

## Aberystwyth University

### *Accelerating fishes increase propulsive efficiency by modulating vortex ring geometry*

Akanyeti, Otar; Putney, Joy; Yanagitsuru, Yuzo R.; Lauder, George V.; Stewart, William J.; Liao, James C.

*Published in:*

Proceedings of the National Academy of Sciences of the United States of America

*DOI:*

[10.1073/pnas.1705968115](https://doi.org/10.1073/pnas.1705968115)

*Publication date:*

2017

*Citation for published version (APA):*

Akanyeti, O., Putney, J., Yanagitsuru, Y. R., Lauder, G. V., Stewart, W. J., & Liao, J. C. (2017). Accelerating fishes increase propulsive efficiency by modulating vortex ring geometry. *Proceedings of the National Academy of Sciences of the United States of America*, 114(52), 13828-13833. <https://doi.org/10.1073/pnas.1705968115>

#### **General rights**

Copyright and moral rights for the publications made accessible in the Aberystwyth Research Portal (the Institutional Repository) are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the Aberystwyth Research Portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the Aberystwyth Research Portal

#### **Take down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

tel: +44 1970 62 2400

email: [is@aber.ac.uk](mailto:is@aber.ac.uk)

1 **ACCELERATING FISHES INCREASE PROPULSIVE EFFICIENCY BY**  
2 **MODULATING VORTEX RING GEOMETRY.**

3

4

5 O. Akanyeti<sup>1,2</sup>, Joy Putney<sup>1,3</sup>, Y.R. Yanagitsuru<sup>1</sup>, G.V. Lauder<sup>4</sup>, W.J. Stewart<sup>1,5</sup>, J.C. Liao<sup>1</sup>

6

7

8 <sup>1</sup> The Whitney Laboratory for Marine Bioscience, Department of Biology, University of Florida,  
9 St. Augustine, FL 32080, USA.

10 <sup>2</sup> The Department of Computer Science, Aberystwyth University, Ceredigion, SY23 3FL, Wales.

11 <sup>3</sup> The School of Biological Sciences, Georgia Institute of Technology, Atlanta, GA 30332, USA.

12 <sup>4</sup> The Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA  
13 02138, USA.

14 <sup>5</sup> The Department of Science, Eastern Florida State College, Melbourne, FL 32935, USA.

15

16

17 Author for correspondence: J.C.L. ([jliao@whitney.ufl.edu](mailto:jliao@whitney.ufl.edu)), O.A. ([ota1@aber.ac.uk](mailto:ota1@aber.ac.uk))

18

19

20

21

22 **Abstract**

23 Swimming animals need to generate propulsive force to overcome drag, regardless of whether  
24 they swim steadily or accelerate forward. While locomotion strategies for steady swimming are  
25 well characterized, far less is known about acceleration. Animals exhibit many different ways to  
26 swim steadily, but we show here that this behavioral diversity collapses into a single swimming  
27 pattern during acceleration regardless of the body size, morphology, and ecology of the animal.  
28 We draw on the fields of biomechanics, fluid dynamics and robotics to demonstrate that there is  
29 a fundamental difference between steady swimming and forward acceleration. We provide  
30 empirical evidence that the tail of accelerating fishes can increase propulsive efficiency by  
31 enhancing thrust through the alteration of vortex ring geometry. Our study provides new insight  
32 into how propulsion can be altered without increasing vortex ring size, and represents a  
33 fundamental departure from our current understanding of the hydrodynamic mechanisms of  
34 acceleration. Our findings reveal a unifying hydrodynamic principle that is likely conserved in  
35 all aquatic, undulatory vertebrates.

36

37

38

39

40

41

42

43

44

45 **Significance Statement**

46 The ability to move is one of the key evolutionary events that led to the complexity of vertebrate  
47 life. The most speciose group of vertebrates, fishes, displays an enormous variation of movement  
48 patterns during steady swimming. We discovered that this behavioral diversity collapses into one  
49 movement pattern when fishes are challenged to increase their swimming speed, regardless of  
50 their body size, shape and ecology. Using flow visualization and biomimetic models, we  
51 provide the first mechanistic understanding of how this conserved movement pattern allows  
52 fishes to accelerate quickly.

53 \body

54

55 **Introduction**

56 Over the course of evolutionary time, patterns of animal locomotion have diversified to take  
57 advantage of the physical environment through the interplay of morphology, physiology and  
58 neural control. Yet, two fundamental principles of locomotion in most animals remain the same:  
59 1) Force is generated by transferring momentum to the environment through repetitive motions  
60 such as body undulations and oscillating appendages (legs, fins, or wings), and 2) the locomotor  
61 speed is modulated by controlling the amplitude and frequency of these periodic motions (1, 2).  
62 Previous studies have demonstrated that the degrees of freedom in amplitude and frequency  
63 control are not limitless, but rather constrained by the physical laws imposed by the environment.  
64 For example, flying animals must maintain a high wing-beat frequency to generate enough lift,  
65 controlling speed primarily by altering the wing's angle of attack(3). In contrast, the morphology  
66 and locomotion strategies of aquatic animals have adapted to moving through a viscous  
67 environment where gravitational forces are negligible. Among these strategies, the ancestral state  
68 of aquatic locomotion is axial undulation, where muscle contractions bend the body into a  
69 mechanical wave that passes from head to tail (4). The interaction of angled body surfaces with  
70 the surrounding fluid propels the animal forward, and the movements of the entire body  
71 contribute to the overall swimming performance (5-10).

72 Over the past several decades, a number of studies have investigated the kinematics (11-  
73 14), muscle activity (15-18) and hydrodynamics (19-21) of tail movements, in particular how tail  
74 beat amplitude and frequency are controlled during steady swimming. Most undulatory  
75 vertebrates such as fishes, alligators, dolphins and manatees control speed by primarily  
76 modulating tail beat frequency while maintaining a relatively low tail beat amplitude (22-25). At  
77 high steady swimming speeds, tail beat amplitude reaches a plateau at around 0.2 body length

78 (L). Computational studies (26-29) and experiments with hydrofoils (30, 31) suggest that  
79 swimming animals operate in this range to maintain high swimming efficiency.

80         How do these mechanisms apply when a steadily-swimming animal accelerates forward,  
81 which is often used to catch prey, avoid predators or save energy during migrations (32, 33)?  
82 One hypothesis is that speed is gained only by further increasing the tail beat frequency (34-37).  
83 Alternatively, an animal can bend its body maximally to accelerate large amounts of fluid, as  
84 seen in Mauthner initiated C-starts (38-41). Yet emerging studies suggest that forward  
85 acceleration exhibits distinct kinematics (42-46) that defy both hypotheses, indicating that  
86 acceleration may have its own optimization strategy. Although forward acceleration has been a  
87 topic of interest for decades in the field of aquatic locomotion (39, 43), a comprehensive  
88 understanding of its prevalence and underlying mechanisms has remained elusive. Here, we  
89 identify a new undulatory locomotion strategy for forward acceleration by integrating  
90 complementary approaches: biological experiments with live fishes and physical experiments  
91 with bio-mimetic fish models.

92

93

94

95

## 96 **Results and Discussion**

### 97 Acceleration kinematics across fish phylogeny

98           We discovered that in fishes tail beat amplitude is consistently higher during acceleration  
99 than during steady swimming (Fig. 1). This pattern is conserved across 51 species examined,  
100 with representatives from a wide range of phylogenetic positions from chondrichthyes (e.g.  
101 bonnethead shark, *Sphyrna tiburo*) to tetraodontiformes (e.g. striped burrfish, *Chilomycterus*  
102 *schoepfi*). These species exhibit vastly different body shapes, ecological habitats and swimming  
103 modes (Table S1). Some species use median or pectoral fins during steady swimming (e.g. clown  
104 knifefish, *Chitala ornata* and sergeant major, *Abudefduf saxatilis*), but always revert to body  
105 undulation when they accelerate forward from steady swimming.

106           When we plot tail beat amplitude during acceleration against steady swimming for all  
107 species, we found that the relationship is linear (Fig. S1a). This suggests that the relative increase  
108 in tail beat amplitude during acceleration is constant at  $34\pm 4\%$ . However, there is substantial  
109 variation in the absolute amplitude values that depends on body length and shape. For example,  
110 when body length is held constant, elongate fishes such as Florida gar (*Lepisosteus platyrhincus*)  
111 and Northern barracuda (*Sphyraena borealis*) accelerate with lower tail beat amplitudes  
112 ( $0.19\pm 0.01 L$ ) compared to more fusiform fishes such as tarpon and red drum ( $0.24\pm 0.01 L$ ). We  
113 also found that during acceleration tail beat amplitude decreases with body length (Fig. S1b).  
114 To better understand if there is a common propulsive strategy across fish diversity, we next  
115 performed a more detailed midline analysis of the entire body during steady swimming and  
116 forward acceleration for 9 species. Despite extreme differences in body shape and swimming  
117 mode, we found that all fishes share similar midline acceleration kinematics. These acceleration  
118 bouts are usually brief, typically less than five tail beats. All points along the body show higher

119 amplitudes compared to steady swimming, but not as high as seen during C-starts (39, 40) (Fig.  
120 S2-4). Further analyses on the travelling body wave and tail movement suggest efficient force  
121 production during acceleration (Table S2). The average values across 10 species for slip ratio,  
122 Strouhal number ( $St$ ) and maximum angle of attack ( $\alpha_{\max}$ ) are  $0.80\pm 0.02$ ,  $0.41\pm 0.01$ , and  
123  $22.71\pm 0.65^\circ$ , respectively. Slip ratios approaching 1 reveal high swimming efficiency, while  
124 experiments with thrust-producing, harmonically oscillating foils show that propulsive efficiency  
125 is maximized when  $St$  falls within the range of 0.2 and 0.5 and  $\alpha_{\max}$  is between  $15^\circ$  and  $25^\circ$  (30).

126 In addition to the species studied here, similar acceleration kinematics was previously  
127 observed in American eels (44). These elevated amplitudes are most notable around the head and  
128 tail. The onset of acceleration (which can be easily recognized because of strong head yaw and a  
129 faster tail beat) provides a reference point to interpret the phase relationship between head and  
130 tail. By doing so, we found that the motion of the head always precedes the motion of the tail,  
131 indicating that the body wave is initiated by strong head movements in all species, though the  
132 timing between head and tail movements is not constant. To more closely investigate the  
133 kinematics and hydrodynamics of acceleration, we chose a generalized teleost fish, the rainbow  
134 trout (*Oncorhynchus mykiss*). The swimming kinematics of this species has been studied in great  
135 detail for steady swimming and other behaviors but not for acceleration (5, 13, 47-54). Like other  
136 species tested in this study, the body amplitudes of trout are higher during acceleration than  
137 during steady swimming (Fig. S5a), and head movements precede the motion of the tail (Fig.  
138 S5b).

139 We next examined how swimming speed and acceleration depend on tail beat amplitude,  
140 given that a range of amplitudes is evident for each behavior (Fig. S5c). As others have shown  
141 previously (44), we found that in general tail beat frequency, not tail beat amplitude, has the



142 most effect during both behaviors (Fig. S5d). Multiple regression analysis revealed that steady  
143 swimming speed increases only with tail beat frequency. This trend is similar during  
144 acceleration, though tail beat amplitude also has a minor effect (Table S3). Our results suggest  
145 that tail beat amplitude does not change during steady swimming or acceleration, but jumps  
146 discretely by ~30% when fish transition from one behavior to another. Thus, trout appear to have  
147 two undulatory gears based on tail beat amplitude; one for steady swimming and another for  
148 acceleration. Our results suggest that this discrete jump in tail beat amplitude during acceleration  
149 is correlated with increased head yaw (Fig. S5e), and these movements are tightly phase-locked,  
150 with the head preceding the tail (Fig. S5f).

151

#### 152 Hydrodynamic effects of increased tail beat amplitude during acceleration

153 We next investigated how increased tail beat amplitude relates to thrust production and  
154 propulsive efficiency by using a combination of quantitative flow visualization experiments on  
155 live fish and experiments with actuated, soft-bodied robotic models. Results from particle image  
156 velocimetry show that fish can reach a maximum acceleration rate of  $20 L s^{-2}$  from initial  
157 swimming speed of  $3 L s^{-1}$ . To accomplish this, fish transfer more axial momentum to the fluid  
158 by generating stronger vortices compared to steadily swimming fish (Fig. 2a). Similar wake  
159 structures were previously observed in zebrafish (55), eel (44) and carp (45). In addition, fish  
160 entrain more fluid around their posterior body to strengthen shed vortices (Fig. 2b). This occurs  
161 because the posterior body has a greater curvature, which creates a low pressure region in the  
162 concavity (Fig. 2b,  $t=12.5$  ms). The entrained fluid in this low pressure region (blue) follows the  
163 traveling body wave until it reaches the trailing edge of the tail ( $t=50$  ms). At the point when the  
164 tail reverses direction, the fluid starts to roll off the tail and into the wake ( $t=56.3$  ms).

165 Concurrently, the body concavity causes flow to build up on the opposite side. This fluid (red)  
166 starts getting released to the wake as the tail increases its velocity ( $t = 68.8$  ms). When the tail  
167 reaches its maximum velocity a vortex is formed ( $t=81.3$  ms), owing to the occurrence of two  
168 bodies of fluid moving in opposite directions. Our results indicate that during acceleration body  
169 undulations of trout are responsible for increased wake velocity and vorticity. This is not  
170 surprising as multiple studies have shown that body-induced flows can enhance vortex shedding  
171 in other species (7, 8, 10, 19, 56, 57).

172         When fish swim, they generate vortex rings (58-60). We see this in two dimensions as  
173 two counter-rotating vortices (i.e. vortex cores) in the wake after each tail beat (61-63). In recent  
174 years, estimating locomotive forces from wake measurements has garnered much interest with  
175 hopes of better understanding the resultant motion of the animal (41, 56, 64-66). Several  
176 methods have been proposed to estimate locomotive forces (56, 64, 67, 68). The one which we  
177 used in this study is based on the classical vortex ring theory (69). We calculated the impulse  
178 (i.e. the average force) applied to the fluid during each tail beat by measuring the circulation, jet  
179 angle ( $\theta$ ), core diameter ( $D_o$ ) and the spacing between the two vortex cores ( $D$ ). We found that  
180 an accelerating trout generates an impulse (along the swimming direction) that is at least 4 times  
181 higher than that required for its initial steady swimming speed (Fig. 2c). This higher impulse is  
182 due to  $172 \pm 16\%$  increase in vorticity. In addition, the jet angle is oriented  $\sim 30 \pm 3\%$  more  
183 downstream, which devotes a greater proportion of the impulse along the swimming direction.

184         We found that  $D$  is reduced by  $\sim 25\%$  from  $0.33 L$  to  $0.25 L$  when fish transition from  
185 steady swimming to acceleration. At first glance this may be surprising given that the impulse  
186 and kinetic energy of a ring is proportional to its size. However, impulse and energy also depend  
187 on the geometry of the vortex ring itself. One key parameter of the ring geometry is the ratio

188 between minor and major axis diameters ( $d/D$ ). When  $d/D$  approaches one, the ring becomes  
189 more axisymmetric, which is favorable because axisymmetric rings possess the maximum  
190 amount of energy relative to other shapes that maintain the same total impulse (70, 71). Given  
191 that  $d$  is always constrained by the span of the tail (7, 58, 59, 62, 72), the axisymmetry of the ring  
192 primarily depends on  $D$ . Our results show that during steady swimming trout generate elliptical  
193 rings ( $d/D=0.66$ ). In contrast, we found that during acceleration the geometry of the vortex rings  
194 become more axisymmetric ( $d/D=0.88$ ).

195         The impulse of a vortex ring is also proportional to the ratio of its core diameter to its  
196 ring diameter ( $D_o/D$ ). In addition to having a more axisymmetric shape, we found that the vortex  
197 rings generated by accelerating trout have thicker cores ( $D_o/D=0.37\pm 0.02$ ) than those generated  
198 by trout swimming steadily ( $D_o/D=0.25\pm 0.01$ ). It has been shown that for vortex rings generated  
199 by a piston pushing a cylinder of fluid through a nozzle there is a limit in generating thicker arms  
200 efficiently, because at some point (piston stroke to diameter ratio  $>3.5$ ) separation occurs and  
201 energy dissipated by a trailing edge of fluid (73-75). For finite-core, axisymmetric vortex rings  
202 which propagate steadily (76), this piston stroke to diameter ratio corresponds to  $D_o/D = 0.42$  in  
203 a vortex ring (77, 78). Perhaps not coincidentally, the vortex rings generated by accelerating  
204 trout have  $D_o/D$  close to 0.42. In order to evaluate whether our fish-generated vortex rings during  
205 acceleration can be compared to nozzle-generated rings, we analyzed their velocity and vorticity  
206 distributions along a center line connecting the two vortex cores, and confirmed that they closely  
207 match the values reported for nozzle-generated rings (73, 79) (Fig. S6a-c). In addition, we  
208 investigated the temporal dynamics of vortex rings once they are shed into the wake, and found  
209 that they translate downstream with a constant velocity while preserving their  $D_o/D$  ratio (Fig.

210 S6d). What this suggests is that the hydrodynamic principles of efficient thrust production in  
211 oscillating fish may be similar to those observed during biological jet propulsion (65, 80-82).

212 Overall, our findings indicate that accelerating trout generate more thrust, not by  
213 generating larger rings but, by modulating their geometry and orientation. To investigate how  
214 common this phenomenon is, we analyzed  $d/D$ ,  $D_o/D$  and  $\theta$  of four additional species with  
215 different swimming modes and body shapes and found similar results (Table S3). In addition,  
216 flow imaging on a similar sized American eel ( $L=23$  cm) shows that during acceleration  
217 anguilliform swimmers also generate vortex rings with comparable  $D_o/D$  ratio ( $\sim 0.4$  based on  
218 Fig. 1b in (44)). It remains to be seen, however, how  $D_o/D$  ratio scales with body size, given that  
219 it is significantly higher (0.6-0.7) for smaller fish such as zebrafish (83) and koi carps (45). Note  
220 that a 2-dimensional geometric analysis of vortex rings provides an initial, albeit qualitative  
221 understanding on how fishes accelerate efficiently. Concatenated, ring-like structures involved in  
222 the wakes of fishes can be highly elongated and 3-dimensional, and may not have the same  
223 properties (e.g. momentum, energy, and stability) as nozzle-generated rings.

224

225 Relationship between tail kinematics and vortex ring geometry We next propose a set of  
226 equations to provide a mechanistic understanding of how the geometry ( $d/D$  and  $D_o/D$ ) and angle  
227 ( $\theta$ ) of a vortex ring depend on the tail kinematics. Because the oscillating tail generates each core  
228 of a vortex ring successively, we used trigonometric relations to define  $D = \sqrt{a^2 + b^2}$  and  
229  $\theta = \tan^{-1}\left(\frac{a}{b}\right)$ , where  $a$  and  $b$  are the vertical and horizontal spacing between the two cores,  
230 respectively. Based on our wake analysis, the vertical spacing depends on the tail beat amplitude  
231 (i.e.  $a$  = half of the tail beat amplitude), and the horizontal spacing depends on the tail beat  
232 frequency and swimming speed (i.e.  $b$  = swimming speed multiplied by half tail beat cycle). To

233 validate our approach, we calculated  $D$  and  $\theta$  for trout swimming steadily at  $3 L s^{-1}$  and  
234 accelerating from the same initial speed. During acceleration we assumed that the swimming  
235 speed was  $4 L s^{-1}$  (i.e. the average between initial and final swimming speeds). We compared the  
236 predicted  $D$  and  $\theta$  to those measured experimentally, and found a good match (Fig. 2D,  $D=0.31$   
237  $L$  and  $\theta=75.07^\circ$  during steady swimming and  $D=0.22 L$  and  $\theta=63.43^\circ$  during acceleration).  
238 Once we validated our approach, we used it to further investigate the contribution of increased  
239 tail beat amplitude during acceleration. We computationally explored an alternative scenario  
240 where the tail beat amplitude was kept constant at the value observed for steady swimming ( $0.16$   
241  $L$ ), and speed was gained by further increasing the tail beat frequency (i.e. hypothetical  
242 acceleration). Given that thrust is proportional to the square of tail beat frequency multiplied by  
243 the square of tail beat amplitude (84, 85), we increased the tail beat frequency from 10 Hz to  
244 12.5 Hz in order to maintain the same effective thrust. We found that this had no effect on the  
245 ring angle ( $\theta=63.43^\circ$ ), but generated a suboptimal  $D=0.18 L$  with  $d/D=1.22$  and  $D_o/D=0.56$  (we  
246 assumed that  $d=0.22 L$  and  $D_o=0.1 L$ ). Therefore, we believe that the increase in tail beat  
247 amplitude observed in trout is the key to geometrically generating the most efficient rings.

248

#### 249 The swimming performance of robotic models increases with tail beat amplitude

250 While it is favorable to generate more thrust by producing vortex rings with optimal  
251 geometry, this does not reveal the overall swimming efficiency of an accelerating fish because  
252 motions that produce them may be costly. It is not unreasonable to imagine that large lateral  
253 body amplitudes would incur large drag penalties (44, 45). To resolve this tradeoff, we employed  
254 experiments with a biomimetic trout model to systematically explore how different tail beat  
255 amplitudes affect steady swimming and acceleration performance (Fig S7). This level of

256 experimental control is impossible to achieve with live fish. We generated undulatory  
257 movements in our flexible fish model from a single actuation point located just posterior to the  
258 head. Therefore, we were able to control tail beat amplitude by modulating the head yaw.

259 We first measured performance during steady swimming and acceleration at yaw  
260 amplitudes very similar to those of live fish ( $10^\circ$  and  $20^\circ$ ). We found that during steady  
261 swimming the model performed better when it is actuated with smaller yaw (Fig. S8a). However,  
262 during acceleration this relationship is reversed; swimming performance is consistently higher  
263 with larger yaw (Fig. S8b). This suggests that there is no convergence of optimum head yaw  
264 between steady swimming and acceleration. While steady swimming seeks to preserve  
265 momentum by streamlining motions, during acceleration additional momentum must be  
266 generated despite drag costs.

267 To determine if there are yaw values that maximize swimming efficiency during  
268 acceleration, we measured efficiency at yaw amplitudes between  $0^\circ$  and  $30^\circ$  at  $3^\circ$  increments.  
269 We found that efficiency increases linearly with yaw amplitudes up to  $20^\circ$ , beyond which values  
270 plateau (Fig. 3). When we map head yaw from live fish onto our model performance curve, we  
271 found that increasing head yaw from steady swimming values to acceleration values can create  
272 an increase in efficiency up to 100%. It is perhaps no accident that the yaw amplitudes chosen by  
273 accelerating fish fall within the range that gives greatly increased propulsive efficiency compared  
274 to steady swimming. We hypothesize that this is due to generating hydrodynamically more  
275 efficient vortex rings, based on our flow measurements in the wake of live fishes. However,  
276 increasing head yaw to accelerate with more optimal vortex rings does not mean that producing  
277 these rings costs less than the rings produced during steady swimming (Figure S9 shows a 50%  
278 increase in mechanical power input for increased head yaw).

279           The ability to move is one of the key evolutionary events that led to the diversity and  
280 complexity of vertebrate life. Given that movement through fluids is energetically costly, fishes  
281 have found many ways to minimize drag during normal, steady swimming, such as keeping the  
282 body straight and using median or paired fin locomotion (86-88). While steady swimming is  
283 optimized for endurance by minimizing the energetic investment, acceleration favors  
284 maximizing force production to escape quickly from predators or capture elusive prey. Here, we  
285 show that the enormous behavioral diversity observed during steady swimming collapses into a  
286 single locomotion strategy when fishes transition to forward acceleration. We believe that this  
287 strategy is likely conserved across all undulatory swimmers and not just fishes because it is  
288 hydrodynamically the optimal solution to maximize propulsive efficiency.

289 **Methods**

290

291 All research protocols were approved by the Institutional Animal Care and Use Committee at the  
292 University of Florida. All data analyses were performed in Matlab (Mathworks) and all values  
293 are shown as mean  $\pm$  standard error of the mean, unless stated otherwise.

294

295 Diversity of swimming kinematics across species Our data set included 51 species of salt and  
296 freshwater fish (105 individuals, from 20 taxonomic orders), which were either obtained from  
297 commercial dealers or wild caught using cast net or hook-and-line. The details about these  
298 species are given in Table S1, and [the research protocols are described in Text S1](#).

299

300

301 Swimming hydrodynamics of rainbow trout We used digital particle image velocimetry to  
302 quantify the flow fields around and behind steady swimming and accelerating trout. We  
303 estimated wake forces as described in (66) (see [Text S2](#) for more details on the experimental  
304 procedures and data analysis).

305

306 Experiments with the physical fish model We performed the experiments in the flow tank at  
307 Harvard University which is customized to house a computer-controlled external actuator. We  
308 used this system in the past to evaluate the swimming performance in a number of swimming  
309 mechanical models (5, 89-91). Here, we systematically moved the physical model with different  
310 tail kinematics and measured the total sum of forces acting on the whole body. For these



311 measurements, we calculated the propulsive force produced by the model and the corresponding  
312 power output of the actuator as described in (92) ([see Text S3 for more details](#)).

313 **Acknowledgements**

314           We thank Sefki Kolozali for his comments on the earlier version of the manuscript. We  
315 thank Mikhaila Marecki and Elias Lunsford for helping to conduct fish experiments and to  
316 digitize fish midlines. We also thank Ashley N. Peterson and Patrick J.M. Thornycroft for  
317 helping to design and fabricate fish models and conduct experiments with them. Wild caught  
318 species were collected with the generous assistance of Craig Barzso, Jessica Long, Adam Pacetti  
319 and John Perkner. This work was supported by ONR N00014-0910352 to G.V.L., Research  
320 Coordination Network Travel grant DBI-RCN 1062052 to O.A. and J.C.L., National Institute on  
321 Deafness and Other Communication Disorders grant RO1-DC-010809 and National Science  
322 Foundation grant IOS 1257150 to J.C.L.

323 **References**

- 324 1. Alexander RM (2003) *Principles of Animal Locomotion* (Princeton University Press).  
325 2. Biewener (2003) *Animal Locomotion* (Oxford University Press).  
326 3. Nudds RL, Taylor GK, & Thomas ALR (2004) Tuning of Strouhal number for high propulsive  
327 efficiency accurately predicts how wingbeat frequency and stroke amplitude relate and scale with  
328 size and flight speed in birds. *Proceedings Royal Society London B* 271:2071-2076.  
329 4. Gray J (1953) The locomotion of fishes. *Essays in Marine Biology*, eds Marshall SM & Orr AP  
330 (Oliver and Boyd, Edinburgh), pp 1-16.  
331 5. Akanyeti O, *et al.* (2016) Fish optimize sensing and respiration during undulatory swimming.  
332 *Nature Communications* 7.  
333 6. Gemmell BJ, Collin SP, Costello JH, & Dabiri JO (2015) Suction-based on propulsion as a  
334 basis for efficient animal swimming. *Nature communications* 6(8790).  
335 7. Kern S & Koumoutsakos P (2006) Simulations of optimized anguilliform swimming. *The*  
336 *Journal of Experimental Biology* 209:4841-4857.  
337 8. Müller UK, Smit J, Stamhuis EJ, & Videler JJ (2001) How the body contributes to the wake in  
338 undulatory fish swimming: flow fields of a swimming eel (*Anguilla anguilla*). *The Journal of*  
339 *Experimental Biology* 204:2751-2762.  
340 9. Nauen JC & Lauder GV (2001) Three-dimensional analysis of finlet kinematics in the chub  
341 mackerel (*Scomber japonicus*). *The Biological Bulletin* 200(1):9-19.  
342 10. Borazjani I & Sotiropoulos F (2009) Numerical investigation of the hydrodynamics of  
343 anguilliform swimming in the transitional and inertial flow regimes. *Journal of Experimental*  
344 *Biology* 212:576-592.  
345 11. Bainbridge R (1958) The speed of swimming of fish as related to size and to the frequency  
346 and amplitude of the tail beat. *The Journal of Experimental Biology* 35:109-133.  
347 12. Videler JJ & Hess F (1984) Fast continuous swimming of two pelagic predators, saithe  
348 (*Pollachius virens*) and mackerel (*Scomber scombrus*): a kinematic analysis. *The Journal of*  
349 *Experimental Biology* 109:209-228.  
350 13. Webb PW, Kosteki PT, & Stevens ED (1984) The effect of size and swimming speed on the  
351 locomotor kinematics of rainbow trout. *The Journal of Experimental Biology* 109:77-95.  
352 14. Jayne BC & Lauder GV (1995) Speed Effects on Midline Kinematics During Steady  
353 Undulatory Swimming of Largemouth Bass, *Micropterus salmoides*. *The Journal of*  
354 *Experimental Biology* 198(2):585-602.  
355 15. Rome LC, Swank D, & Corda D (1993) How fish power swimming. *Science* 261:340-343.  
356 16. Jayne BC & Lauder GV (1996) New data on axial locomotion in fishes: how speed affects  
357 diversity of kinematics and motor patterns. *American Zoologist* 36(6):642-655.  
358 17. Altringham J & Ellerby DJ (1999) Fish swimming: patterns in muscle function. *The Journal*  
359 *of Experimental Biology* 202(Pt 23):3397-3403.  
360 18. Coughlin DJ (2002) Aerobic muscle function during steady swimming in fish. *Fish and*  
361 *Fisheries* 3:63-78.  
362 19. Videler JJ, Müller UK, & Stamhuis EJ (1999) Aquatic vertebrate locomotion: Wakes from  
363 body waves. *The Journal of Experimental Biology* 202(23):3423-3430.  
364 20. Drucker EG & Lauder GV (2002) Experimental Hydrodynamics of Fish Locomotion:  
365 Functional Insights from Wake Visualization. *Integrative and Comparative Biology* 42(2):243-  
366 257.

- 367 21.Lauder GV & Tytell ED (2005) Hydrodynamics of Undulatory Propulsion. *Fish Physiology*,  
368 (Academic Press), Vol Volume 23, pp 425-468.
- 369 22.Bainbridge R (1963) Caudal fin and body movements in the propulsion of some fish. *The*  
370 *Journal of Experimental Biology* 40:23-56.
- 371 23.Fish FE (1984) Kinematics of Undulatory Swimming in the American Alligator. *American*  
372 *Society of Ichthyologists and Herpetologists* 4:839-843.
- 373 24.Fish FE (1998) Comparative kinematics and hydrodynamics of odontocete cetaceans:  
374 morphological and ecological correlates with swimming performance. *Journal of Experimental*  
375 *Biology* 201:2867-2877.
- 376 25.Kojeszewski T & Fish FE (2007) Swimming kinematics of the Florida manatee (*Trichechus*  
377 *manatus latirostris*): hydrodynamic analysis of an undulatory mammalian swimmer. *Journal of*  
378 *Experimental Biology* 210:2411-2418.
- 379 26.Eloy C (2013) On the best design for undulatory swimming. *Journal of Fluid Mechanics*  
380 717:48-89.
- 381 27.Schultz WW & Webb PW (2002) Power Requirements of Swimming: Do New Methods  
382 Resolve Old Questions? *Integrative and Comparative Biology* 42:1018-1025.
- 383 28.van Rees WM, Gazzola M, & Koumoutsakos P (2015) Optimal morphokinematics for  
384 undulatory swimmers at intermediate Reynolds numbers. *Journal of Fluid Mechanics* 775:178-  
385 188.
- 386 29.Tytell ED, Hsu C-Y, Williams TL, Cohen AH, & Fauci LJ (2010) Interactions between  
387 internal forces, body stiffness, and fluid environment in a neuromechanical model of lamprey  
388 swimming. *National Academy of Sciences* 107(46):19832–19837.
- 389 30.Anderson JM, Streitlien K, Barrett DS, & Triantafyllou MS (1998) Oscillating foils of high  
390 propulsive efficiency. *Journal of Fluid Mechanics* 360:41-72.
- 391 31.Taylor GK, Nudds RL, & Thomas AL (2003) Flying and swimming animals cruise at a  
392 Strouhal number tuned for high power efficiency. *Nature* 425(6959):707-711.
- 393 32.Weih D & Webb PW (1983) Optimization of Locomotion. *Fish Biomechanics*, eds Webb  
394 PW & Weih D (Praeger Publishers, New York).
- 395 33.Gleiss AC, *et al.* (2011) Convergent evolution in locomotory patterns of flying and swimming  
396 animals. *Nature Communications* 2.
- 397 34.Rome LC, *et al.* (1988) Why animals have different muscle fibre types. *Nature* 335:824 - 827.
- 398 35.Johnson TP, Syme DA, Jayne BC, Lauder GV, & Bennett AF (1994) Modeling red muscle  
399 power output during steady and unsteady swimming in largemouth bass. *American Journal of*  
400 *Physiology- Regulatory, Integrative and Comparative Physiology* 267(2 pt 2):R481-R488.
- 401 36.Weih D (1974) Energetic Advantages of Burst Swimming of Fish. *Journal of Theoretical*  
402 *Biology* 48:215-229.
- 403 37.Videler JJ & Weih D (1982) Energetic advantages of burst-and-coast swimming of fish at  
404 high speeds. *Journal of Experimental Biology* 97:169-178.
- 405 38.Eaton RC, Bombardieri RA, & Meyer DL (1977) The Mauthner-initiated startle response in  
406 teleost fish. *Journal of Experimental Biology* 66(1):65-81.
- 407 39.Domenici P & Blake RW (1997) The Kinematics and Performance of Fish Fast-Start  
408 Swimming. *The Journal of Experimental Biology* 200(pt 8):1165-1178.
- 409 40.Wakeling JM (2006) Fast-start mechanics. *Fish Biomechanics*, eds Shadwick RE & Lauder  
410 GV (Academic Press, San Diego), pp 333-368.
- 411 41.Tytell ED & Lauder GV (2008) Hydrodynamics of the escape response in bluegill sunfish,  
412 *Lepomis macrochirus*. *Journal of Experimental Biology* 211:3359-3369.

413 42.Fierstine HL & Walters V (1968) Studies in locomotion and anatomy of scombroid fishes.  
414 *Memoirs of the Southern California Academy of Science* 6:1-31.  
415 43. Videler JJ (1993) *Fish Swimming* (Chapman and Hall, New York).  
416 44.Tytell ED (2004) Kinematics and hydrodynamics of linear acceleration in eels, *Anguilla*  
417 *rostrata*. *Philosophical Transactions Royal Society London B* 271:2535-2540.  
418 45.Wu G, Yang Y, & Zeng L (2007) Kinematics, hydrodynamics and energetic advantages of  
419 burst-and-coast swimming of koi carps (*Cyprinus carpio koi*). *Journal of Experimental Biology*  
420 210:2181-2191.  
421 46.van Leeuwen JL, Lankheet MJM, Akster HJ, & Osse JWM (1990) Function of red axial  
422 muscles of carp (*Cyprinus carpio* L.): recruitment and normalized power output during  
423 swimming in different modes. *Journal of Zoology London* 220(123-145).  
424 47.Drucker EG & Lauder GV (2003) Function of pectoral fins in rainbow trout: behavioral  
425 repertoire and hydrodynamic forces. *Journal of Experimental Biology* 206(Pt 5):813-826.  
426 48.Drucker EG & Lauder GV (2005) Locomotor function of the dorsal fin in rainbow trout:  
427 kinematic patterns and hydrodynamic forces. *The Journal of Experimental Biology* 208(Pt  
428 23):4479-4494.  
429 49.Coughlin DJ (2000) Power production during steady swimming in largemouth bass and  
430 rainbow trout. *The Journal of Experimental Biology* 203:617-629.  
431 50.Ellerby DJ & Altringham JD (2001) Spatial variation in fast muscle function of the rainbow  
432 trout *Oncorhynchus mykiss* during fast-starts and sprinting. *The Journal of Experimental Biology*  
433 204(Pt 13):2239-2250.  
434 51.Liao JC, Beal DN, Lauder GV, & Triantafyllou MS (2003) The Kármán gait: novel body  
435 kinematics of rainbow trout swimming in a vortex street. *The Journal of Experimental Biology*  
436 206(6):1059-1073.  
437 52.Akanyeti O & Liao JC (2013) Effect of flow speed and body size on Kármán gait kinematics  
438 in rainbow trout. *The Journal of Experimental Biology* 216:3442-3449.  
439 53.Stewart WJ, Tian F, Akanyeti O, Walker CJ, & Liao JC (2016) Refuging rainbow trout  
440 selectively exploit flows behind tandem cylinders. *Journal of Experimental Biology*  
441 219(14):2182-2191.  
442 54.Akanyeti O & Liao JC (2013) A kinematic model of Kármán gaiting in rainbow trout. *The*  
443 *Journal of Experimental Biology* 216(24):4666-4677.  
444 55.Müller UK, Stamhuis EJ, & Videler JJ (2000) Hydrodynamics of unsteady fish swimming  
445 and the effects of body size: Comparing the flow fields of fish larvae and adults. *The Journal of*  
446 *Experimental Biology* 203(2):193-206.  
447 56.Tytell ED & Lauder GV (2004) The hydrodynamics of eel swimming: I. Wake structure  
448 *Journal of Experimental Biology* 207:1825-1841.  
449 57.Gemmell BJ, *et al.* (2016) How the bending kinematics of swimming lampreys build negative  
450 pressure fields for suction thrust. *Journal of Experimental Biology* 219:3884-3895.  
451 58.Flammang BE, Lauder GV, Troolin DR, & Strand TE (2011) Volumetric imaging of fish  
452 locomotion. *Biology Letters* 7(5):695-698.  
453 59.Mendelson L & Techet AH (2015) Quantitative wake analysis of a freely swimming fish  
454 using 3D synthetic aperture PIV. *Experiments in Fluids* 56(135):1-19.  
455 60.Tytell ED, Standen EM, & Lauder GV (2008) Escaping Flatland: three dimensional  
456 kinematics and hydrodynamics of median fins in fishes. *Journal of Experimental Biology*  
457 211(2):187-195.

458 61. Blickhan R, Krick C, Zehren D, Nachtigall W, & Breithaupt T (1992) Generation of a vortex  
459 chain in the wake of a Subundulatory swimmer. *Naturwissenschaften* 79(5):220-221.

460 62. Nauen JC & Lauder GV (2002) Hydrodynamics of caudal fin locomotion by chub mackerel,  
461 *Scomber japonicus* (Scombridae). *The Journal of Experimental Biology* 205(12):1709-1724.

462 63. Müller UK, Van den Heuvel BLE, Stamhuis EJ, & Videler JJ (1997) Fish foot prints:  
463 morphology and energetics of the wake behind a continuously swimming mullet (*Chelon*  
464 *labrosus* Risso). *The Journal of Experimental Biology* 200(22):2893-2906.

465 64. Drucker EG & Lauder GV (1999) Locomotor forces on a swimming fish: three-dimensional  
466 vortex wake dynamics quantified using digital particle image velocimetry. *Journal of*  
467 *Experimental Biology* 202(Pt 18):2393-2412.

468 65. Bartol IK, Krueger PS, Stewart WJ, & Thompson JT (2009) Hydrodynamics of pulsed jetting  
469 in juvenile and adult brief squid *Lolliguncula brevis*: evidence of multiple jet 'modes' and their  
470 implication of propulsive efficiency. *Journal of Experimental Biology* 212:1889-1903.

471 66. Epps BP & Techet AH (2007) Impulse generated during unsteady maneuvering of swimming  
472 fish. *Experiments in Fluids* 43:691-700.

473 67. Noca F, Shiels D, & Jeon D (1999) A comparison of methods for evaluating time-dependent  
474 fluid dynamic forces on bodies, using only velocity fields and their derivatives. *Journal of Fluids*  
475 *and Structures* 13:551-578.

476 68. Dabiri JO (2005) On the estimation of swimming and flying forces from wake measurements.  
477 *Journal of Experimental Biology* 208:3519-3532.

478 69. Batchelor GK (2000) *An Introduction to Fluid Dynamics* (Cambridge University Press).

479 70. Kelvin L (1880) Vortex statistics. *Philosophical Magazine* 10:97-109.

480 71. Dabiri JO (2009) Optimal vortex formation as a unifying principle in biological propulsion.  
481 *Annual Review of Fluid Mechanics* 41:17-33.

482 72. Borazjani I & Daghooghi M (2013) The fish tail motion forms an attached leading edge  
483 vortex. *The Royal Society Proceedings B* 280(1756):20122071.

484 73. Gharib M, Rambod E, & Shariff K (1998) A universal time scale for vortex ring formation.  
485 *Journal of Fluid Mechanics* 360:121-140.

486 74. Krueger PS & Gharib M (2005) Thrust augmentation and vortex ring evolution in a fully  
487 pulsed jet. *The Journal of American Institute of Aeronautics and Astronautics* 43(4):792-801.

488 75. Mohseni K & Gharib M (1998) A model for universal time scale of vortex ring formation.  
489 *Physics of Fluids* 10:2436-2438.

490 76. Norbury J (1973) Family of steady vortex rings. *Journal of Fluid Mechanics* 57:417-431.

491 77. Linden PF & Turner JS (2004) 'Optimal' vortex rings and aquatic propulsion mechanisms.  
492 *Proceedings of The Royal Society B* 271(1539):647-653.

493 78. Linden PF & Turner JS (2001) The formation of 'optimal' vortex rings, and the efficiency of  
494 propulsion devices. *Journal of Fluid Mechanics* 427:61-72.

495 79. Weigand A & Gharib M (1997) On the evolution of laminar vortex rings. *Experiments in*  
496 *Fluids* 22:447-457.

497 80. Dabiri JO, Collin SP, Katija K, & Costello JH (2010) A wake-base correlate of swimming  
498 performance and foraging behavior in seven co-occurring jellyfish species. *Journal of*  
499 *Experimental Biology* 213:1217-1225.

500 81. Gharib M, Rambod E, Kheradvar A, Sahn DJ, & Dabiri JO (2006) Optimal vortex formation  
501 as an index of cardiac health. *Proceedings of the National Academy of Sciences of the United*  
502 *States of America* 103:6305-6308.

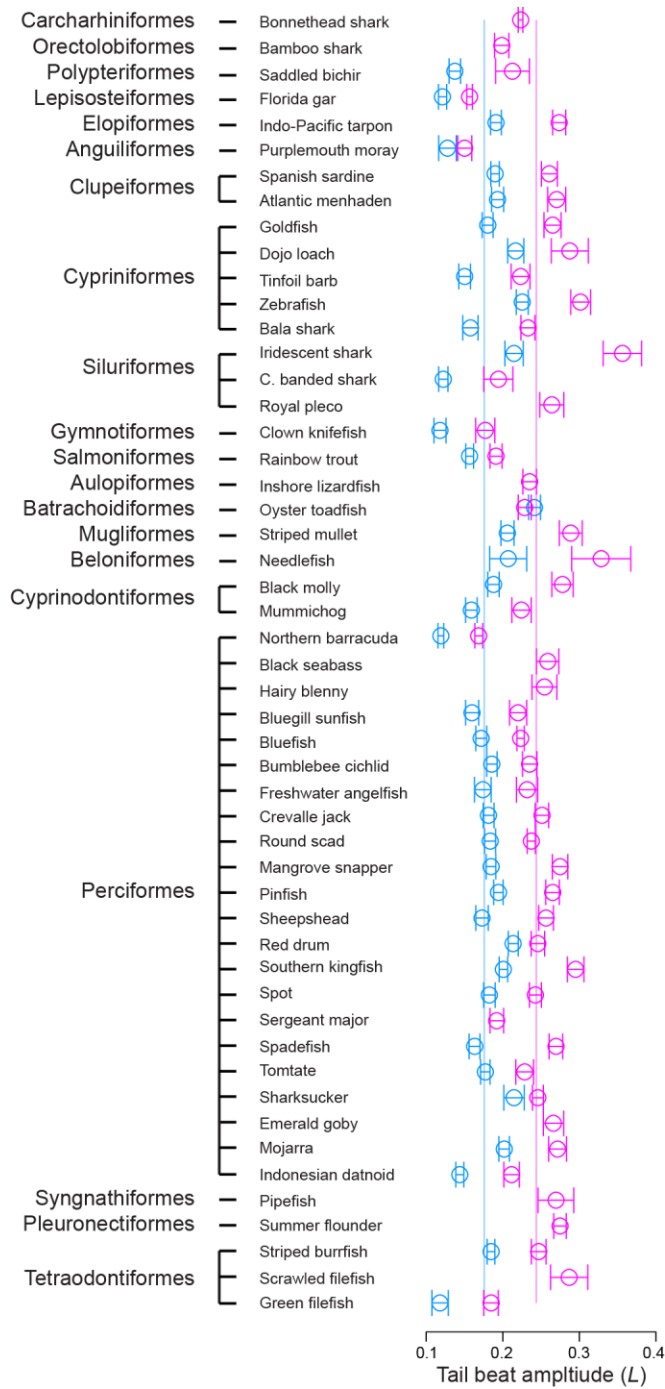
- 503 82.Dabiri JO, Collin SP, & Costello JH (2006) Fast-swimming hydromedusae exploit velar  
504 kinematics to form an optimal vortex wake. *Journal of Experimental Biology* 209:2025-2033.
- 505 83.Müller UK & van Leeuwen JL (2004) Swimming of larval zebrafish: ontogeny of body waves  
506 and implications for locomotory development. *The Journal of Experimental Biology* 207(Pt  
507 5):853-868.
- 508 84.Wu TY (1977) Introduction to scaling of aquatic animal locomotion. *Scale Effects of Animal*  
509 *Locomotion*, ed Pedley TJ (Academic Press, New York, NY), pp 203-232.
- 510 85.Lighthill J (1971) Large-amplitude elongated body theory of fish locomotion. *Proceedings of*  
511 *the Royal Society B: Biological Sciences* 179(1055):125-138.
- 512 86.Lighthill J (1993) Estimates of Pressure Differences across the Head of a Swimming Clupeid  
513 Fish. *Philosophical Transactions of the Royal Society B: Biological Sciences* 341(1296):12.
- 514 87.Webb PW (1992) Is the high cost of body/caudal fin undulatory swimming due to increased  
515 friction drag or inertial recoil? *The Journal of Experimental Biology* 162:157-166.
- 516 88.Fish FE (1998) Imaginative solutions by marine organisms for drag reduction. *Proceedings of*  
517 *the International Symposium on Seawater Drag Reduction*:443-450.
- 518 89.Lauder GV, Flammang BE, & Alben S (2012) Passive robotic models of propulsion by the  
519 bodies and caudal fins of fish. *Integrative and Comparative Biology* 52:576-587.
- 520 90.Shelton RM, Thornycroft JMP, & Lauder VG (2014) Undulatory locomotion of flexible foils  
521 as biomimetic models for understanding fish propulsion. *Journal of Experimental Biology*  
522 217:2110-2120.
- 523 91.Lauder GV & Tangorra JL (2015) Fish locomotion: biology and robotics of body and fin-  
524 based movements. *Robot Fish - Bioinspired Fishlike Underwater Robots*, eds Du R, Li Z,  
525 Youcef-Toumi K, & Valdivia Y Alvarado P (Springer-Verlag, Berlin), pp 25-49.
- 526 92.Read DA, Hover FS, & Triantafyllou MS (2003) Forces on oscillating foils for propulsion  
527 and maneuvering. *Journal of Fluids and Structures* 17:163-183.

528  
529  
530

531

532 **Figures**

533 **Figure 1**



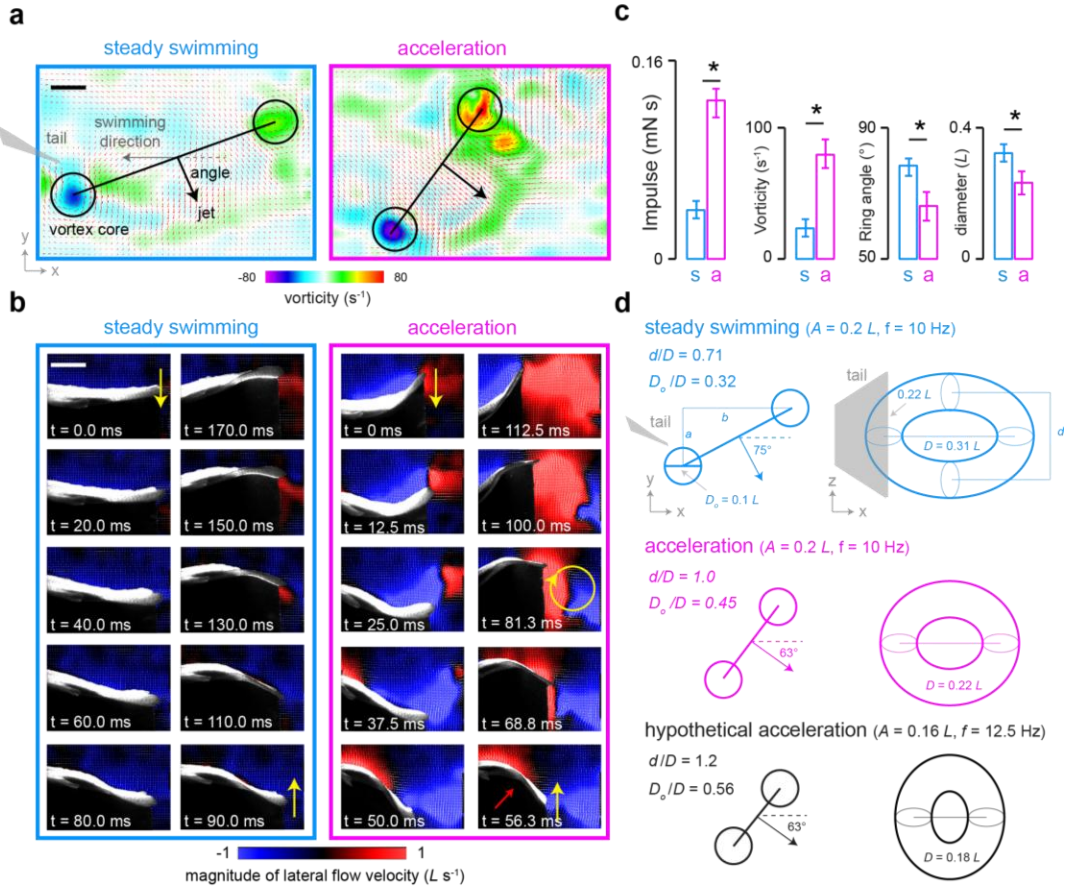
534  
535



536 Figure 2.

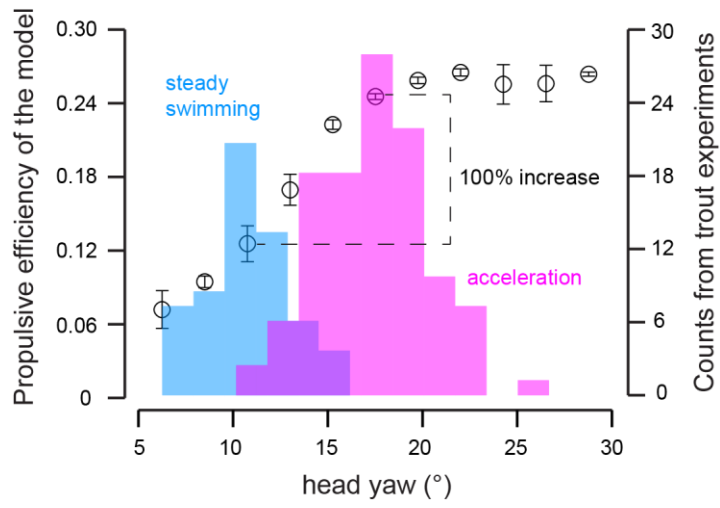
537

538



539  
540

541 Figure 3.



542

543 **Figure Legends**

544

545 Figure 1. Fishes have higher tail beat amplitude during acceleration. (a) This phenomenon was  
546 confirmed across a wide range of fishes from 20 taxonomic orders with different body shapes,  
547 swimming modes and ecologies. Blue and magenta lines indicate the mean tail beat amplitudes  
548 for steady swimming ( $0.181 \pm 0.004 L$ ) and acceleration ( $0.244 \pm 0.006 L$ ), respectively. Mean  
549 tail beat amplitudes for steady swimming and acceleration are statistically different (unpaired T-  
550 test,  $P < 0.001$ ). During steady swimming, it was not possible to measure the tail beat amplitude  
551 of few species (black seabass, sergeant major, pipefish, summer flounder and filefish), as they  
552 use primarily median or pectoral fins for propulsion. Error bars are  $\pm$  one standard error of the  
553 mean.

554 Figure 2. Hydrodynamics of steady swimming versus acceleration. (a) Representative flow fields  
555 behind a rainbow trout ( $L=32$  cm) swimming steadily at  $3 L s^{-1}$  (left) and accelerating (right)  
556 from the same initial speed. The heat map denotes vorticity where negative (magenta) and  
557 positive (red) values indicate clockwise and counter-clockwise rotation, respectively. The length  
558 of the scale bar is 2 cm. (b) Body movements of the same fish during steady swimming (left  
559 column) and acceleration (right column) over one representative tail beat cycle. Yellow arrows  
560 indicate the direction of tail movement. The blue and red denote the magnitude of left and right  
561 flow fields, respectively, in the fish frame of reference. In each video frame, the body of the trout  
562 is visible from the dorsal fin to the tail, which represents the 30% of the total length. The length  
563 of the scale bar is 4.5 cm. (c) Mean impulse, vorticity, angle and diameter of an average vortex  
564 ring for steady swimming and acceleration (10 tail beats from each fish,  $n=2$  fish). \* denotes  
565 significant at  $P<0.01$ , unpaired T-test. Error bars are  $\pm$  one standard error. (d) Hypothesized  
566 vortex ring geometry and orientation behind fish swimming steadily (blue) and accelerating  
567 (magenta). Hypothetical acceleration with lower tail beat amplitude is also shown for  
568 comparison (black).  
569

570 Figure 3. Fishes adopt acceleration kinematics tuned for high propulsive efficiency. Propulsive  
571 efficiency of the physical model as a function of head yaw at flow speed  $1.2 L s^{-1}$  (left axis, black  
572 points; error bars are  $\pm$  one standard error); propulsive efficiency increases with increasing head  
573 yaw. A histogram of head yaw (right axis) is shown for live trout during steady swimming (blue)  
574 and acceleration (magenta). Note that the overlapped region between the distributions steady  
575 swimming and acceleration appears darker. The average head yaw for steady swimming and  
576 acceleration is  $12.469 \pm 0.370^\circ$  and  $17.805 \pm 0.352^\circ$ , respectively (unpaired T-test,  $P < 0.01$ ).  
577