

How fish exploit vortices to save energy, and under what conditions

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1 **How fish exploit vortices to save energy, and under what conditions**

2

3 **Abstract**

4 Fish are known to extract energy from vortices to reduce swimming costs, but the
5 underlying physical mechanism has remained unclear for decades. Here we address this
6 question by combining experiments on live fish, dead fish, and passive bionic models
7 in a flow tank, using four different bluff-body geometries to generate Kármán vortex
8 streets. Observing fish behavior across 20 species and systematically varying body
9 properties and wake conditions, we discover that Kármán gait is not an active choice
10 but a physically gated resonant state: the incident wake drives the body as a damped
11 oscillator near resonance, and stable entrainment requires three conditions—sufficient
12 flexibility, frequency matching, and appropriate body–wake scale. When these
13 conditions are not met, the gait fails to appear. These findings reveal a general principle
14 for how flexible bodies exploit environmental flows, with implications for fish ecology
15 and underwater robotics.

16 **Introduction**

17 Turbulence is everywhere in aquatic environments—generated by rocks, vegetation,
18 other animals, and even human-made structures ^{1, 2, 3, 4, 5, 6, 7}. Fish can exploit these
19 environmental vortices to reduce swimming costs, yet the physical mechanisms
20 underlying this interaction have remained unclear for decades ^{5, 6, 8, 9}. A prominent
21 example is Kármán gait, in which fish hold station behind an obstacle by slaloming
22 through its wake and synchronizing their body motion with alternating vortices while
23 reducing axial muscle activity ^{9, 10, 11}. Dead fish and passive flexible foils can also
24 exhibit organized responses in vortex wakes, suggesting that this behavior arises in
25 large part from fluid–structure coupling rather than active control alone ^{7, 9, 12, 13, 14}.
26 However, live and dead fish have not been directly compared under matched wake
27 conditions, leaving unresolved which features of the gait are organized by the wake and
28 which are actively modified by the living fish.

29 Understanding this interaction is important not only for fish locomotion and habitat use,
30 but also for a broader problem in fluid–structure interaction: how flexible bodies
31 convert unsteady environmental forcing into stable, organized motion ^{6, 13, 14, 15, 16}.
32 Previous studies have characterized the distinctive kinematics of Kármán gait and
33 shown that fish motion varies systematically with the position and frequency of incident
34 vortices ^{9, 10, 11, 17, 18}. Numerical and theoretical studies further indicate that vortex wakes
35 can deform flexible fish-like bodies and generate hydrodynamic forces or thrust that
36 depend on the phase between body motion and incident vortices ^{12, 13, 14, 19}. However,
37 experimental studies have generally focused on body kinematics and wake organization
38 without directly resolving the associated hydrodynamic loading ^{3, 10, 11, 20}, whereas
39 theoretical studies have often considered constrained, prescribed, or simplified body
40 deformation ^{19, 21}. Recent work has proposed an inertial mechanism through which
41 cross-stream vortex forcing may contribute to dynamic station holding ¹⁸, but a unified
42 framework linking wake-associated loading, passive body–wake mechanics, active

stabilization, and the conditions for stable entrainment remains lacking. Moreover, most detailed evidence remains concentrated on rainbow trout, with only isolated observations in other taxa, leaving the taxonomic breadth and physical limits of Kármán gait poorly understood^{3, 8, 9, 10, 11, 17, 18}. Resolving these questions may also guide the design of flow-adaptive robots and underwater vehicles that exploit, rather than resist, unsteady wakes^{21, 22, 23, 24, 25, 26, 27}.

Here, we test the hypothesis that Kármán gait is a wake-forced, phase-locked state whose emergence is gated by physical compatibility between the incident vortex street and the flexible body. Under this framework, the vortex street provides a structured hydrodynamic template that organizes body motion, while body mechanics determine whether this external forcing can be inherited as a stable response. Specifically, we propose that stable Kármán gait depends on three coupled conditions: (i) sufficient body compliance for wake entrainment, (ii) frequency matching between vortex shedding and the body's natural response, and (iii) body–wake scale matching for spatial synchronization.

To test this framework, we combined cross-species kinematic analyses, matched live–post-mortem comparisons, flow-field and pressure reconstruction, reduced-order modelling, and passive bionic-fish experiments (**Fig. 1**). We quantified the occurrence and phase organization of Kármán gait across diverse fish species and bluff-body wakes, and used live–dead fish comparisons to assess the respective contributions of passive body–wake mechanics and active stabilization. Dynamic mode decomposition of reconstructed pressure fields was used to identify dominant wake-associated modes and forcing signatures²⁸, while a forced damped-oscillator model was developed to interpret the observed forcing–response phase relation^{15, 29, 30}. Finally, by varying stiffness and density in passive bionic models and examining body–wake scale in live fish, we characterized the mechanical and geometric conditions associated with stable Kármán gait. Our results support a framework in which Kármán gait emerges as a

physically gated, wake-forced state with near-resonant dynamics, providing a mechanical explanation for how flexible swimmers exploit external vortical forcing.

Results

Kármán gait is a widespread phase-locked response with a strong passive component

Kármán gait was observed across phylogenetically and morphologically diverse fishes, indicating that it is a reproducible response to vortex forcing rather than an incidental behavior. Across the 20 surveyed species, the temporal probability ranged from approximately 3.3% to 41.7% (**Fig. 2a**). The behavior occurred within a bounded geometric and hydrodynamic window, with a characteristic fish-to-obstacle size ratio of 2.0–2.5 and an incoming flow velocity of 0.3–0.6 m s⁻¹ (**Fig. 2a**, inset). Kármán gait also occurred behind multiple bluff-body geometries with no significant difference in occurrence probability (**Fig. 2b**), consistent with the similarity of their wake structures. These results indicate that Kármán gait is not restricted to a particular fish morphology or obstacle geometry, but emerges as a repeatable wake-forced response within a definable flow–geometry window.

Kármán gait showed clear kinematic synchronization with the incident vortex street. Tail-beat frequency matched vortex-shedding frequency, and body-wave velocity closely followed vortex convection velocity (**Fig. 2c,d**), indicating synchronization in both time and space under external vortex forcing. However, frequency and wave-speed matching alone do not distinguish whether the gait is actively generated or primarily organized by the wake. We therefore next examined the phase organization between body-center and tail motion.

A more fundamental distinction emerged from the body-center (BC)–tail phase relationship. We defined the phase difference as $\varphi = \varphi_{\text{tail}} - \varphi_{\text{BC}}$. Active undulatory

swimming clustered near a positive phase branch ($\varphi \approx +0.5\pi$), whereas both live- and dead-fish Kármán-gait responses converged toward a negative branch ($\varphi \approx -0.5\pi$; **Fig. 2e**; ANOVA, $P < 0.00005$). The convergence of live and dead fish toward the same phase branch indicates that this organization does not arise from active tail beating alone. Instead, Kármán gait represents a wake-forced phase-locked state distinct from active undulatory swimming.

Body-configuration analysis further supported this interpretation (**Fig. 2f**). Active swimming exhibited a pronounced undulatory profile, whereas Kármán gait showed an inclined body configuration shared by both live and dead fish. The primary live–dead difference was localized to the head region, indicating that anterior-body motion retains active modulation while the global body configuration is reorganized by the wake. Thus, Kármán gait is not completely passive, but its overall body organization is strongly shaped by passive body–wake interaction.

Consistent with this, oscillation amplitudes showed the largest live–dead difference at the head, with a $\sim 106\%$ increase in dead fish relative to live fish (**Fig. 2g**). By contrast, body-center and tail amplitudes were more similar between the two Kármán conditions, although both exceeded those observed in active swimming. These results indicate that active regulation is concentrated mainly in the anterior body, whereas the global body–tail oscillation during Kármán gait is largely organized by interaction with the incident vortex street. Together, these results identify Kármán gait as a vortex-synchronized, passive-dominated phase-locked response to wake forcing.

Vortex-street pressure modes provide a structured forcing template

Having shown that Kármán gait exhibits a passive-dominated phase-locked response to vortex forcing, we next asked what hydrodynamic structure within the incident wake organizes this state. Because wakes generated by the four bluff-body geometries were similar, the D-shaped cylinder was used as a representative case. Time-resolved PIV

showed that *Squalidus argentatus* slalomed regularly through the wake (**Fig. 3a**). The vorticity field revealed alternating counter-rotating vortices arranged around the centerline, with a characteristic spacing of ~ 0.08 m and normalized vorticity of approximately -40 and $+40$. Tail motion was phase-aligned with the incoming vortices rather than opposing them, and the presence of the fish did not substantially alter the large-scale wake topology (**Supplementary Fig. S6**). Similar slaloming patterns were observed in both live and passive dead fish (**Supplementary Figs. S16–S17**).

CFD-based pressure reconstruction further showed that the fish body moved through alternating high- and low-pressure regions associated with the incident vortex street (Fig. 3b; validation in **Supplementary Fig. S10**). Periodic low-pressure zones were distributed above and below the wake centerline, with pressure near vortex cores reaching approximately -200 Pa. During each half-cycle, the fish body passed through these alternating pressure regions, indicating that Kármán gait arises from coherent body–wake interaction rather than isolated body motion. To resolve the force structure underlying this interaction, we decomposed the reconstructed pressure field into dominant hydrodynamic modes.

Dynamic mode decomposition (DMD) identified three leading pressure modes (Fig. 3c). Pressure-gradient signatures were used as proxies for the local hydrodynamic forcing associated with each mode. Mode 1 formed a low-pressure restoring corridor that confined the lateral position of the fish body. At the representative cross-section $x=0.08$ m, the pressure-gradient profile varied approximately linearly with lateral position, with a fitted slope of -7.72×10^5 Pa/m² and $R^2=0.9844$ (**Fig. 3d**). This mode therefore provides an effective restoring structure that defines the lateral boundary of the Kármán-gait corridor.

Modes 2 and 3 provided the oscillatory components of the wake-force architecture. Mode 2 was associated with a periodic lateral forcing proxy, $F_y(\omega)$, synchronized with the passage of successive vortices. Mode 3 generated a streamwise forcing component,

$F_x(2\omega)$, associated with body curvature and downstream body-wave propagation. The pressure-gradient signatures of Modes 2 and 3 were well described by $A_y \cos(\omega t)$ and $A_x \cos(2\omega t - 0.5\pi)$, respectively, indicating that the incident vortex street contains a coupled lateral–streamwise forcing structure rather than a single dominant forcing event.

These hydrodynamic modes mapped directly onto the characteristic kinematics of Kármán gait (**Fig. 3e,f**). Mode 1 defined the downstream corridor in which Kármán gait occurred most frequently, with occurrence probabilities of 66% in C1 and 52% in C2 and negligible occurrence in the lateral regions. Mode 2 drove periodic body-center oscillation, with a lateral amplitude of approximately 0.3 BL and a forcing–response phase lag of approximately 0.5π . Mode 3 promoted body-wave propagation toward the tail, with a tail-wave amplitude of approximately 0.15 BL and a propagation velocity matching that of the shed vortices, consistent with the velocity matching shown in Fig. 2d. Similar Mode-2 and Mode-3 kinematic features were also observed in passive dead-fish responses (**Supplementary Fig. S15**).

Together, these results demonstrate that the incident vortex street does not merely disturb the fish; it imposes a hydrodynamic template - a structured $F_y(\omega) - F_x(2\omega)$ force architecture - that organizes body-center oscillation, body curvature, and tail-mediated amplitude regulation into a coherent gait. Mode 1 defines the restoring corridor, Mode 2 supplies periodic lateral forcing, and Mode 3 promotes streamwise body-wave propagation and tail-mediated amplitude development. This tripartite modal architecture provides an explicit representation of Kármán gait as a wake-forced oscillator, wherein the body-center response is simultaneously driven by vortex forcing, confined by a pressure-defined corridor, and regulated by tail-mediated forcing.

A wake-forced oscillator model captures the phase lag and bounded amplitude of Kármán gait

The modal wake-force architecture identified above provides a reduced-order basis for the lateral dynamics of Kármán gait. Mode 1 defines an effective restoring corridor, Mode 2 supplies periodic lateral vortex forcing $F_y(\omega)$, and Mode 3 promotes body curvature and tail-amplitude development. We therefore asked whether these modal components could explain the characteristic forcing–response phase lag and bounded lateral amplitude observed during Kármán gait.

We modelled the body-center displacement L_c as a wake-forced oscillator (**Fig. 4b**), in which the lateral dynamics are governed by effective inertia, damping and restoring stiffness, and driven by the net forcing generated by lateral vortex forcing and tail-mediated regulation:

$$m_{eff}\ddot{L}_c + c_{eff}\dot{L}_c + k_{eff}L_c = F_y(t) - F_t(t) \quad (1)$$

Here, F_t is an effective tail-mediated force inferred from the Mode-3-associated body deformation and tail-amplitude variation (**Fig. 4a**). Because F_t scales with tail amplitude and acts opposite to the primary lateral vortex forcing F_y , it was treated as a kinematically constrained regulatory term rather than an independent fitting parameter. After normalization by the effective mass, the equation can be written as a standard forced-oscillator model,

$$\ddot{L}_c + 2\beta\dot{L}_c + \omega_0^2 L_c = f_0 \cos(\omega t) \quad (2)$$

where β is the effective damping coefficient, ω_0 is the effective natural frequency, and f_0 is the net forcing amplitude. Full derivations and parameter definitions are provided in the Supplementary Information.

The model predicts that L_c oscillates at the forcing frequency, consistent with the frequency matching observed in **Fig. 2c**. It also predicts that the forcing–response phase lag φ_c approaches 0.5π near the resonance condition $\omega \approx \omega_0$ (**Fig. 4c,d**). Here, φ_c denotes the phase lag between lateral vortex forcing and body-center response, and is distinct from the BC–tail phase difference $\varphi = \varphi_{tail} - \varphi_{BC}$ used in Fig. 2. Thus, the near- 0.5π forcing–response lag arises naturally from wake-forced resonance, rather than from an imposed kinematic constraint.

The same framework explains why the resonant amplitude remains bounded (**Fig. 4e**). Under weak damping, the predicted response becomes excessively large, making the fish prone to leaving the Kármán-gait corridor defined by Mode 1. Under strong damping, the response is suppressed and inconsistent with the pronounced lateral displacement observed experimentally. The observed motion is therefore most consistent with an intermediate-damping regime, in which resonance is present but amplitude remains controlled.

We further evaluated how F_t modifies the resonant amplitude (**Fig. 4f**). At resonance, the amplitude can be characterized by the relative ratio of the tail-mediated force (f_t) and the mass-normalized vortex forcing (f_y). For *Squalidus argentatus*, the values of f_t/f_y were estimated from the difference in lateral amplitude between live and dead fish during Kármán gait, as detailed in **Supplementary Results VI**. Using the values of f_t/f_y of *Squalidus argentatus*, under the observed regulated condition as a reference, we showed that removing the opposing tail-mediated force increased the amplitude by 89%, whereas reversing its direction increased it by 177% (**Fig. 4f**). These results suggest that F_t offsets the vortex forcing, thereby reducing the net excitation and limiting excessive lateral motion.

Together, these results support the interpretation of Kármán gait as an amplitude-regulated, wake-forced resonant response. Mode 1 confines the body within a low-pressure corridor, Mode 2 provides lateral excitation, and Mode 3 contributes tail-

mediated amplitude regulation. This resonant response links the $F_y(\omega)$ – $F_x(2\omega)$ wake-force architecture to the opposite BC–tail phase branches reported above in **Fig. 2e**.

Physical gating of Kármán gait by compliance, frequency, and scale matching

The wake-forced oscillator model suggests that stable Kármán gait should depend not only on incident vortex forcing, but also on the physical properties of the body that determine whether it can be entrained by the wake. We therefore combined passive bionic-fish experiments with live-fish observations to examine how body stiffness, body density and body–wake scale affect Kármán-gait occurrence (**Fig. 5a**). For the bionic fish, the occurrence probability of Kármán gait (P_{KG}), was quantified using the same temporal-probability criterion as in the live-fish experiments. In total, we tested 5×7 stiffness–density combinations, with three repeated trials for each condition. The corresponding forcing-to-natural frequency ratio, (ω_s/ω_n) , was calculated to evaluate the degree of frequency matching between the incident vortex street and the flexible body.

The density–stiffness phase map showed that stable Kármán gait was restricted to a limited region of parameter space (**Fig. 5b**). High occurrence probabilities appeared near neutral density ($\rho/\rho_0 \approx 1$) and low-to-moderate stiffness, whereas density mismatch or excessive stiffness reduced P_{KG} . Specifically, the high-probability region was centered near $\rho/\rho_0 = 1.0$ and $EI/EI_0 = 1.0$, where (P_{KG}) reached 31.23%. By contrast, P_{KG} decreased to 0% under the sampled density-mismatched and high-stiffness conditions. This indicates that Kármán gait is not a generic passive response to the vortex street, but requires specific physical matching between the body and the wake.

Body stiffness had a strong suppressive effect on Kármán-gait occurrence (**Fig. 5c**). (P_{KG}) remained high for sufficiently compliant bodies but decreased markedly as normalized stiffness increased. Increasing stiffness reduced (P_{KG}) from 32.71% at

$EI/EI_0 = 0.5$ to 0% at $EI/EI_0 > 5.0$. This result indicates that sufficient compliance is required for wake entrainment: a flexible body can be deformed and organized by the incident vortex street, whereas an overly stiff body cannot readily develop the wake-forced body motion needed for stable phase locking.

Body density produced a distinct matching effect (**Fig. 5d**). (P_{KG}) peaked near $\rho/\rho_0 = 1$, where the forcing-to-natural frequency ratio approached $\omega_s/\omega_n \approx 1$. More specifically, (P_{KG}) reached 31.23% at $\rho/\rho_0 = 1.0$, corresponding to ($\omega_s/\omega_n = 1.0$). Both lighter and heavier bodies showed lower occurrence probabilities, with P_{KG} decreasing to 0% at $\rho/\rho_0 = 0.5$ and $\rho/\rho_0 = 2.0$, respectively. This suggests that density matching promotes frequency matching between the incident vortex street and the natural response of the flexible body, thereby facilitating stable wake-forced phase locking.

Live-fish observations further supported the role of body–wake scale matching (Fig. 5e). Kármán-gait occurrence was elevated within an intermediate range of relative body length, BL/W , whereas very small or very large relative lengths showed lower occurrence probabilities. In live fish, Kármán-gait occurrence was highest within $BL/W = 2.0$ - 2.5 , reaching 20.24%, whereas smaller and larger (BL/W) ranges showed lower occurrence probabilities. Although the live-fish data exhibited larger variability than the bionic-fish experiments, this trend suggests that body length must be compatible with the spatial scale of the vortex street for stable Kármán gait to occur.

Together, these results identify a triadic physical gate for Kármán gait (**Fig. 5f**). Stable wake-forced phase locking requires sufficient body compliance for wake entrainment, density-dependent frequency matching for near-resonant responsiveness, and appropriate body–wake scale matching for spatial synchronization. Thus, Kármán gait emerges only when the flexible body is physically compatible with both the temporal and spatial structure of the incident vortex street.

272 Discussion

273 Our results support the interpretation of Kármán gait as a physically gated, vortex-
274 forced resonant state - a regime in which an organized vortex street and a mechanically
275 compatible flexible body interact through phase-locked dynamics. This conclusion rests
276 on four lines of evidence. First, the gait occurs across diverse species, in dead fish, and
277 in passive bionic models, indicating a passive mechanical basis. Second, the incident
278 vortex street imposes a characteristic $F_y(\omega) - F_x(2\omega)$ forcing architecture that defines
279 a wake corridor, drives lateral oscillation, and promotes body-wave propagation. Third,
280 the near-quarter-cycle forcing-response lag follows naturally from a forced-oscillator
281 model near resonance, without requiring active tuning as the sole explanation. Fourth,
282 stable entrainment occurs only when body compliance, density-dependent natural
283 frequency, and body-wake scale match the incident wake—demonstrating that Kármán
284 gait is not an unconditional passive response, but a state gated by physical compatibility.

285 Rather than being simply a behavioral response to an upstream obstacle or a passive
286 drift within a low-velocity wake, Kármán gait emerges when the temporal and spatial
287 structure of the incident wake can be inherited by the body. Across live fish, dead fish
288 and passive bionic models, stable Kármán gait was associated with synchronized body
289 oscillation, organized body curvature and a consistent relationship between vortex
290 forcing and body motion. These findings extend previous observations that fish can
291 exploit wakes generated by upstream obstacles by showing that the incident vortex
292 street acts as a hydrodynamic template capable of organizing flexible-body dynamics^{8,}
293 ^{10, 11, 12, 13, 14, 17}.

294 The hydrodynamic analyses reveal how this template is structured. The incident vortex
295 street produced a lateral forcing component at the vortex-shedding frequency and a
296 streamwise component at approximately twice this frequency, forming a characteristic
297 $(F_y(\omega) - F_x(2\omega))$ force architecture. This architecture created a wake-defined corridor

in which the body could oscillate laterally while maintaining a stable streamwise position. Thus, the vortex street does not merely disturb the fish; it provides an organized mechanical input that can drive a flexible body into a stable phase-locked response. This interpretation is consistent with broader studies showing that vortex formation and vortex–body interactions are central organizing principles in biological propulsion and flow-mediated locomotion^{12, 13, 14, 16, 31, 32}.

Flexible bodies exploit this vortical input through phase-locked energy transfer rather than simple passive drifting. When the body response is properly phased relative to the incident forcing, the vortex street can perform positive mechanical work on the body over part of each cycle, driving lateral oscillation and body bending while reducing the active power required for station holding. The forced-oscillation analysis supports this interpretation: the body-center response approached a near-quarter-cycle phase lag relative to the external forcing, consistent with the response of a forced damped oscillator near resonance^{15, 29, 30}. At the same time, live–dead comparisons indicate that Kármán gait is passive-dominated but not fully passive. Dead fish and passive bionic models reproduced much of the global body–tail oscillation, whereas live fish differed most clearly in the anterior body region. This suggests that body–wake mechanics organize the main oscillatory state, while neural and sensory control stabilize posture, orientation and corridor position^{7, 8, 33}. This stabilizing role of body-wave propagation parallels broader findings that undulatory body motion can enhance locomotor stability, as shown in flying snakes where aerial undulation stabilizes glide dynamics and improves performance³⁴. In Kármán gait, tail-mediated body waves may similarly help regulate lateral amplitude and maintain the fish within the wake-defined corridor.

A key implication of this framework is that Kármán gait does not occur for arbitrary flexible bodies exposed to a vortex street. Instead, access to this state is gated by compliance, frequency matching and body–wake scale matching. Increasing stiffness reduced Kármán-gait occurrence, indicating that sufficient compliance is required for

wake entrainment. Density affected Kármán gait through inertial and frequency matching: occurrence peaked near neutral density, where the forcing-to-natural frequency ratio approached ($\omega_s/\omega_n \approx 1$). Live-fish observations further suggested that Kármán gait occurs most frequently within an intermediate range of relative body length, indicating that the body must also be spatially compatible with the vortex street. This compliance requirement also distinguishes wake-inherited Kármán gait from stiffness tuning in active fish-like propulsion. In actively driven swimmers, appropriate or tunable stiffness can enhance speed and efficiency by optimizing internally generated propulsion, whereas in Kármán gait, sufficient compliance gates access to an externally forced phase-locked state^{16, 23, 25, 27}.

This framework has implications for both fish ecology and bioinspired propulsion. In natural aquatic environments, wakes generated by rocks, vegetation, bridge piers and other submerged structures are common, but our results suggest that wake exploitation depends not only on the presence of vortices, but also on whether body compliance, inertial response and body length are compatible with the wake structure^{1, 2, 3, 4, 5, 6}. For robotic swimmers, efficient wake use therefore requires more than placing a flexible body in a vortex street; body compliance, effective inertia and body–wake scale must be jointly tuned to enable stable wake entrainment and phase locking^{13, 14, 22, 23, 24, 25, 26, 27}. More broadly, our findings suggest a general principle for flexible bodies in unsteady flows: external vortical forcing can be inherited as organized motion only when the body's mechanical properties are temporally and spatially compatible with the forcing structure. This "physical compatibility" principle may extend beyond fish swimming to other flow-structure interactions, including bird flight in turbulent wakes, plant reconfiguration in wind, and the design of flow-adaptive robots.

Several limitations should also be noted. The present experiments focused mainly on controlled bluff-body vortex streets, whereas natural aquatic flows are often three-dimensional, intermittent and turbulent. Active muscle control was inferred from

kinematics and live–dead comparisons rather than directly measured. In addition, the density and stiffness effects were tested using passive bionic models, and whether extremely low stiffness disrupts phase transmission remains to be tested over a wider compliance range. Overall, Kármán gait emerges when an organized vortex street, a sufficiently compliant body and compatible temporal–spatial scales jointly produce stable wake-forced phase locking.

Methods summary

We combined comparative wake experiments, live–post-mortem comparisons, flow reconstruction, reduced-order modelling and passive bionic-fish tests to examine the physical basis of Kármán gait. Experiments were conducted in a recirculating flow tank using four bluff-body geometries to generate vortex streets. Kármán-gait bouts were identified by sustained body-center slaloming through alternating vortices, frequency locking between tail-beat and vortex-shedding frequencies, and maintenance of the synchronized pattern for at least three vortex-shedding cycles. Fish midlines were extracted from high-speed videos to quantify head, body-center and tail motion, body-wave propagation and the body-center–tail phase difference.

Time-resolved PIV was used to characterize the incident vortex street, and CFD-based pressure reconstruction was used to estimate pressure fields and hydrodynamic force proxies around the fish body. Dynamic mode decomposition was applied to reconstructed pressure fields to identify leading wake-associated pressure modes linked to lateral confinement, periodic lateral excitation and body-wave-related forcing. A reduced-order forced-oscillator model was then used to interpret the phase and amplitude relationship between vortex forcing and body-center motion.

To test physical constraints on access to Kármán gait, passive bionic fish with controlled stiffness and density were placed downstream of a D-shaped cylinder, and Kármán-gait occurrence probability was quantified across stiffness–density

combinations. Live-fish observations were further used to evaluate the effect of body–wake scale, BL/W. Data are reported as mean $\pm$ s.d. Statistical units and detailed procedures for animal handling, image processing, PIV, CFD, DMD, modelling and statistical analyses are provided in the Supplementary Methods.

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453 **Supplementary Materials**

454 Symbols

455 Supplementary Methods

456 Supplementary Results I to VI

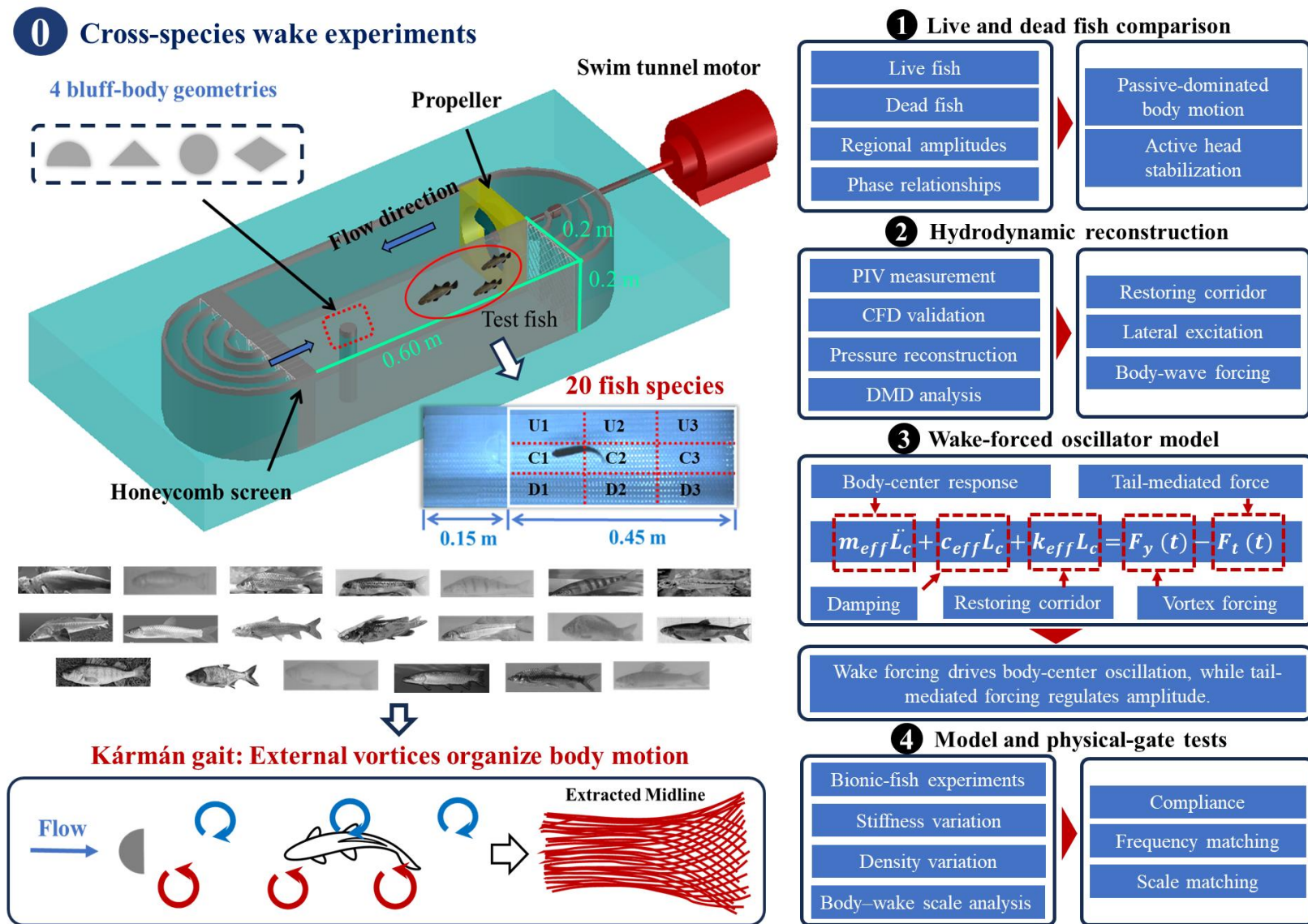
457 Figs. S1 to S20

458 Tables S1 to S6

459 Legends for supplementary figures S1 to S20

460 Legends for supplementary tables S1 to S6

461 Movies S1 to S3



462

463 **Figure 1 Framework for testing Kármán gait as a wake-forced, physically gated state.** Cross-species experiments, live–dead
 464 comparisons, hydrodynamic reconstruction and passive bionic-fish tests were integrated to examine how vortex streets organize fish
 465 body motion. The framework links wake-induced confinement and forcing to an oscillator model and tests the roles of compliance,
 466 frequency matching and body–wake scale matching in stable Kármán gait.

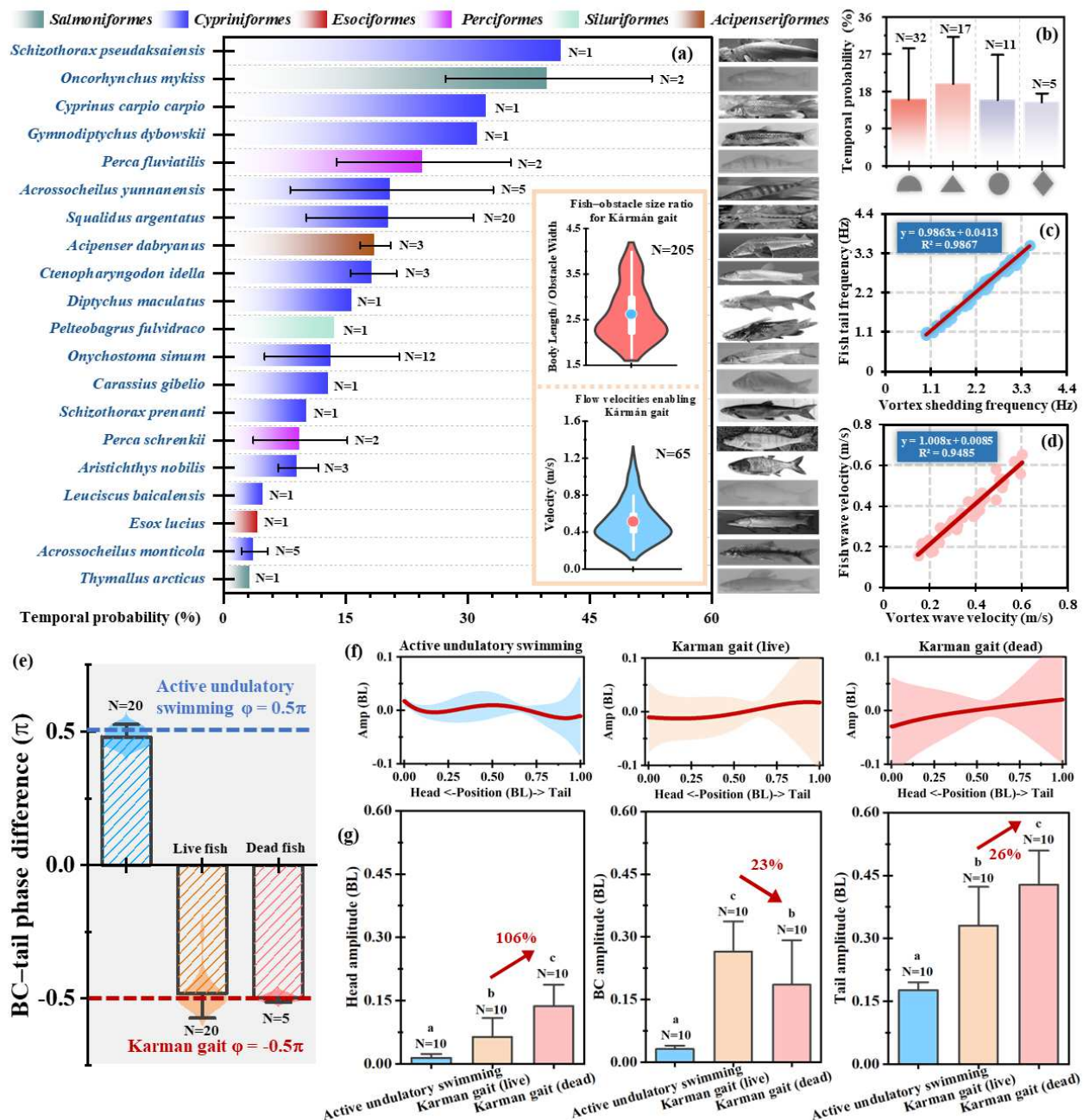


Figure 2 Kármán gait is a vortex-synchronized phase-locked response with a strong passive component. (a) Temporal probability of Kármán gait across representative fish species. Insets show the fish-to-obstacle size ratio and incoming flow velocity associated with Kármán-gait bouts. (b) Occurrence probability behind four bluff-body geometries. (c) Tail-beat frequency versus vortex-shedding frequency, showing frequency locking. (d) Body-wave velocity versus vortex convection velocity, showing spatial synchronization. (e) Body-center–tail phase difference, defined as $\phi_{BT} = \phi_{tail} - \phi_{BC}$, during active undulatory swimming, live-fish Kármán gait and dead-fish Kármán-gait-like responses. Active swimming and Kármán gait occupy opposite phase branches. (f) Spatial profiles of lateral body-oscillation amplitude under the three locomotor conditions. (g) Head, body-center and tail oscillation amplitudes; red arrows indicate relative changes in post-mortem fish compared with live fish during Kármán gait. Data are mean $\pm$ s.d. where applicable; different letters indicate significant differences among groups.

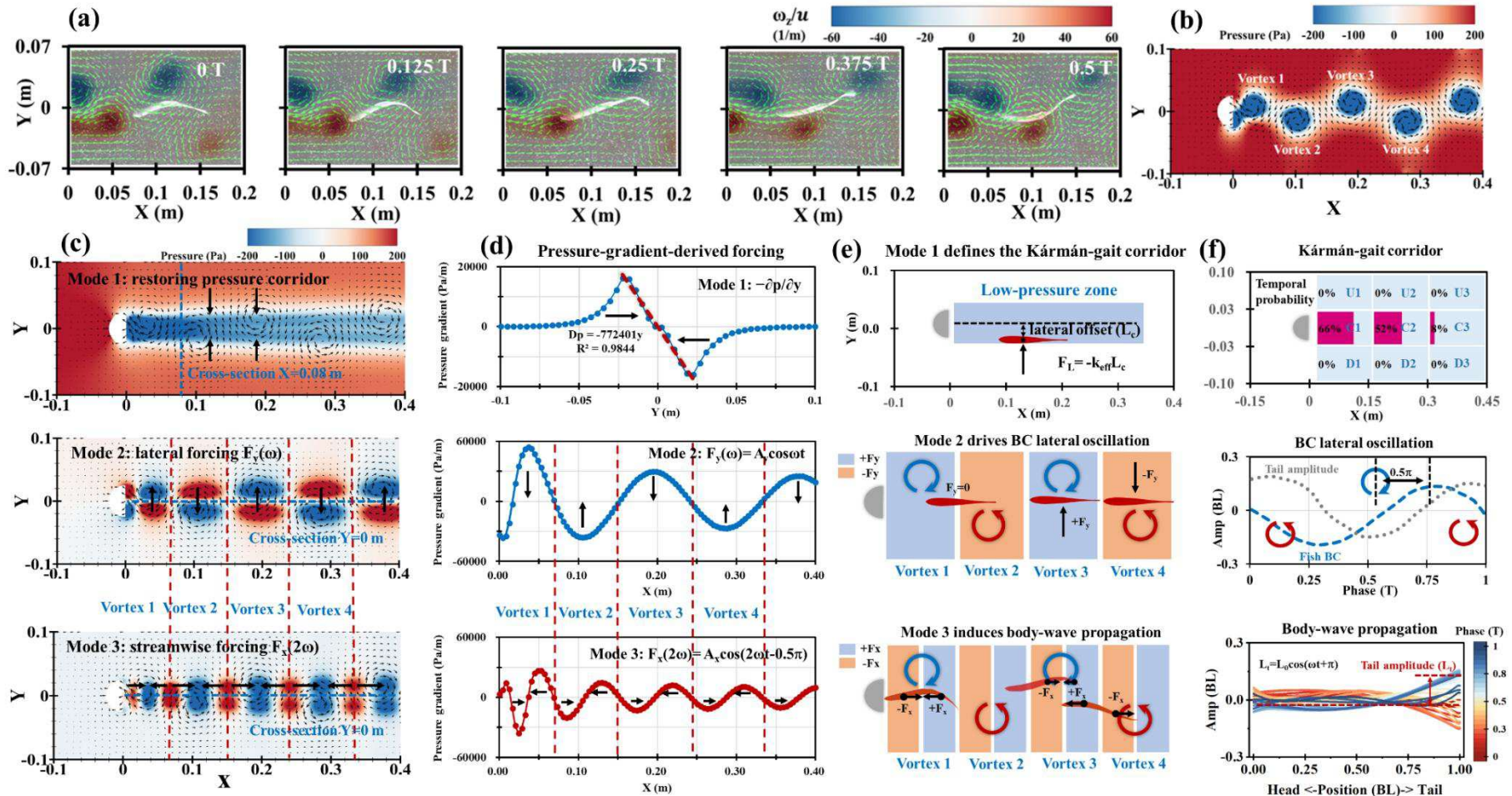


Figure 3 The incident vortex street provides a $(F_y(\omega) - F_x(2\omega))$ force architecture for Kármán gait. (a) Time-resolved vorticity fields over one half-cycle, showing the fish slaloming through successive vortices. (b) Reconstructed pressure field around the fish body, showing alternating high- and low-pressure regions in the incident vortex street. (c) Pressure-mode decomposition identifies three dominant wake-associated modes: a lateral restoring corridor, a periodic lateral forcing proxy, $F_y(\omega)$, and a streamwise forcing proxy, $F_x(2\omega)$. (d) Pressure-gradient profiles along representative cross-sections show the direction and relative magnitude of mode-associated forcing proxies. (e) Schematic interpretation of the three modal components, including effective lateral confinement, body-center excitation and body-wave-related forcing. (f) Correspondence between the leading wake modes and characteristic Kármán-gait kinematics, including corridor confinement, body-center oscillation, downstream body-wave propagation and tail-amplitude development.

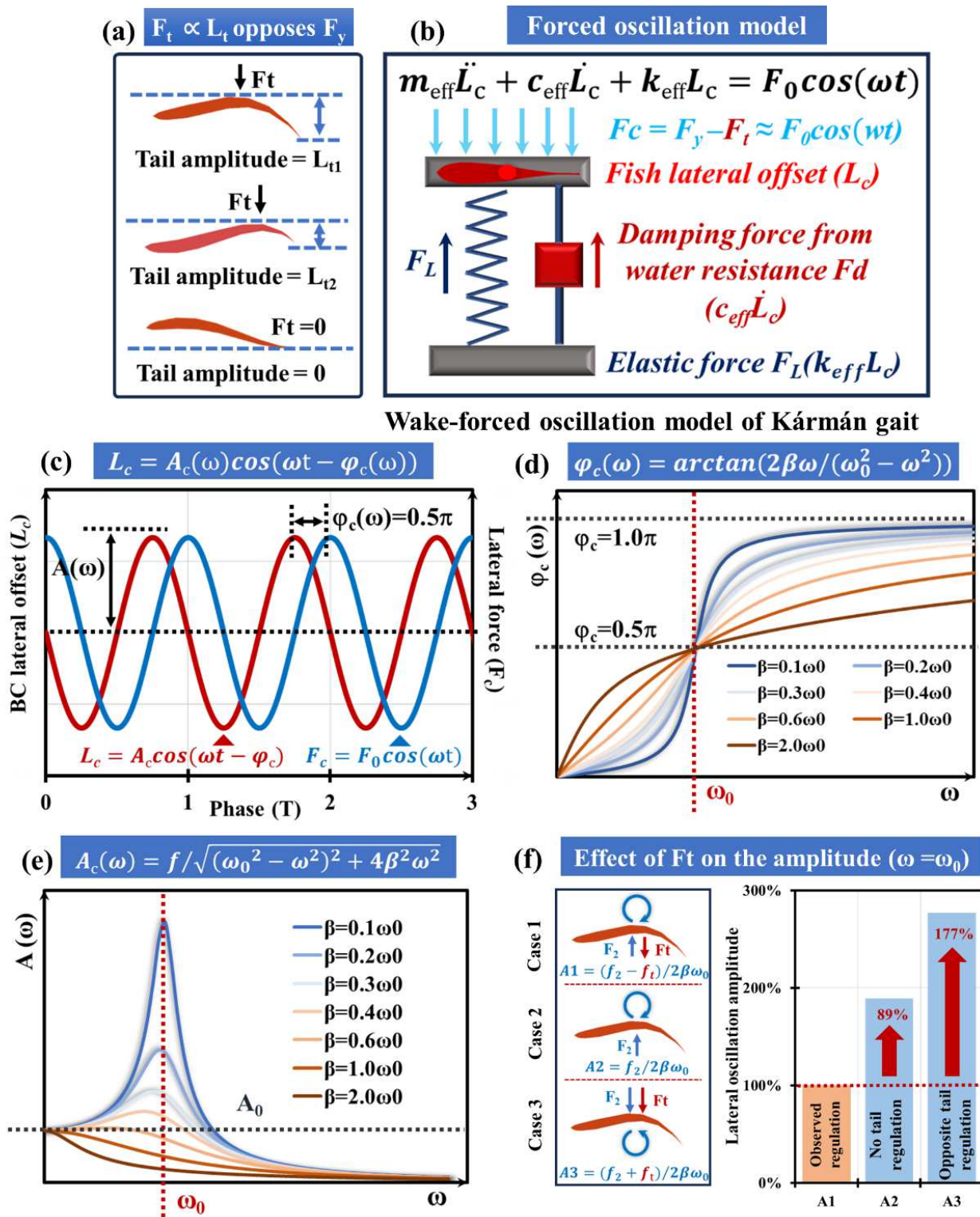
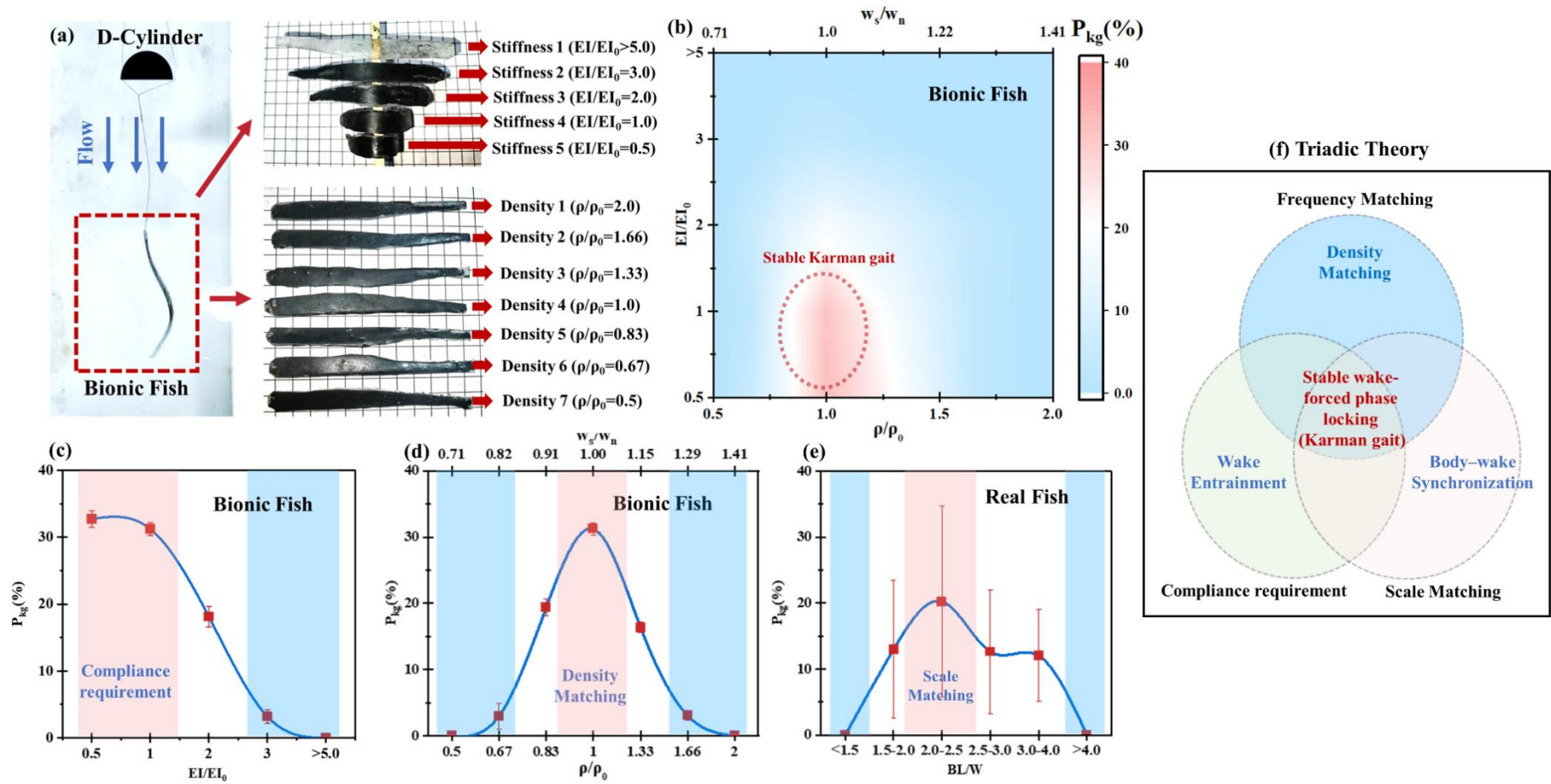


Figure 4 Wake-forced oscillation model of Kármán gait. (a) Tail-mediated force F_t was inferred from tail-amplitude variation and treated as acting opposite to the lateral vortex forcing F_y . (b) Reduced-order model describing body-center displacement L_c as a damped oscillator driven by the net lateral forcing $F_c(t) = F_y(t) - F_t(t)$. (c) Predicted phase lag between the effective lateral forcing and body-center response. (d,e) Phase and amplitude responses of the forced-oscillation model, showing a near-quarter-cycle phase lag and damping-dependent amplitude limitation near the effective resonance frequency. (f) Predicted effect of tail-mediated forcing on resonant amplitude. The observed regulated condition was normalized to 100%; removing or reversing the tail-mediated counterforce increased the predicted amplitude relative to this condition.



499

500 **Fig. 5. Physical constraints on access to Kármán gait.** (a) Experimental design for passive bionic-fish tests with varied body stiffness and density
 501 downstream of a D-shaped cylinder. (b) Density–stiffness phase map of Kármán-gait occurrence probability, P_{KG} , with the upper axis showing
 502 the forcing-to-natural frequency ratio, ω_s/ω_n . (c,d) Effects of body stiffness and density on P_{KG} . (e) Relationship between live-fish Kármán-gait
 503 occurrence and relative body–wake scale, BL/W . (f) Proposed physical-gate framework linking compliance, frequency matching and body–wake
 504 scale matching to stable Kármán gait. Error bars indicate mean $\pm$ s.d.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [Video1.mp4](#)
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