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Fish Swimming in a Kármán Vortex Street
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1 **FISH SWIMMING IN A KÁRMÁN VORTEX STREET: KINEMATICS, SENSORY**

2 **BIOLOGY AND ENERGETICS**

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Abstract

Fishes often live in environments characterized by complex flows. To study the mechanisms of how fishes interact with unsteady flows, the periodic shedding of vortices behind cylinders has been employed to great effect. In particular, fishes that hold station in a vortex street (i.e. Kármán gaiting) show swimming kinematics that are distinct from their patterns of motion during freestream swimming in uniform flows, although both behaviors can be modelled as an undulatory body wave. Kármán gait kinematics are largely preserved across flow velocities. Larger fish have a shorter body wavelength and slower body wave speed than smaller fish, in contrast to freestream swimming where body wavelength and wave speed increases with size. The opportunity for Kármán gaiting only occurs under specific conditions of flow velocity and depends on the length of the fish; this is reflected in the highest probability of Kármán gaiting at intermediate flow velocities. Fish typically Kármán gait in a region of the cylinder wake where the velocity deficit is about 40% of the nominal flow. The lateral line plays a role in tuning the kinematics of the Kármán gait, since blocking it leads to aberrant kinematics. Vision allows fish to maintain a consistent position relative to the cylinder. In the dark, fish do not show the same preference to hold station behind a cylinder though Kármán gait kinematics are the same. When oxygen consumption level is measured, it reveals that Kármán gaiting represents about half of the cost of swimming in the freestream.

Introduction

Understanding how fishes swim in unsteady flows has attracted attention from many disciplines, ranging from biologists interested in fish ecology to engineers working on the

48   principles of efficient propulsion [1-5]. Because the hydrodynamics of a cylinder wake is well-

49   characterized [6], examining how fish interact with cylinder vortices has provided a tractable way

50   to begin to understand fish-fluid interactions under complex, yet predictable flow conditions [7-9].

51   This is because the relationships between flow velocity, cylinder diameter, and vortex shedding

52   frequency are already known. Flow moving past the cylinder creates vortices that shed

53   alternately from each side of the cylinder, with the vortices staggered as two columnar arrays [6,10].

54   For Reynolds numbers of 40 – 100,000 in which many fishes swim, the Strouhal number (*St*) for

55   cylinders is 0.2, where *f* is the vortex shedding frequency, *d* is the diameter of the cylinder, and *U*

56   is the nominal flow velocity.

57

58   $$St = \frac{fd}{U} \qquad (1)$$

59

60   The spacing of the vortices, or wake wavelength (*λ*) can be calculated from the flow velocity

61   divided by the vortex shedding frequency.

62

63   $$\lambda = U/f \qquad (2)$$

64

65   This enables experimenters the ability to control the frequency and spacing of vortices by

66   altering the flow speed and cylinder size, and has provided a unique opportunity to study how

67   fish behave in an unsteady, periodic environment.

68   Previous studies revealed that fishes adopt novel body kinematics behind a cylinder,

69   termed the Kármán gait. Kármán gaiting can save energy for station holding fishes, and occurs

70   under certain conditions of flow velocity, body length, and cylinder size [8,11-13]. To identify

71   Kármán gaiting, five criteria are used: 1) the fish is holding station and not drifting upstream or

72   downstream, 2) there is a traveling wave along the body, 3) the body displays a large lateral

73   displacement ($> \frac{1}{2} L$), 4) the body posture adopts a long wavelength (>1 L), and 5) there are no

74   transient small-amplitude, high-frequency tail beats.

75

76   *Body wave kinematics of Kármán gaiting versus freestream swimming*

77   A travelling wave along the body can describe both freestream swimming and Kármán

78   gaiting kinematics for subcarangiform swimming fishes. This equation, with an arbitrary initial

79   phase (ϕ), takes the form:

80

81    $$h(x,t) = A(x) * \sin\left(\frac{2\pi}{\lambda}x - 2\pi f t + \phi\right) \qquad (3)$$

82

83   where t and x denote time and position along the body, respectively. The wave initiation point

84   varies with the locomotor mode (thunniform, carangiform, anguilliform), which is defined

85   according to how much of the body participates in the undulatory wave [14]. Tail beat frequency (f)

86   and body wavelength (λ) define the temporal and spatial periodicity of the equation. The speed of

87   the travelling wave (V) is defined by

88

89                                $$V = \lambda f \qquad (4)$$

90

91   The amplitude envelope ($A(x)$) also depends on the locomotor mode. For subcarangiform

92   swimmers such as rainbow trout and mackerel, it is described by a second order polynomial

93    $A(x) = c_1 x + c_2 x^2$ [15].

94   Whether the travelling wave is generated actively through muscular activity or passively

95   due to flow-induced motions varies depending on the flow regime. In freestream swimming, an

96   antero-posterior wave of red muscle activity drives the propagation of the wave [16]. In contrast,

97   during Kármán gaiting undulatory waves are generated passively as a result of lateral

98   acceleration while the fish is being buffeted from side to side by the fluid [8]. Several findings

99   support this argument. First, muscle recordings indicate that Kármán gaiting fish activate only

100   the anterior red axial muscles [12]. Second, dead trout temporarily generate a mechanical wave

101   similar to live fish [17]. Third, there is a high correlation between the lateral acceleration and tail

102   beat amplitude of the fish.

103   Freestream swimming and Kármán gaiting differ in that they are separated in the

104   parameter space; the amplitude, wavelength and frequency values of the travelling wave

105   equation are substantially different for each behavior [18]. During Kármán gaiting, the wave is

106   initiated at the body centre, which is $0.2\,L$ (where L = total body length) further down the body

107   compared to the initiation point in freestream swimming. Fourier analysis on the motions of a

108   dead trout towed behind a cylinder shows that in a completely passive body, the wave starts at

109   the base of the cranium similar to freestream swimming (Fig. 1). This suggests that the location

110   of the wave initiation point during Kármán gaiting is not due to the passive fish-fluid

111   interactions. When live fish Kármán gait they activate their anterior muscles in order to adopt a

112   straight posture in the mid-body region; as a result this arrangement changes the location of the

113   initiation point. In this way, the interaction between fish and fluid in the mid-body region is more

114   critical than the posterior region. Fish appear to keep the mid-body region from bending in order

115   to provide a local axial control surface to harness the appropriate fluid forces. In addition to

116 undulation, Kármán gaiting fish also exhibit substantial lateral translations and body rotations,

117 which can constitute up to 75% of the behavior.

118

119 *Body wave speed increases with flow speed*

120   Kármán gaiting fish respond to increasing flow speed by increasing the speed of their

121 traveling body wave. To do so, fish increase tail-beat frequency while keeping body wavelength

122 and amplitude constant. Why does tail-beat frequency change and not body wavelength? Kármán

123 gaiting is a flow-dominated behavior, where cylinder wake wavelength and vortex shedding

124 frequency drives the body wavelength and tail-beat frequency. The cylinder vortex shedding

125 frequency, but not wavelength, increases with flow speed, setting up a condition where the body

126 wavelength is preserved across flow speed.

127   Experiments have shown that even a rigid foil positioned in a vortex street can generate

128 thrust [17]. What, then, is the role of the traveling wave in Kármán gait? In uniform flow, the ratio

129 of the traveling wave to the forward body speed (i.e. slip) approaches unity when swimming is

130 efficient because more momentum is directed towards forward thrust. This concept is less useful

131 in a vortex street environment, where the contributions of passive versus powered thrust

132 generation are harder to differentiate. The traveling wave is not entirely passive, given that

133 across flow velocities body wave speed is consistently 25% greater than the speed of the vortices

134 drifting at the nominal flow speed [19].

135 *The effect of fish length on body wavelength*

136   Fish relate to the vortex street in different ways depending on their body length. Kármán

137 gaiting fish require cylinder-to-body length ratios that range from 1:2 to 1:4 [11,19]. The body

138 wavelength of the fish affects its ability to properly interact with vortices to produce thrust. In

139   order to Kármán gait, small fish interact differently with cylinder vortices than larger fish. When

140   small fish Kármán gait, they have a longer body wavelength than larger fish, reflecting the

141   relatively larger size and spacing of the cylinder vortices. Hypothetically, a larger fish may be

142   able to adopt a shorter wavelength because the body spans to interact with two successive

143   vortices, while a smaller fish must adopt a longer wavelength because its body can only interact

144   with one vortex. This is the opposite of what is found in freestream swimming, where body

145   wavelength increases with fish size [20]. As mention above, during the Kármán gait less of the

146   body participates in the traveling wave than observed for freestream swimming. Therefore, a

147   longer body length does not correspond to a longer body wavelength as it seems to do for

148   freestream swimming (Fig. 4).

149   Regardless of body size, Kármán gaiting fish possess a body wavelength that is longer

150   than the wake wavelength at intermediate flow speeds. This relationship seems critical to hold

151   station and likely orients the body to create more thrust-generating interactions with passing

152   vortices.

153   ***Probability of Kármán gaiting depends on flow speed***

154   One of the most important factors determining how often fish prefer to Kármán gait is the

155   nominal flow speed to which the cylinder is exposed. Figure 2 shows that the highest probability

156   of Kármán gaiting occurs at intermediate flow speeds between 2-5 body lengths per second [19].

157   The body center of the fish is typically located 4-6 cylinder diameters downstream from the

158   cylinder regardless of flow velocity level (Fig. 3A). This region corresponded to a velocity

159   deficit of about 40% of the nominal velocity (Fig. 3B). At low flow velocities fish did not

160   Kármán gait often and their motions resembled freestream swimming. This is because vortical

161   flows must be sufficiently developed before fish can exploit them [8,11-13]. Kinematic results

162   support this interpretation; at lower flow speeds the tail-beat frequency was considerably higher

163   than the vortex shedding frequency[19]. The tail-beat frequency at the low flow speed was identical

164   to that of a freestream swimming fish [20]. Furthermore, body wavelength and tail-beat amplitude

165   were very similar to those found in freestream swimming fish. At the highest speeds, trout do not

166   hold station continuously and are either drawn upstream into the suction zone behind the

167   cylinder, or ejected laterally from the vortex street. Under these higher Reynolds number flow

168   conditions the wake can adopt complex, three-dimensional vortex dynamics such as braid

169   vortices and other hydrodynamic instabilities [21]. Merging and pairing between initial shear layer

170   vortices can give rise to secondary structures that contribute to irregular vortex shedding

171   frequencies and amplitudes [6,22]. The resulting turbulent vortex street exceeds the stabilization

172   abilities of fishes.

173

174   *Sensory feedback during the Kármán gait*

175   What roles do vision and the lateral line play in the ability to exploit vortices in a cylinder

176   wake? Theoretically, the hydrodynamic conditions of an oscillating wake make it possible for

177   any foil-shaped object of the appropriate size to generate thrust passively [23,24]. Experimental

178   evidence shows that a dead trout towed behind a cylinder can momentarily synchronize its body

179   kinematics to the oscillating flow of a vortex street to generate thrust [12,17]. However, for a fish to

180   remain in the cylinder wake for sustained periods requires sensory feedback from the visual and

181   lateral line systems.

182   In general fishes rely heavily on both visual [25,26] and hydrodynamic [27-29] cues to adapt

183   their swimming movements to their immediate environment. Kármán gait kinematics change

184   when the lateral line is blocked, indicating that hydrodynamic feedback is used to alter motor

185 output accordingly in turbulent flows. The greater variability in body wavelength for trout with a

186 blocked *vs.* intact lateral line underscores the importance of detecting local flow along the body

187 in adjusting Kármán gait kinematics to maintain a favorable posture to facilitate vortex capture.

188 In addition, trout with a blocked lateral line hold station further downstream from the cylinder

189 than fish with an intact lateral line. These lines of evidence reiterate that a proportion of Kármán

190 gait kinematics are under active control and are not the sole result of passive buffeting of the

191 body by vortices. Longer body wavelength and faster wave speed suggest that Kármán gaiting is

192 less efficient or more energetically costly without a functional lateral line. The fact that trout in

193 the light with a blocked lateral line do not spend as much time Kármán gaiting as trout with a

194 functional lateral line (Fig. 5) provides behavioral evidence in support of this hypothesis.

195 Whether altered Kármán gait kinematics reflect muscle activity and changes in energy

196 expenditure for the individual is currently not known. When lateral line functionality is held

197 constant (i.e. within fish with an intact or blocked lateral line), the presence or absence of light

198 does not change Kármán gait kinematics. This provides further evidence that when trout hold

199 station in a vortex street the lateral line, rather than vision, plays a larger role in body kinematics.

200   One exception occurs where vision alone can alter Kármán gait kinematics. Fish with a

201 blocked lateral line in the dark have a greater variability in body wavelength than fish in the

202 light. These fish seem to have more difficulty exploiting vortices, often drifting position within

203 the vortex street, displaying "corrective" motions, or switching to traditional undulatory

204 swimming such as seen in uniform flow. Vision allows fish to maintain a consistent position

205 relative to the cylinder. This may minimize the exposure to flow variation and thus variation in

206 body wavelength, since the predictability and energy of the vortices decreases with downstream

207 distance from the cylinder.

Energetics of Kármán gaiting

209   The cost of Kármán gaiting can be measuring directly and non-invasively in live fishes

210   by employing the technique of respirometry, which measures the oxygen consumed during a

211   particular behavior. There are several regions around a cylinder that fish choose to hold station.

212   Figure 6 illustrates that for a given flow speed, oxygen consumption during Kármán gaiting is

213   higher than entraining near the suction region, but lower than bow waking in the front of the

214   cylinder [13]. Kármán gaiting represents about half of the cost (47%) of swimming in the

215   freestream away from the cylinder. When compared to freestream swimming in flow equivalent

216   to the reduced velocity behind the cylinder (which is about 40% of the nominal flow velocity),

217   Kármán gaiting represents about 79% of the cost [11]. Therefore, by exploiting vortices Kármán

218   gaiting fish used significantly less oxygen than predicted if there were only benefiting from

219   swimming in the reduced velocity of the cylinder wake.

220

221   *Future directions*

222   Our work on the midline kinematics of Kármán gaiting, sensory biology and energetics

223   can be used by roboticists to develop control algorithms that can move bio-inspired robots and

224   by computational fluid dynamics modelers to simulate fluid-structure interactions. Given that the

225   majority of the body waves during Kármán gaiting are generated passively, it is more important

226   for a flexible robot to control its head and the anterior body than control its posterior body. If

227   hydrodynamic forces are harnessed appropriately at the anterior body, a travelling wave is

228   generated passively at the posterior body starting from the body centre. This represents a

229   paradigm shift in the field of autonomous robotics locomotion which traditionally emphasize the

230   control of the posterior body [30-32]. What Kármán gaiting studies teach us is that head control is

231   critical for steering and improving stability in unsteady flows by counter-balancing body

232   rotations and lateral translation, and that control functionality can be outsourced to the visco-

233   elastic properties of the body itself.

234   The study of biological locomotion in unsteady flow regimes is a promising one that

235   stands to shed light on new mechanisms of hydrodynamic propulsion. Though vortex streets

236   generated by cylinders has proven to be a production experimental system, overall the responses

237   of fishes to unsteady flows remains largely unexplored. Around a single cylinder, already three

238   distinct energy-saving behaviors are observed. What if the wakes behind three-dimensional

239   objects, arranged in aggregations, or varying in flexibility, were investigated in more species? It

240   is apparent that the diversity of maneuvering, wake-exploitation and drag-reduction behaviors

241   would reflect the inexhaustible number of scenarios between over 33,000 species of fishes and

242   unsteady flow conditions. Along this vein, experiments into more natural flow conditions stand

243   to be well rewarded. For example, investigating the behavior of fish holding station behind two

244   cylinders in tandem, only a slightly more involved experiment than a single cylinder but closer to

245   mimicking flows from more natural object aggregations such as large woody debris in streams,

246   already reveals new principles of fluid-solid interactions and wake exploitation that could not be

247   predicted [33]. Another promising topic is the investigation of how fishes navigate waves in the

248   surf zone during foraging. With the application of Digital Particle Image Velocimetry, high

249   speed videography and physiological techniques such as respirometry and electromyography,

250   new insights into the mechanisms of fish locomotion are now more accessible to marine

251   technology applications.

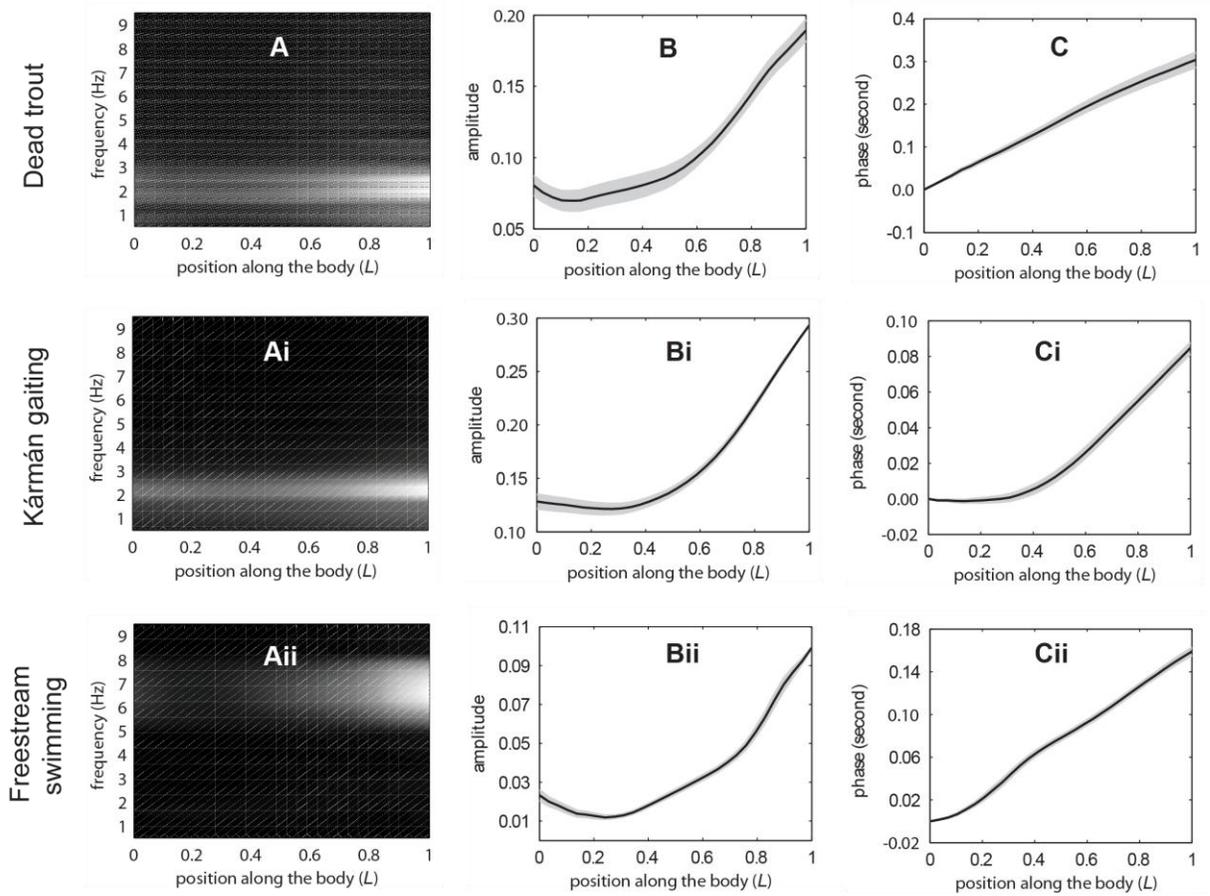252

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Figures

261   Fig. 1

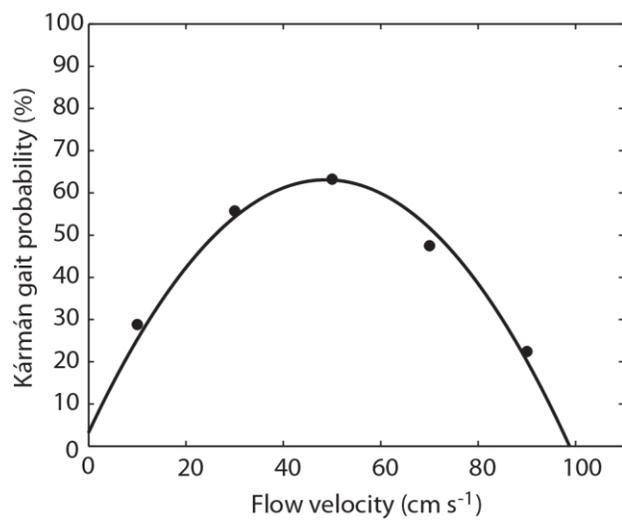FIG 1

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264　　Fig. 2

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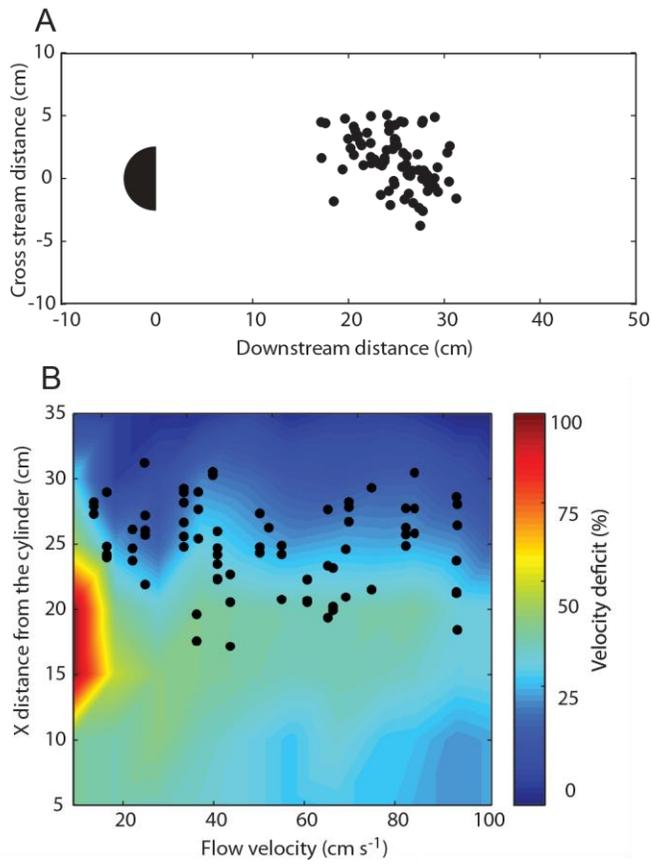
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269   Fig. 3

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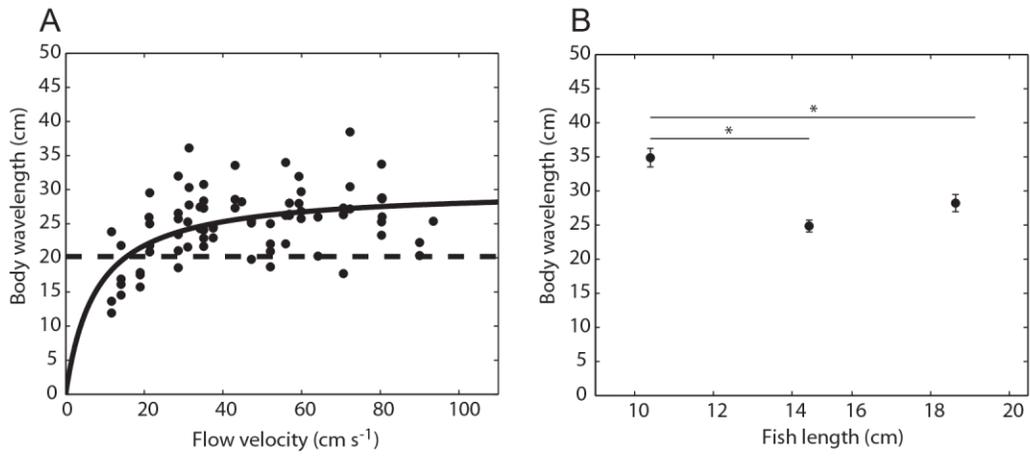
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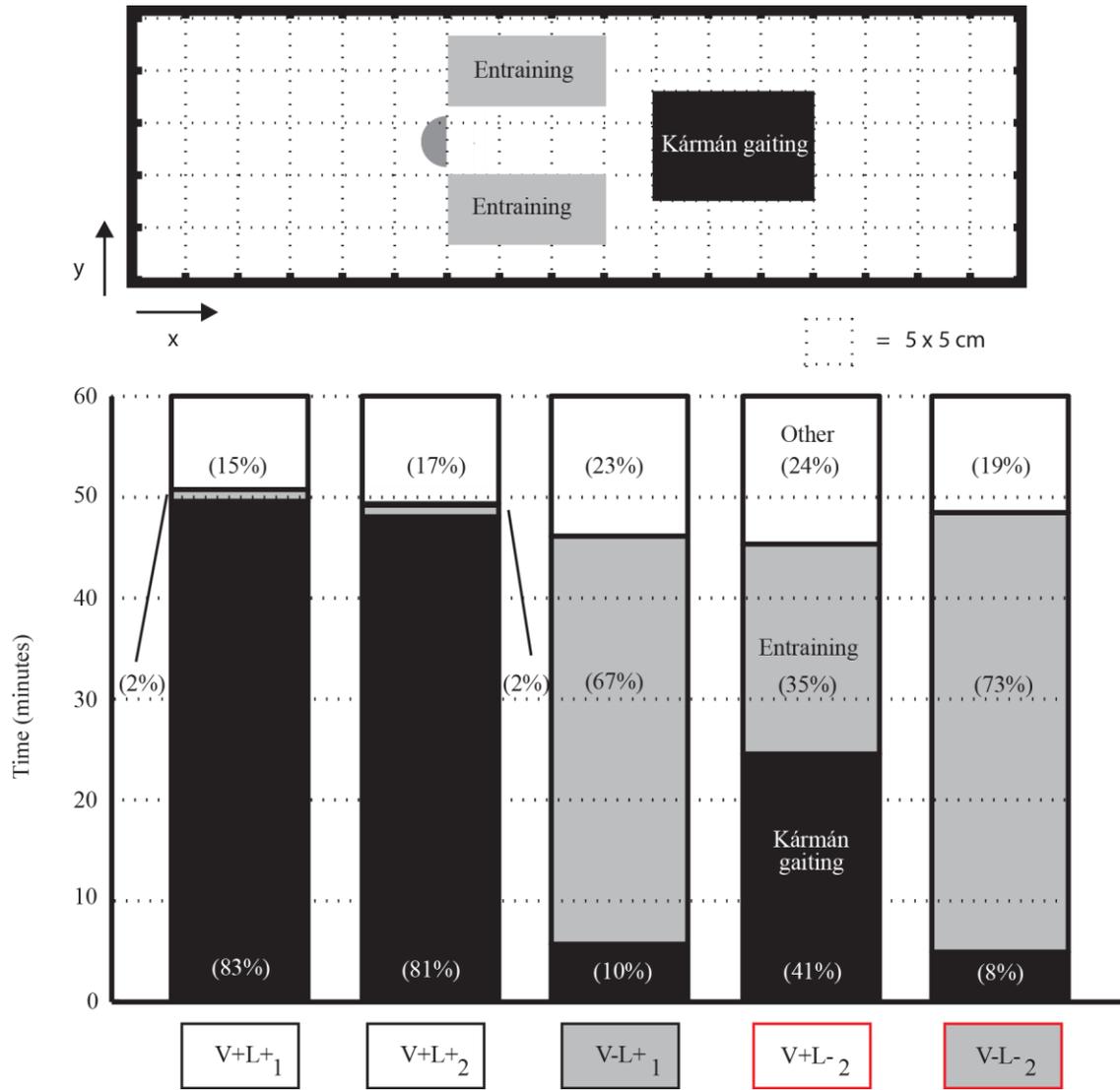281   Fig. 4

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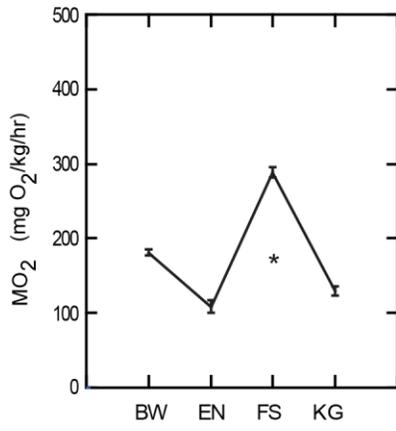285

286   Fig. 5

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289   Fig. 6

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Figure Legends

295

296   Fig. 1. Fourier analysis of a dead trout midline kinematics while in the vortex street (L = 17.8

297   cm, flow speed = 57 cms^{-1} and cylinder diameter = 5 cm [17]). (A) Normalized frequency spectrum

298   (black = frequency with smallest lateral amplitude and white = largest amplitude) revealed that

299   the dominant frequency is 2.20±0.10 Hz, similar to a live Kármán gaiting trout (A_i). (B) Mean

300   amplitude curve (solid line) across 6 tail beat cycles (gray shaded area shows ± standard error of

301   the mean) indicated that body amplitudes of dead trout were smaller than those of live trout (B_i).

302   (C) Increasing phase lag from head to tail in the mean phase curve (solid line, gray shaded area

303   shows ± standard error of the mean) indicated that the travelling wave along the body was

304   initiated more anteriorly than in a live trout (C_i). This suggests that live fish actively control the

305   anterior body to prevent wave formation. (A_{ii}) Normalized frequency spectrum shows both

306   freestream swimming and Kármán gaiting fish (L = 10.0±0.3 cm) at 4.5 Ls^{-1} exhibited periodic

307   lateral oscillations, where the dominant frequency was 6.6±0.1 Hz and 2.2±0.05 Hz,

308   respectively. (B_{ii}) Mean amplitude curves (solid line) at dominant frequency (gray shaded area

309   shows ± standard error of the mean). In both behaviours, the amplitude of lateral oscillations was

310   smallest at the mid-body region and increased gradually towards tail. During Kármán gaiting,

311   body amplitudes at all locations were larger than during freestream swimming. (C_{ii}) Mean phase

312   curves (solid line) at dominant frequency (gray shaded area shows ± standard error of the mean).

313   A travelling wave was evident for both behaviours. In Kármán gaiting, the wave started at the

314   body centre (0.4 L), which was about 0.2 L posterior to the starting point of freestream

315   swimming fish. In both behaviours, the wave speed was constant along the posterior body (~60

316   cms^{-1} for freestream swimming and ~75 cms^{-1} for Kármán gaiting fish). The freestream

317 swimming amplitude and phase curves of trout are very similar to those of saithe and mackerel

318 presented in [15].

319

320 Fig. 2. The probability of Kármán gaiting changes with flow speed. Fish Kármán gait the most at

321 intermediate flow speeds (~30 - 70 cm s^{-1} for trout with total body length of 15.7 ± 0.8 cm) and

322 the least at extreme speeds. Videos were binned into 5 flow speed categories, where each

323 category consisted of a minimum of 50 videos from at least 5 different fish.

324

325 Fig. 3. (A) Location of the body centre (BC, black circles) of the body relative to the D-cylinder

326 for all trials. The x and y axes show the downstream and lateral position, respectively, where 0

327 corresponds to the cylinder axis. (B) Downstream position of the BC relative to the cylinder as

328 flow velocity increases. The BC positions are superimposed on a heat map illustrating the

329 magnitude of the velocity deficit behind the cylinder as a percentage of the freestream velocity,

330 where red represents the greatest relative flow reduction. The location of greatest flow reduction

331 remains in a consistent region downstream of the cylinder across most flow speeds. Note that this

332 plot does not distinguish the reversal in flow direction that is established in the suction region

333 directly behind the cylinder. At the lowest speed, flow reduction can equate to no flow (100%

334 reduction), whereas at higher speeds the largest flow reduction still results in some flow

335 magnitude.

336

337 Fig. 4. Body wavelength across speed and body size. (A) Body wavelength (solid line) starts

338 lower than the cylinder wake wavelength (dashed line) and then rises above as flow speed

339 increases ($r^2 = 0.28$, n = 9 fish). At the lowest swimming speeds, the absence of a strong vortex

340   street likely requires use of a shorter body wave similar to freestream swimming fish (see text).

341   (B) At a flow speed of ~50 cm s^{-1}, smaller fish have a longer body wavelength than larger fish (p

342   < 0.05, n = 15 fish). Values shown are the mean ± S.E.M.

343

344   Fig. 5. Regions around a cylinder in flow that trout will either entrain or Kármán gait (defined as

345   two rectangular regions on either side of the cylinder, 7x15 cm, or a single rectangle centered

346   along the midline of the cylinder wake, 10x15cm, respectively). In the light, fish prefer to

347   Kármán gait in the vortex street downstream from the cylinder (black fill) for the majority of the

348   time during a 60-minute experiment, especially when the lateral line is intact (V+L+$_1$). Values

349   for fish in the light with an intact lateral line exposed to the cylinder for two consecutive days

350   (V+L+$_2$) are almost identical to those exposed for one day (V+L+$_1$), indicating that previous

351   experience in the flow tank does not alter the preference to Kármán gait. In contrast to

352   experiments performed in the light, fish in the dark do not spend much time in the vortex street

353   regardless of lateral line functionality (V-L+$_1$ or V-L-$_2$), preferring to entrain (gray fill) just

354   downstream and to the side of the cylinder. The time that fish spent exploring other regions of

355   the flow tank (white) is similar across treatments.

356

357   Fig. 6. Statistical comparison of MO_2 values between Kármán gaiting (KG) and other behaviors

358   at 3.5 L s^{-1}. Compared to other behaviors at 3.5 L s^{-1}, Kármán gaiting requires significantly less

359   oxygen than swimming in the free stream (FS, 47%) and bow waking (BW, 73%), but requires

360   more oxygen than entraining (EN, 116%). Kármán gaiting fish use less oxygen (79%) compared

361   to fish swimming in the free stream at 1.8 L s^{-1} (asterisk). Values are reported as the mean ± the

362   standard error.

363   **References**

364

365   1   Streitlien, K. & Triantafyllou, G. S. Efficient foil propulsion through vortex control.
366   *AIAA Journal* **34**, 2315-2319, doi:10.2514/3.13396 (1996).
367   2   Heggenes, J. Flexible summer habitat selection by wild, allopatric brown trout in lotic
368   environments. *Transactions of the American Fisheries Society* **131**, 287-298, doi:10.1577/1548-
369   8659(2002)131<0287:FSHSBW>2.0.CO;2 (2002).
370   3   McMahon, T. E. & Hartman, G. F. Influence of cover complexity and current velocity on
371   winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). *Canadian Journal of*
372   *Fisheries and Aquatic Sciences* **46**, 1551-1557, doi:10.1139/f89-197 (1989).
373   4   Triantafyllou, M. S., Techet, A. H. & Hover, F. S. Review of experimental work in
374   biomimetic foils. *IEEE Journal of Oceanic Engineering* **29**, 585 - 594,
375   doi:10.1109/JOE.2004.833216 (2004).
376   5   Pavlov, D. S., Lupandin, A. I. & Skorobogatov, M. A. The effects of flow turbulence on
377   the behavior and distribution of fish. *Journal of Ichthyology* **40**, S232-S261 (2000).
378   6   Williamson, C. H. K. Vortex dynamics in the cylinder wake. *Annual Review of Fluid*
379   *Mechanics* **28**, 477-539, doi:10.1146/annurev.fl.28.010196.002401 (1996).
380   7   Webb, P. W. Entrainment by river chub *Nocomis micropogon* and smallmouth bass
381   *Micropterus dolomieu* on cylinders. *The Journal of experimental biology* **201**, 2403-2412 (1998).
382   8   Liao, J. C., Beal, D. N., Lauder, G. V. & Triantafyllou, M. S. Fish Exploiting Vortices
383   Decrease Muscle Activity. *Science* **302**, 1566-1569, doi:10.1126/science.1088295 (2003).
384   9   Sutterlin, A. M. & Waddy, S. Possible role of the posterior lateral line in obstacle
385   entrainment by brook trout (*Salvelinus fontinalis*). *Journal of the Fisheries Research Board of*
386   *Canada* **32**, 2441-2446, doi:10.1139/f75-281 (1975).
387   10   Zdravkovich, M. M. *Flow Around Circular Cylinders : A Comprehensive Guide Through*
388   *Flow Phenomena, Experiments, Applications, Mathematical Models, and Computer Simulations*.
389   Vol. 1 (Oxford University Press, 1997).
390   11   Liao, J. C., Beal, D. N., Lauder, G. V. & Triantafyllou, M. S. The Kármán gait: novel
391   body kinematics of rainbow trout swimming in a vortex street. *The Journal of experimental*
392   *biology* **206**, 1059-1073, doi:10.1242/jeb.00209 (2003).
393   12   Liao, J. C. Neuromuscular control of trout swimming in a vortex street: implications for
394   energy economy during the Kármán gait. *The Journal of experimental biology* **207**, 3495-3506,
395   doi:10.1242/jeb.01125 (2004).
396   13   Taguchi, M. & Liao, J. C. Rainbow trout consume less oxygen in turbulence: the
397   energetics of swimming behaviors at different speeds. *The Journal of experimental biology* **214**,
398   1428-1436, doi:10.1242/jeb.052027 (2011).
399   14   Breder, C. M. J. The locomotion of fishes. *Zoologica* **4**, 159-256 (1926).
400   15   Videler, J. J. & Hess, F. Fast continuous swimming of two pelagic predators, saithe
401   (*Pollachius virens*) and mackerel (*Scomber scombrus*): a kinematic analysis. *The Journal of*
402   *experimental biology* **109**, 209-228 (1984).
403   16   Jayne, B. C. & Lauder, G. V. Red Muscle Motor Patterns During Steady Swimming in
404   Large Mouth Bass: Effects of Speed and Correlations with Axial Kinematics. *The Journal of*
405   *experimental biology* **198**, 1575-1587 (1995).

406   17   Beal, D. N., Hover, F. S., Triantafyllou, M. S., Liao, J. C. & Lauder, G. V. Passive
407   propulsion in vortex wakes. *Journal of Fluid Mechanics* **549**, 385-402,
408   doi:10.1017/S0022112005007925 (2006).
409   18   Akanyeti, O. & Liao, J. C. A kinematic model of Karman gaiting in rainbow trout. *The*
410   *Journal of experimental biology* **216**, 4666-4677, doi:10.1242/jeb.093245 (2013).
411   19   Akanyeti, O. & Liao, J. C. The effect of flow speed and body size on Karman gait
412   kinematics in rainbow trout. *The Journal of experimental biology* **216**, 3442-3449,
413   doi:10.1242/jeb.087502 (2013).
414   20   Webb, P. W., Kostecki, P. T. & Stevens, E. D. The effect of size and swimming speed on
415   the locomotor kinematics of rainbow trout. *The Journal of experimental biology* **109**, 77-95
416   (1984).
417   21   Wei, T. & Smith, C. R. Secondary vortices in the wake of circular cylinders. *Journal of*
418   *Fluid Mechanics* **169**, 513-533 (1986).
419   22   Blevins, R. D. *Flow Induced Vibration*. Second Edition edn, (Krieger Publishing
420   Company, 2001).
421   23   Bose, N. & Lien, J. Energy absorption from Ocean Waves: A Free Ride for Cetaceans.
422   *Proceedings of the Royal Society B* **240**, 591-605, doi:10.1098/rspb.1990.0054 (1990).
423   24   Wu, T. Y. & Chwang, A. T. *Extraction of flow energy by fish and birds in a wavy stream*.
424   Vol. 2 (Plenum Press, 1975).
425   25   Roeser, T. & Baier, H. Visuomotor behaviors in larval zebrafish after GFP-guided laser
426   ablation of the optic tectum. *The Journal of Neuroscience* **23**, 3726-3734 (2003).
427   26   Ingle, D. *Vision: the experimental analysis of visual behavior*. Vol. 5 (Academic Press,
428   1971).
429   27   Dijkgraaf, S. The functioning and significance of the lateral-line organs. *Biological*
430   *Reviews* **38**, 51-105, doi:10.1111/j.1469-185X.1963.tb00654.x (1963).
431   28   Coombs, S., Braun, C. B. & Donovan, B. The Orienting response of Lake Michigan
432   mottled sculpin is mediated by canal neuromasts. *The Journal of experimental biology* **204**, 337-
433   348 (2001).
434   29   Engelmann, J., Hanke, W., Mogdans, J. & Bleckmann, H. Hydrodynamic stimuli and the
435   fish lateral line. *Nature* **408**, 51-52, doi:10.1038/35040706 (2000).
436   30   Alvarado, P. V. *Design of Biomimetic Compliant Devices for Locomotion in Liquid*
437   *Environments* Ph.D. thesis, MIT, (2007).
438   31   Liu, J. & Hue, H. Biologically inspired behaviour design for autonomous robotic fish.
439   *International Journal of Automation and Computing* **4**, 336-347 (2006).
440   32   Stefanini, C., Orofino, S., Manfredi, L., Mintchev, S., Marrazza, S., Assaf, T., L.
441   Capantini, Sinibaldi, E., Grillner, S., Walén, Peter & Dario, Paolo. . A novel autonomous
442   bioinspired swimming robot developed by neuroscientists and bioengineers. *Bioinspiration and*
443   *Biomimetics* **7** (2012).
444   33   Stewart, W. J., Tian, F. B., Akanyeti, O., Walker, C. J. & Liao, J. C. Refuging rainbow
445   trout selectively exploit flows behind tandem cylinders. *The Journal of experimental biology*
446   **219**, 2182-2191, doi:10.1242/jeb.140475 (2016).
447