INVITED PAPER

Fish without Tail Fins—Exploring the Function of Tail Morphology of the First Vertebrates

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Synopsis We use a series of hydrodynamic experiments on abstracted models to explore whether primitive vertebrates may have swum under various conditions without a clearly-differentiated tail fin. Cambrian vertebrates had post-anal stubby tails, some had single dorsal and ventral fins, but none had yet evolved a clearly differentiated caudal fin typical of post-Cambrian fishes, and must have relied on their long and flexible laterally-compressed bodies for locomotion, i.e., by bending their bodies side-to-side in order to propagate waves from head to tail. We approach this problem experimentally based on an abstracted model of Metaspriggina walcotti from the 506-million-year old Burgess Shale by using oscillating thin flexible plates while varying the tail fin geometry from rectangular to uniform, and finally to a no tail–fin condition. Despite a missing tail fin, this study supports the observation that the abstracted Metaspriggina model can generate a strong propulsive force in cruise conditions, both away from, and near the sea bed (in ground effect). However, when the abstracted Metaspriggina model moves in ground effect, a weaker performance is observed, indicating that Metaspriggina may not necessarily have been optimized for swimming near the sea bed. When considering acceleration from rest, we find that the Metaspriggina model’s performance is not significantly different from other morphological models (abstracted truncate tail and abstracted heterocercal tail). Statistical analysis shows that morphological parameters, swimming modes, and ground effect all play significant roles in thrust performance. While the exact relationships of Cambrian vertebrates are still debated, as agnathans, they share some general characteristics with modern cyclostomes, in particular an elongate body akin to lampreys. Lampreys, as anguilliform swimmers, are considered to be some of the most efficient swimmers using a particular type of suction thrust induced by the traveling body wave as it travels from head to tail. Our current experiments suggest that Metaspriggina’s ability in acceleration from rest, through possibly a similar type of suction thrust, which is defined as the ability to generate low pressure on upstream facing sections of the body, might have evolved early in response to increasing predator pressure during the Cambrian Explosion.

Introduction

The elongated tail bearing fin rays is found in a wide variety of early vertebrate fossils ranging from homocercal tails to heterocercal tails (Lauder 2000). However, for Metaspriggina walcotti, a primitive fish from the Cambrian of North America, no fins have been recognized (Conway Morris and Caron 2014). Thus, the function of tail morphology in swimming performance, possible aspects of Metaspriggina ecology, and how tail shapes might have evolved in early vertebrates are of considerable interest.

Muscle types in early chordates

Through abstraction, this study provides insight into the hydrodynamics of flexible bodies dating back to the Cambrian Explosion (~506 MYA). Metaspriggina walcotti, as shown in Fig. 1B and C, is believed to be one of the most basal and best known early vertebrates in the fossil record (Conway Morris and...
Metaspriggina has a flexible body (Fig. 1C) and lacks any evidence of fins, although it has a roughly symmetrical stubby post-anal tail (Fig. 1A and B in Conway Morris and Caron 2014). This tail is reminiscent to the protocercal condition known in cephalochordates (Fig. 1D), or to the slightly hypocercal conditions known in lampreys, the primitive chordate Pikaia gracilens as shown in Fig. 1A (Conway Morris and Caron 2012), conodonts, and early skeletonized vertebrates (Pradel et al. 2007), showing that primitively the notochord probably extended to the very tip of the posterior end into a small notochordal lobe. Closely-related early vertebrate species from the lower Cambrian of China show basically the same tail end as in Metaspriggina, although these fishes preserve a single ventral and dorsal fin, which do not seem to extend to the posterior end (Shu et al. 1999; Shu 2003). The possible aspects of Cambrian chordates ecology, in particular Metaspriggina, have not, to date, been explored using quantitative methods, although particular types of myomeral configurations have provided some initial elements.

Anatomical comparisons suggest that early vertebrates may have swum like extant swimmers. The Cambrian chordates from the Burgess Shale
showcase two broad types of myomeres, as shown in Fig. 1. In *Pikaia* (Fig. 1A), the myomeral configuration has segmented muscle blocks, which are gently-curved (Conway Morris and Caron 2012). These have been interpreted as narrow slow-twitch fibers (Lacalli 2012). Myomeres in *Metaspriggina* (Fig. 1B and C), on the other hand, have a clear chevron or V-shaped arrangement and the caudal region shows myomeres which are more steeply inclined (Conway Morris and Caron 2014). This configuration is close to *Branchiostoma* (Fig. 1D) (Lacalli 2012) and more directly comparable to fishes (Van Leeuwen 1999), suggesting that *Metaspriggina* would have likely been capable of swimming rapidly operating in the fast-twitch mode for escape. Since *Metaspriggina* is considered a true vertebrate (Conway Morris and Caron 2014), the myomere configuration offers an opportunity to illuminate the origin of high-performance swimming in basal fishes.

**Abstraction of fish locomotion**

Many studies have illustrated the power of using an abstracted robotic oscillating model in order to explore the dynamics of self-propelled flexible bodies. Researchers have confirmed that we can use abstracted mechanical models to understand the integrated function of muscle, water, and skeleton (Madden and Lauder 2003; Thorsen and Westneat 2005). McHenry et al. found that the changes in body flexural stiffness can control propulsive wavelength, wave speed, Froude efficiency, and consequently, swimming speed (McHenry et al. 1995). Long et al. measured flexural stiffness and flexural damping of a hagfish notochord under *in vitro* conditions that mimicked the body curvature and bending frequency measured during steady undulatory swimming (Long et al. 2002). Although the notochord is important for flexural stiffness, Long and Nipper (1996) found that fishes can increase body stiffness by using their muscles to generate negative mechanical work. Erickson et al. used a three-point bending test to measure stiffness, ultimate strength, and yield strain of the pelvic metapterygium of *Polypterus* (Erickson et al. 2002). Lauder et al. investigated the effect of altering flexural stiffness on swimming speed (Lauder et al. 2011; Wen et al. 2018; Mignano et al. 2019; Han et al. 2020; Ibrahim et al. 2020; Wolf et al. 2020). Leftwich et al. (2012) used a robotic lamprey, based on the silver lamprey, to investigate the influence of passive tail flexibility on the wake structure and thrust production during anguilliform swimming. Lauder et al. (2011) confirmed that analysis of propulsion using flexible models allows investigation of the effect of altering flexural stiffness on swimming speed. Even though the skeletal systems of fishes are complex, these studies on mechanical properties and flexibility have led to the consideration of the whole fish as a resonating cantilevered beam.

Although significant progress has been made on modeling the mechanical properties of skeletal tissue and structures, a comprehensive study of coupled vortex shedding and swimming dynamics in fluid–structure interactions is still far from complete. Notwithstanding, the investigations of fluid–flexible body interactions have much improved our understanding of biological propulsion. In many cases, the pressure-field variations associated with flexible-body deformation in the form of waves play a significant role in the fluid–structure interaction process (Muller et al. 2002; Tytell and Lauder 2004; Lauder and Tytell 2006; Flammang 2010; Tytell et al. 2010; Eloy 2013; Gemmell et al. 2015, 2016). Understanding the structure and dynamics of adjacent vortices is thus important in order to accurately assess the time-dependent forces acting on the body with wave-like motions. The studies of Gemmell et al. explore the mechanisms associated with traveling body waves, which bend the lamprey body, thus generating and controlling vortices (Gemmell et al. 2015, 2016). Their investigations also indicate that the nonoptimal, passive bending of the tail section can also generate thrust, suggesting that thrust can still effectively be generated through passively-bending bodies as used in this study. Du Clos et al. compared the kinematics and hydrodynamics of larval sea lampreys with those of lampreys accelerating from rest during escape swimming (Du Clos et al. 2019). Their study shows that a high-pressure mechanism, such as the one used for acceleration from rest, could also be important for low-speed maneuvering when drag-based turning mechanisms are less effective. The study of Flammang (2010) found that activity of caudal musculature in sharks can play a significant role in the formation of vortices during swimming. Thus, the adjacent vortices, and the forces they exert on the body, are of considerable interest for biological propulsion (Gemmell et al. 2015, 2016; Du Clos et al. 2019).

**Morphological features of tail fins**

The shapes of the caudal fin can have a significant effect on the mechanics and hydrodynamics of locomotion. The flapping panels are usually used to model the morphologies of flying and swimming animals for locomotion through a fluid (Li and Lu...
Hartloper and Rival (2014) indicates that the shapes of rigid flapping plates have a significant impact on the development of vortical structures in the wake. Their simulation results found that more sweptback configurations (an increase in the area moment of inertia), resulted in weaker leading-edge vortices and stronger trailing-edge vortices, suggesting that overall thrust and therefore performance could be modified through this modification in shape. Hartloper and Rival (2013) studied vortex development on pitching plates with lunate and truncate planforms in starting motions. Their experimental investigation indicated that a spanwise leading-edge curvature may result in a favorable lift-to-drag ratio during the force-relaxation phase of escape, which in turn sheds light on the evolutionary convergence towards spanwise leading-edge curvatures on biological appendages. The lack of plate stiffness in the above studies adds further caution regarding the generalizability of these findings. These studies would have been more convincing if they had included discussions on flexible plates. In the study reported here, flexible plates were used as a reduced-order flexible model toward further resolving this knowledge gap.

Studies on wakes generated by flexible bodies are also common across a wide variety of extant and extinct swimmers (Fish and Lauder 2006; Wu 2011), but few comprehensive studies have been conducted to explore the origins of, and an evolutionary pathway toward, tail fins. Affleck (1950) outlined the possible derivation of tails in fishes. However, he also pointed out that his study cannot show the evolution of the groups, because parallel evolution has almost certainly taken place. Affleck (1950) speculated that the earliest chordates probably spent most of the time on the bottom of rivers or lakes and made only occasional swimming movements (Affleck 1950). The study reported here seeks to obtain data that will help to assess the claim that these animals may be described as intermittent swimmers in contradistinction to later continuous swimmers. Many studies showed the significance of functional data and analytical techniques in early vertebrates and major evolutionary patterns to tail morphology (Lauder 2000; Lauder et al. 2002, 2003). Lauder (2000) discussed the function and evolution of the caudal fin using quantitative flow measurements. His experimental data indicated that the function of homocercal tails is considerably more complex than previously appreciated by phylogenetic analysis. The study of Lauder et al. (2003) revealed that many long-standing hypotheses about the function and evolution of the fins of fishes can be evaluated mechanistically. Their study also showed that the heterocercal tails of sharks and sturgeon function so differently in propulsive performance, which cannot be detected by previous phylogenetic analysis.

### Swimming at the sea floor

Another significant impact on hydrodynamic propulsion is the gap between the swimmer and the sea floor. The morphology of the branchial area in *Metaspriggina* suggests a microphagous feeding habit (Conway Morris and Caron 2014). The eyes are high on their bodies, suggesting that *Metaspriggina* likely lived swimming directly above the sea floor (Ahlberg 2001). Quinn et al. (2014) investigated ground-effect performance for a rigid pitching model. Their results show that ground effect is advantageous for efficient thrust production, and could allow for higher cruise speeds with no loss in efficiency. According to the study of Affleck (1950), the earliest chordates may spend most of the time on the bottom of rivers or lakes. Thus, exploring ground effect on these abstracted flexible bodies is a key feature of this study.

### Objectives

The basic elements of our current approach were thus inspired by the above studies. We propose that the study of thrust generation of aquatic swimmers is a key to understanding the impact of multiple factors (morphological parameters, swimming modes, and ground effect) on propulsive performance. It is clear from existing work that thrust generation is crucial to the dynamics of self-propelled flexible bodies (Lauder et al. 2007; Gemmell et al. 2016; Du Clos et al. 2019). We thus propose that an abstraction of fish locomotion that mimics fish-like locomotion with significant wake-vortex formation, together with high-fidelity thrust measurements, provides a reasonable simplification for the evaluation of swimming dynamics. Furthermore, this model provides valuable insights on the pathway for early vertebrate swimmers, as well as high-performance swimmers, observed today. The specimen shown in Fig. 1C presents a realistic undulation of the body, which in turn inspired us to use a flexible model to present the locomotion of *Metaspriggina*. Thus, the objective of this study is to use abstracted, flexible models to explore how tail shapes might have evolved in early vertebrates. The current state of our knowledge draws us to the following open questions: To what extent do morphological features in this fish affect thrust performance? Can abstracted models help us understand whether *Metaspriggina* could swim effectively near the sea bed and/or in free conditions?
Methodology

Experimental setup

We used time-resolved force measurements to study the performance of *Metaspriggina* and other abstracted models as detailed herein. Figure 2 presents the general shape of *Metaspriggina* and the four abstracted morphological models. The experimental setup incorporated plunging flexible models as shown in Fig. 3. All models were made using a 1-mm-thick Polyethylene terephthalate glycol (PETG) plastic sheet, with a width of \( S = 6 \text{cm} \) and a chord length of \( c = 30 \text{cm} \). The flexural stiffness \( EI \) is the product of the Young’s modulus \( E \) (\( E = 2000 \text{ MPa} \) for PETG Plastic) and the area moment of inertia of the beam cross-section \( I \). In this study, the flexural stiffness is \( 1/10 \text{Ncm}^2 \), which is similar to that of real fish estimated during locomotion (Shelton et al. 2014; Wolf et al. 2020). Note that all experiments were conducted in the optical towing tank at Queen’s University (15-m long with a 1 m × 1 m cross-section). The tank has a covered ceiling to minimize free-surface effects, admitting an opening only large enough for the sting, in turn, connected to a motorized traverse. The steady-state speed chosen was \( U_\infty = 0.1 \text{m/s} \), yielding a Reynolds number based on maximum body length \( (c) \) of \( Re = 30,000 \). The largest *Metaspriggina* specimens are estimated to be \( \sim 10 \text{cm} \) (one-third of the abstracted model chord length). The selection of Reynolds number was based on extant locomotion (\( Re = 10^4 \rightarrow 10^6 \)) (Gazzola et al. 2014) and previous plunging model experiments (\( Re = 25,000 \rightarrow 64,000 \)) (Wen and Lauder 2013). The plastic models were driven by a linear actuator with a plunge motion of

\[
h(t) = H \cos(2\pi ft),
\]

where \( h(t) \) presents the plunge motion of the plastic model in the lateral direction. The amplitude of the plunge motion \( (H) \) was set at 4.5 cm (0.15c) and the plunge frequency \( (f) \) was set at 0.4 Hz, corresponding to a Strouhal number range of \( St = 0.3 \rightarrow 0.4 \). The amplitude and frequency were chosen according to the Strouhal number of fish locomotion ranging from 0.2 to 0.4 (Eloy 2012; Gazzola et al. 2014). The Strouhal number is defined by

\[
St = fa / U_\infty,
\]

where \( a \) is the characteristic width of the wake (often represented by the peak-to-peak amplitude of the trailing-edge deflection). The proximity to the sea bed in this study is taken as the distance between the model and the tank wall, as shown in Fig. 3.

In this study, we use the “fixed propulsion” platforms, as described in the study of Lauder et al. (2007) for aquatic locomotion, along with force/moment measurements. The plastic model was attached to a sting (a rod holding the plastic model horizontally from the plunge mechanism). In cruise conditions, the model was towed at a constant velocity on a moving carriage. The model enters the field of view from right
and leaves on the left at a constant speed \((U_\infty = 0.1 \text{m}/\text{s})\), as shown in Fig. 4. To emulate an acceleration from rest, the model is fixed in place while forces are measured on the sting (see Fig. 5). For both cases, the model was not self-propelled, but rather moved at an externally-imposed speed.

**Thrust measurements**

The flexible plastic models were attached via a stainless-steel clip to an ATI Nano 17 six-axis force/moment sensor (ATI Industrial Automation Inc., Apex, NC) and submerged at mid-depth in the tank as seen in Fig. 3B and C. Mid-depth placement offers a minimum of wall interference with symmetric oscillations. The sensor was connected to a linear actuator using a stainless sting, which allowed for three forces and three moments to be measured in the XYZ coordinate plane \((x, y\) is the towing direction, \(y\) is the plunge direction, and \(z\) is the lateral direction). The sensor resolution for forces and moments were 6.25 mN and 31.25 mN/m, respectively. The F/M measurements were sampled at 1000 Hz. The force/moment data acquisition (DAQ) system, which simultaneously acquires forces \((F_x, F_y, F_z)\) and moments \((M_x, M_y, M_z)\), consists of a force and moment (F/M) sensor, an interface power supply, a USB DAQ device (NI 6212) and LabVIEW software. The F/M sensor outputs six amplified strain gage voltages to the DAQ device; these gauge voltages are then processed through the ATI-supplied six-by-six calibration matrix using LabVIEW to obtain the F/M measurements \((F_x, F_y, F_z, M_x, M_y, M_z)\). The force data were filtered using a low-pass filter at 2.5 Hz. In this sensor mounting arrangement, the \(x\)-axis is the direction of thrust. Thus, \(F_x\) is the thrust \(T\) for the model. We present the propulsive performance by examining the thrust coefficient, which is normalized by the swimming speed. In this study, we use the time-averaged thrust coefficient to assess the overall propulsive performance during particular time intervals. The mean thrust coefficient was time-averaged over six periods for cruise conditions and the first half period in acceleration when starting from rest. The mean thrust coefficient \((\bar{C}_T)\) is defined as

\[
\bar{C}_T = \frac{T}{\frac{1}{2} \rho U_\infty^2 A}, \tag{3}
\]

where \(T\) is the mean thrust, \(\rho\) is the density of water in the tank, and \(A\) represents the overall areas of
each of the models. The reference speed ($U_r = 0.1 \text{m/s}$) is the same for both cruise and starting conditions.

**Statistical methods**

We used analysis of variance (ANOVA) and Tukey HSD post hoc test to analyze the statistical differences among various models. A global ANOVA $F$-test was used to investigate the effects of multiple factors for the thrust coefficient: model shape, swimming mode (cruising/acceleration from rest), and ground effect condition. We then used Tukey HSD to determine whether the thrust between two models/gap treatments are significantly different from each other for each of the cruising/start datasets. Statistical analysis was performed using MATLAB and a $P < 0.05$ was considered significant.

**Results**

**Thrust performance**

In this study, we examine the thrust performance as a key performance indicator for biological locomotion of aquatic vertebrates. Figure 6 shows the mean thrust coefficient defined in “Thrust measurements” section with error bars determined by standard deviation, based on the categorization of multiple factors including morphological shape, swimming mode, and ground effect condition. Figure 6A presents the mean thrust coefficients for all models in cruise and start conditions. Note that the mean thrust coefficient in start conditions is calculated for the first half period. Only Model 1, which provides the nearest analog to *Metaspriggina*, presents the minimum thrust coefficient in cruise conditions but comparable thrust coefficient to Models 2 and 3 in start conditions. In contrast, Model 4 (the rectangular model) has the maximum thrust coefficient in cruise conditions but, conversely, the minimum thrust coefficient in start conditions.

The influence of two levels of ground effect on thrust is shown in Fig. 6B and C. The solid wall always reduces performance in both cruise and start conditions. Model 2 outperforms Models 1 and 3 both in cruise and start conditions, for the medium gap ($B = 0.1c$) condition. Ground effect can also induce large variation in thrust, as represented by the error bars in Fig. 6, both in cruise and start conditions, especially for Model 1. The complex vortex interaction between the model and the wall may result in a large fluctuation in the thrust coefficient. The time-averaged thrust is reduced by $\approx 20\%$ for Model 1 in start conditions while it approaches zero in cruise conditions (where there is a $B = 0.1c$ gap). The results indicate that *Metaspriggina* may not necessarily be optimized for cruising near the sea floor. In contrast, the data does suggest that *Metaspriggina* was able to escape rapidly when near the sea floor. Figure 6D shows the mean thrust coefficient for all gaps in cruise and start conditions. Model 3 generally outperforms Model 1 in cruise conditions. However, due to the large error bars, this speculation has to be further verified by the statistical tests.

Statistical analysis was performed to test the effects of multiple factors on the mean thrust. Table 1 shows the ANOVA result for morphological shape, ground effect, and swimming mode. The ANOVA analysis was then followed by Tukey HSD post hoc tests, which provide pairwise comparisons among various morphological shapes and gap treatments, as shown in Tables 2 and 3. Figure 7 presents...
the estimates of the mean thrusts with comparison intervals determined by the Tukey HSD post hoc tests.

First, we investigated how the abstracted *Metaspriggina* tail morphology affects thrust compared to other models. There are significant differences among various morphological shapes at the $P = 0.003$ level in Table 1. The pairwise comparison in Table 2 also confirms this point for cruise conditions. The $P$-value of 0.002 indicates that the mean thrusts for Models 1 and 3 are significantly different when swimming at constant speed. When accelerating from rest, the difference was less significant ($P = 1.000$). Figure 7 further supports the above statements. The disjoint comparison intervals indicate that Model 1 results are significantly different from those recorded for Model 3 when considering mean thrust in cruise conditions (as shown in Fig. 7A). In contrast, Models 1–4 results are not significantly different because their intervals overlap for acceleration from rest (see Fig. 7B). It
Thus would appear that the Metaspriggina abstraction was more optimized for an acceleration from rest.

Another interesting question is how ground effect influences thrust performance among models. The ANOVA in Table 1 shows that the ground effect is statistically significant for the mean thrust ($P < 0.001$). The further pairwise comparison in Table 3 detects statistical differences among ground treatments. In cruise conditions, the 0.067c gap has a significantly smaller mean thrust ($P < 0.001$) when compared with free conditions. When the gap increases to 0.1c, the difference becomes less significant ($P = 0.058$). For acceleration from rest, both of the two-gap treatments (0.067c and 0.1c) are statistically significant from the free conditions when considering mean thrust. Figure 7 also supports the above statements through visualization. In cruise conditions, the intervals for the 0.067c gap and free conditions are statistically distinct from one another. For the acceleration from rest, both of the two-gap treatments (0.067c and 0.1c) do not overlap with the intervals for the free conditions. This lack of overlap indicates that the thrusts for both ground

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<th>Table 2</th>
<th>Pairwise comparison results from a Tukey HSD post hoc test for morphological shapes</th>
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<td>Cruise</td>
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<th>Acceleration from rest</th>
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The first two columns show the groups that are compared. The fourth column shows the difference between the estimated group means. The third and fifth columns show the lower and upper limits for 95% confidence intervals for the true mean difference. The sixth column contains the $P$-value for a hypothesis test that the corresponding mean difference is equal to zero.

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<th>Table 3</th>
<th>Pairwise comparison results from a Tukey HSD post hoc test for various gap conditions</th>
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<td>Cruise</td>
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treatments (0.067c and 0.1c) are statistically different from those recorded for the free conditions.

Finally, the statistical tests were used to address the open question: What are the differences between cruise conditions and the acceleration from rest cases on thrust performance among the various models? The ANOVA shown in Table 1 revealed that the mean thrust in cruise conditions is significantly different from that for the acceleration from rest. The data in Fig. 6 also confirm that the mean thrust under acceleration from rest is much larger than that in cruise conditions.

**Time history of thrust**

The behavior of time-dependent thrust performance is shown in Fig. 8A. The curves are plotted during one cycle starting from a stationary state. For the first half of the period, the *Metaspriggina* model (Model 1) outperforms all other models. For long-distance cruising, the data in Fig. 6A indicate that the tail section of *Metaspriggina* would generate minimum thrust, which represents poor performance in cruise conditions. The significant difference on thrust performance between the half-cycle starting from rest and the cruise state suggests that *Metaspriggina* is more likely to have a burst-and-coast locomotion behavior. In this mode, *Metaspriggina* would use bursts of acceleration from rest and then glide over short distances. The possible intermittent swimming mode suggests an initial condition for self-propelled thrust performance, but also limits propulsion speed and distance.

In this study, the plunge amplitude was held constant at 4.5 cm ($H = 0.15c$) at the leading edge of the model. However, the deflection at the trailing edge varied between the different models. It is necessary to elucidate the thrust performance for the same trailing-edge deflection. The kinematics of the moving models show that the trailing-edge deflection is approximately the same for all models at $t = 0.33T$, where $T$ is the period for one single cycle (see Fig. 8B). The thrust coefficients are $\sim 0.9$ among...
Models 1, 2, and 3 without ground effect. The mean thrust coefficient for the rectangular model is much smaller than for the *Metaspriggina* model. It appears that the abstracted *Metaspriggina* model is able to generate thrust when swimming above the sea floor. The *Metaspriggina* model can also generate strong thrust in cruise conditions, both away from, and near the sea floor (ground effect). The data in Fig. 8B suggest that trailing-edge shapes may exert greater influence on thrust performance with a more moderate gap with the sea bed \((B = 0.1c)\). The statistical analysis in Fig. 6 is consistent with this finding. For maximum ground effect \((0.067c)\), the thrust results are not statistically significant among Models 1–3. In contrast, there are significant differences in thrust between Models 1 and 2 with the medium ground effect condition \((0.1c)\).

**Discussion**

Simulation data (see Li et al. 2014) indicates that the mean thrust coefficient increases monotonically with the area moment for rigid models (from protocercal tails to homocercal tails) in cruise conditions. Our flexible-model experiments confirm this point and are also consistent with rigid pitching model experiments (see Van Buren et al. 2017) on thrust. The observed thrust coefficients for Models 2 and 3 indicate that the presence of a tail fin promotes thrust performance in cruise conditions and also maintains high thrust for start conditions. Van Buren et al. (2017) suggest that rigid fish caudal fin shapes do not generate optimum propulsive performance. In fact, our experimental results show that the flexible slanted tail (Model 1) is no worse than more sophisticated tail shapes (Models 2 and 3) on the propulsive performance during acceleration from rest, although Model 1 tends to perform worst among all models in cruise conditions (see Fig. 6). Our current experiments suggest that *Metaspriggina*’s greater ability to escape might have evolved early in response to increasing predator pressure during the Cambrian Explosion. Furthermore, the thrust data suggests that *Metaspriggina* is more likely to have had an intermittent swimming gait.

Despite the fact that anguilliform swimmers, such as lampreys, use a traveling body wave for propulsion, thrust is generated mainly near their tail (Du Clos et al. 2019). Thus, the impact of caudal fin shape on thrust production is key in understanding anguilliform swimming modes. The study of Du Clos et al. (2019) suggests that, during the transition from rest to steady swimming, the initial body waves produced by lampreys were visibly larger and slower than those produced during steady swimming, with a significantly greater wavelength. Thus, our morphological investigation on thrust performance for acceleration from rest may also benefit the understanding of thrust generation of lampreys during escape motions.

**Conclusions**

Abstracted morphological models were developed and tested in order to investigate the function of tail morphology in cruise and start conditions. The study sheds light on the evolutionary pathway toward extant (vertebrate) swimmers with tail fins. The *Metaspriggina* configuration was found to exhibit competitive performance in acceleration from rest, while its thrust coefficient was slightly lower in cruise conditions. When in ground effect, thrust capabilities of the flexible models were shown to decrease compared to values far from the sea bed. It
appears that the ground effect might have been disadvantageous for efficient thrust production in cruise conditions and thus decreased cruise performance. A burst-and-glide strategy thus may have been used.

A statistical analysis shows that morphological shape, swimming modes, and ground effect treatments are all significant on thrust performance. For morphological shape, a significant difference was found between Models 1 and 3 ($P < 0.001$) in cruise conditions. In contrast, the morphological shape (see Models 1–3) has no significant impact on the thrust during acceleration from rest.

Finally, our experiments reveal that the Metaspriggina configuration may offer performance gains for acceleration from rest, while only suffering a slight loss for swimming near the sea bed. The thrust data suggests that Metaspriggina is more likely to have had an intermittent swimming gait and that fins likely evolved for cruise performance. The poor thrust performance in cruise conditions also indirectly supports the microphagous life-habit of Metaspriggina previously implied (Conway Morris and Caron 2014).

Three-dimensional effects can—and often do—play an important role in vortex-wake dynamics. To better understand this issue, going forward further numerical and/or three-dimensional experimental studies of the flow around flexible models are needed in order to investigate these wake characteristics in greater detail. This study has only examined the impact of the pure-plunge motion on thrust performance. The prescribed undulatory locomotion did not include any pitching motion (rotation of the sting). In terms of future work, it would be worthwhile to expand the experiments described here by adding more degrees of freedom in the swimming motion.

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References


