, the covariance matrix narrows down towards the best quality sample. In our case, the best sample is the swimming motion parameters that move the simulated plesiosaur the farthest in a straight line through the water.

To converge to the optimal motion, CMA requires many samples to be evaluated. Each sample evaluation requires a full simulation of the specified motion, and each such plesiosaur/fluid simulation requires roughly one hour of computation. We used 31 samples per iteration of CMA, and we found that a typical optimization run converged in about 70 iterations, after which the quality of the motion samples does not improve. This means that a full optimization requires more than two thousand swimming simulations. We made use of a compute cluster with 32 nodes, so that the computations for a single iteration were all calculated in parallel on separate nodes. (One of these computer nodes coordinates the simulations of the other 31 nodes.) Even with the compute cluster, performing CMA optimization for a single set of joint ranges requires three days to run.

Although CMA converges to high quality samples, there is no guarantee that it will find the best possible sample in our 26-dimensional search space. This explains why, for the wide joint range, the best forelimb-only swimmer that was found is slightly faster than the all-limbs swimmer (Fig 5). To verify that this was due to small variations between optimization runs, we ran a total of three optimization runs for each of these two cases for the wide joint range. The three optimization runs for all-limbs gave speeds of 0.745, 0.75, and 0.785 (m/s), and the three runs for forelimbs-only resulted in speeds of 0.745, 0.80, and 0.84. Note that these ranges overlap. Fig 5 reports the fastest speeds from each of these sets of three optimization runs.

Supporting Information

S1 Video. Efficient swimming motions. Animation showing the most efficient swimming motions that were found in each of the three joint ranges (wide, medium, and narrow). For each joint range, animations are shown for both sets of limbs, for only forelimbs, and for only hindlimbs. White streamlines show the motion of the surrounding fluid.
(MP4)

S2 Video. Tip traces. Animation showing the motion of the tips of the limbs for the most efficient swimming motions in each of the three joint ranges. The camera view is locked to move with the plesiosaur model to more clearly show these tip traces. For each swimming motion, both a lateral view and a posterolateral view are shown.
(MP4)

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Author Contributions

Conceived and designed the experiments: SL ASS YG JT CKL GT. Performed the experiments: SL JT. Analyzed the data: SL ASS YG JT CKL GT. Wrote the paper: SL ASS JT CKL GT. Plesiosaur body layout and joint ranges: ASS. Created digital models: YG. Wrote simulation software: JT SL.

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