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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.

45

Introduction

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

48 principles of efficient propulsion¹⁻⁵. Because the hydrodynamics of a cylinder wake is well-
49 characterized⁶, 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 conditions⁷⁻⁹.
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

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

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

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

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 gating 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

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

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 wave¹⁴. 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

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

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

$$93 \quad A(x) = c_1 x + c_2 x^2 \text{ }^{15}.$$

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 thrust¹⁷. 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 speed¹⁹.

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 size²⁰. 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 second¹⁹.
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 frequency¹⁹. The tail-beat frequency at the low flow speed was identical
164 to that of a freestream swimming fish²⁰. 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 instabilities²¹. 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 hydrodynamic²⁷⁻²⁹ 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.

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Energetics of Kármán gaiting

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Future directions

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The cost of Kármán gaiting can be measuring directly and non-invasively in live fishes by employing the technique of respirometry, which measures the oxygen consumed during a particular behavior. There are several regions around a cylinder that fish choose to hold station. Figure 6 illustrates that for a given flow speed, oxygen consumption during Kármán gaiting is higher than entraining near the suction region, but lower than bow waking in the front of the cylinder¹³. Kármán gaiting represents about half of the cost (47%) of swimming in the freestream away from the cylinder. When compared to freestream swimming in flow equivalent to the reduced velocity behind the cylinder (which is about 40% of the nominal flow velocity), Kármán gaiting represents about 79% of the cost¹¹. Therefore, by exploiting vortices Kármán gaiting fish used significantly less oxygen than predicted if there were only benefiting from swimming in the reduced velocity of the cylinder wake.

Our work on the midline kinematics of Kármán gaiting, sensory biology and energetics can be used by roboticists to develop control algorithms that can move bio-inspired robots and by computational fluid dynamics modelers to simulate fluid-structure interactions. Given that the majority of the body waves during Kármán gaiting are generated passively, it is more important for a flexible robot to control its head and the anterior body than control its posterior body. If hydrodynamic forces are harnessed appropriately at the anterior body, a travelling wave is generated passively at the posterior body starting from the body centre. This represents a paradigm shift in the field of autonomous robotics locomotion which traditionally emphasize the control of the posterior body³⁰⁻³². 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 predicted³³. 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.

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254

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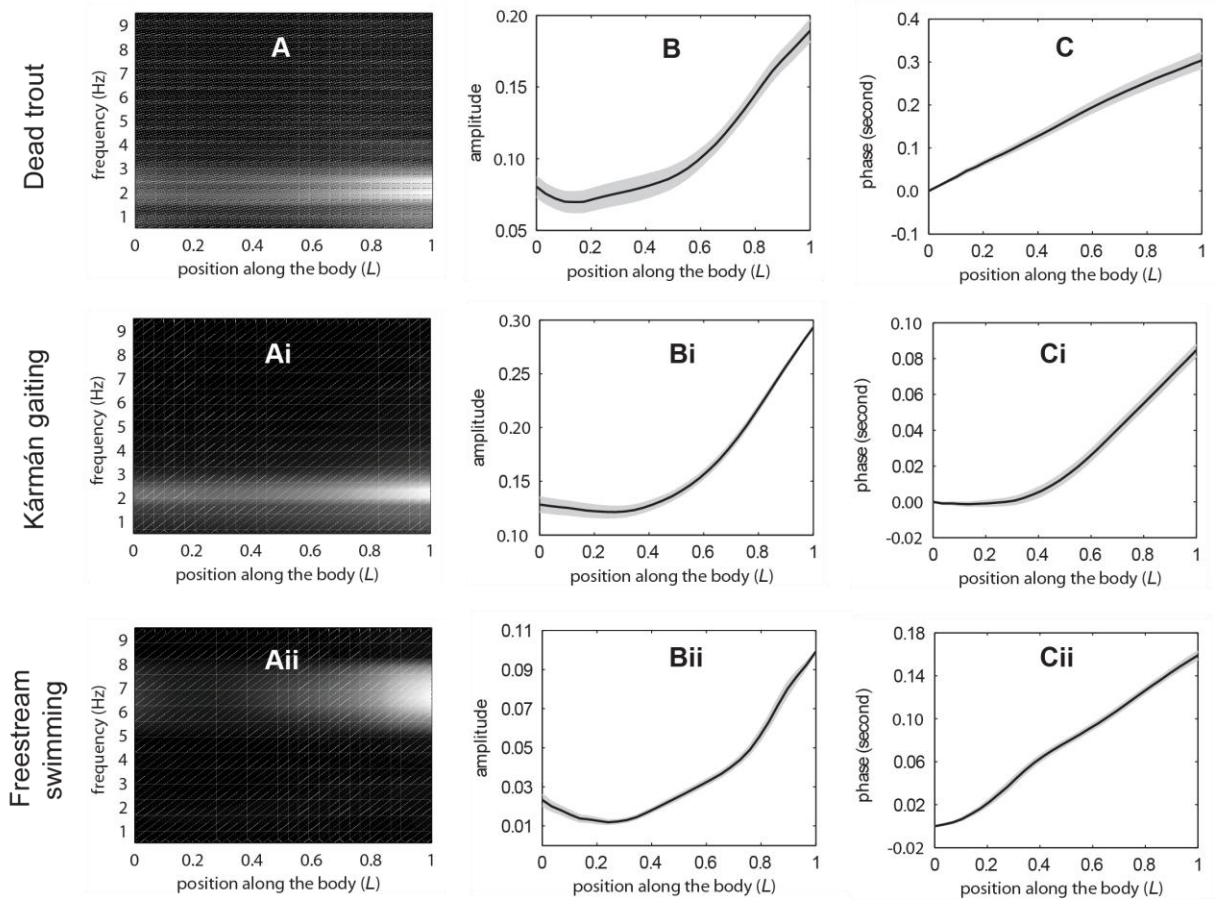
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Figures

261 Fig. 1

FIG 1

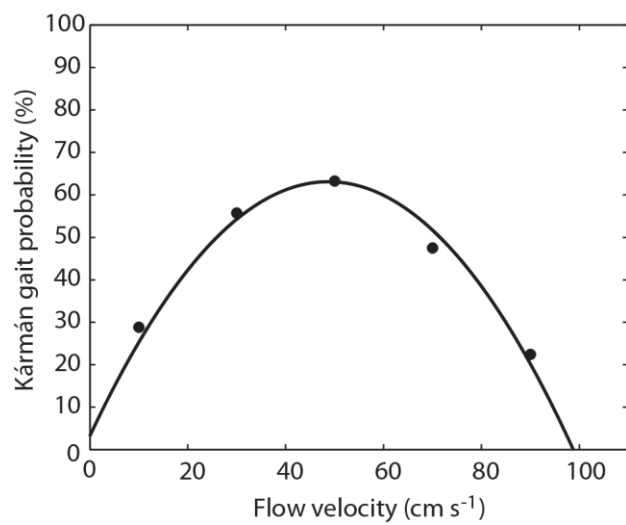


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264 Fig. 2

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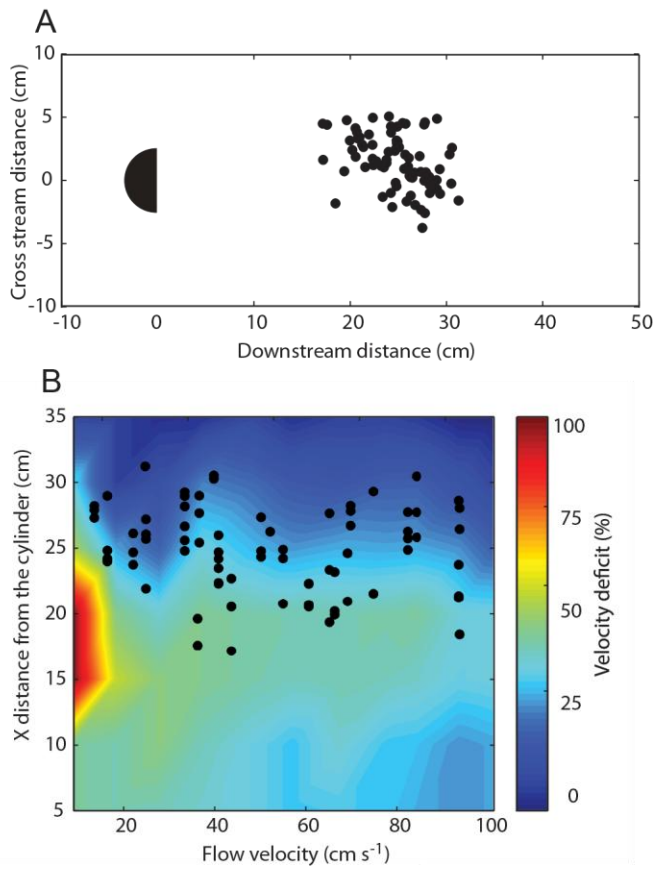
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269 Fig. 3

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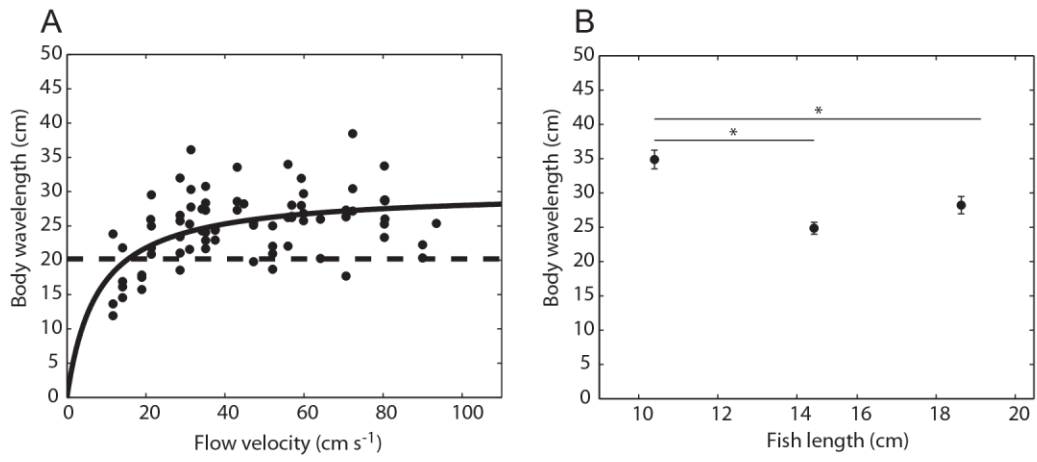
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281 Fig. 4

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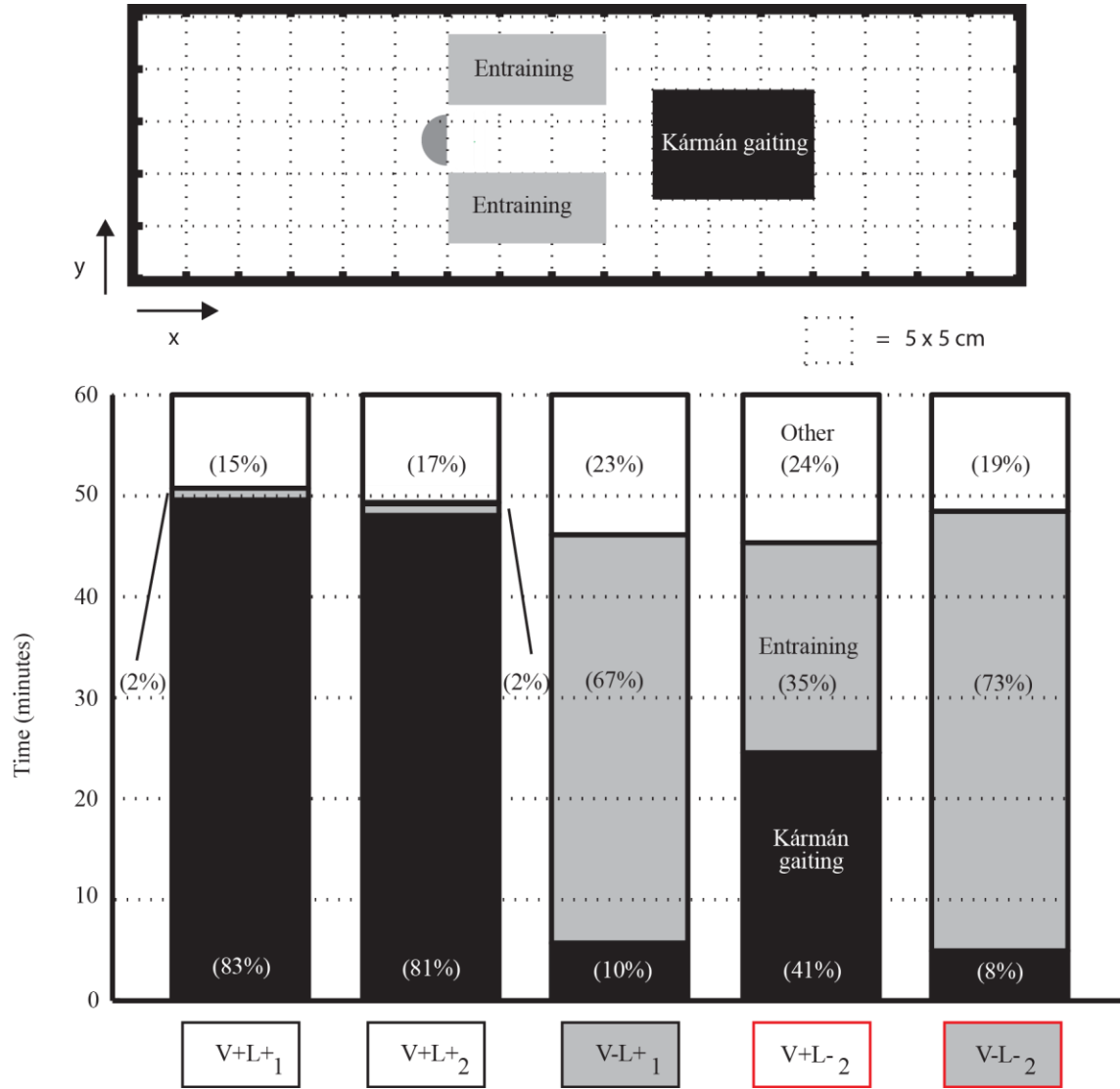


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286 Fig. 5

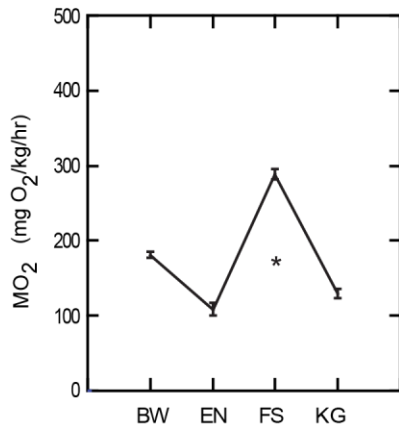


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289 Fig. 6

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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 $2.20 \pm 0.10 \text{ Hz}$, 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 \pm 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 \pm 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 ($L = 10.0 \pm 0.3 \text{ cm}$) at 4.5 Ls^{-1} exhibited periodic

307 lateral oscillations, where the dominant frequency was $6.6 \pm 0.1 \text{ Hz}$ and $2.2 \pm 0.05 \text{ Hz}$,

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

309 shows \pm 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 \pm 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 $\sim 75 \text{ cms}^{-1}$ 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 ($\sim 30 - 70 \text{ cm s}^{-1}$ for trout with total body length of $15.7 \pm 0.8 \text{ cm}$) 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 $\sim 50 \text{ cm s}^{-1}$, smaller fish have a longer body wavelength than larger fish (p
342 < 0.05 , $n = 15$ fish). Values shown are the mean \pm 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, $7 \times 15 \text{ cm}$, or a single rectangle centered
346 along the midline of the cylinder wake, $10 \times 15 \text{ cm}$, 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 \pm the
362 standard error.

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