

The fish Strouhal number as a criterion for hydraulic fishway design

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23 both species. However, in the complex, three-dimensional altered flows observed in
24 fishways, swimming performance is likely to vary from the free flow case due to the
25 adoption of distinctive swimming gaits, variation in swimming styles, and the
26 potentially destabilizing effects of wake vortices. In order to improve criteria for
27 hydraulic design of fishways for multiple species we study the behavior and tail beat
28 kinematics of *C. galusdae* and *B. microlepidotus* (juveniles), in the wake of vertical
29 and bottom-mounted cylinders in an open channel flow. *Cheirodon galusdae* swam
30 using a burst-and-coast style. This species avoided the cylinder wakes, searching for
31 more favorable flow conditions. *Basilichthys microlepidotus* adopted a Kármán gait-
32 like swimming strategy to swim in the cylinder wake. Tail beat frequency was constant
33 in all experiments for both species, but in the presence of cylinders >2 cm in diameter,
34 *C. galusdae* diminished the duration of the coast phase evidencing a higher propulsive
35 effort. Tail beat amplitude of both species increased with the vortex length scale and
36 decreased linearly with vortex shedding frequency. The fish Strouhal number
37 correlated well with the relative vortex size and shedding frequency, compiling the
38 swimming effort of species with very different behaviors, indicating that it is a suitable
39 criterion for fishway design.

40

41 **Keywords:** Multispecies fishways; Design criteria; Fish behavior in wakes; Tail beat
42 kinematics; Turbulence.

43

44 **1. Introduction**

45 The decline of freshwater fish biodiversity is occurring at an alarming and persistent
46 rate (Butchart et al., 2010). Given that most fish must undertake some form of movement to
47 complete their life cycle, the high proliferation of hydropower schemes is of particular
48 concern since longitudinal river fragmentation through physical barriers is a major issue for
49 the conservation of aquatic species. Moreover, impacts of hydropower facilities and other
50 instream structures, such as weirs and culverts, which block fish movements are especially
51 complex in regions with diverse and poorly understood fish stocks (Castro-Santos et al.,
52 2009). Several locations in the southern hemisphere such as Brazil, Perú and Chile, are
53 among the major global hotspots of hydropower development (Zarfl et al., 2015) and are
54 home to some of the least studied ‘non-sport’ fish communities in the world (Link and
55 Habit, 2015).

56 Even when considered ‘half-way’ technologies (Brown et al., 2013) fishways,
57 especially nature-like designs, are a promising alternative for provision of riverine
58 connectivity to mitigate the critical impacts of barriers, such as longitudinal fragmentation
59 (Baki et al., 2013; Baki et al., 2014). One of the greatest challenges in fish passage
60 technology is the development of structures and design concepts suitable for a broad range
61 of species (Castro-Santos et al., 2009; Russon and Kemp, 2011). The reasons explaining
62 why some fishways work better than others and why some species perform better than
63 others in particular fishways is still poorly understood. Some of the factors that affect fish
64 passage in a fishway include: (1) biological characteristics as for instance the migration and
65 movement patterns, body length, swimming and non-swimming (e.g. climbing) modes,
66 circadian rhythms, and response to olfactory and acoustic stimuli; (2) ecological

67 characteristics, such as habitat and food preferences, light intensity and water temperature,
68 and presence of conspecifics and predators; and (3) hydraulic properties of the fishway,
69 including geometry, substrate and vegetation, length, slope, water depth, velocity and
70 turbulence (Bunt et al., 2012; Noonan et al., 2012; Goettel et al., 2015; Link and Habit,
71 2015).

72 Of the aforementioned factors body length and hydraulics have received much
73 attentions as, within a given species, fish swimming speed is proportional to body length
74 (Videler & Wardle, 1991; Wardle et al., 1995; Stafkiotakis et al., 1999). This is especially
75 important in the context of ensuring passage for non-sport fish that, by definition, are small-
76 bodied (<150 mm total length at maturity) and have been described as having
77 correspondingly weak swimming abilities in absolute terms (e.g. Mitchell 1989, Nikora et
78 al., 2003; Plew et al., 2007). Laborde et al. (2016), however, have recently shown that two
79 non-sport species native to Chile exhibit relatively strong swimming capacity during
80 swimming tests in free flow in the laboratory. The swimming ability of the two species,
81 *Cheirodon galusdae* and *Basilichthys microlepidotus*, under controlled conditions was
82 similar, leading to the suggestion that an effective fishway could be designed to
83 accommodate both species simultaneously. However, in the complex, three-dimensional
84 altered flows observed in fishways (Feurich et al., 2012; Bretón et al., 2013; Baki et al.,
85 2013; Baki et al., 2014) the swimming performance of fish is likely to vary from the free
86 flow case due to the adoption of distinctive swimming gaits (Liao et al., 2003a; Liao et al.,
87 2003b; Liao et al., 2007; Taguchi and Liao, 2011), variation in swimming styles (Weihs
88 and Webb, 1983; Videler, 1993), and the potentially destabilizing effects of wake vortices
89 (Pavlov et al., 2000; Lupandin, 2005; Tritico and Cotel, 2010). Depending on the intensity,

90 predictability (periodicity), orientation and scale of the turbulence relative to fish
91 characteristics (e.g. body shape and length), swimming performance may be enhanced,
92 diminished or unaffected in altered flows (Lacey et al., 2012; Wilkes et al., 2013; Enders
93 and Boisclair, 2016).

94 An important aspect of swimming performance is related to propulsion through the
95 caudal fin and thus, to tail beat kinematics, including tail beat frequency (f_{TB}) and amplitude
96 (λ) in relation to swimming speed (U) (Bainbridge, 1958; Hunter and Zweifel, 1971;
97 Videler and Wardle, 1991). Note that swimming speed would typically be equal to the flow
98 velocity as, due to rheotaxis, the fish tends to hold position in the flow. In the following, U
99 is the section averaged flow velocity. In particular, the fish Strouhal number, $St_{fish} = f_{TB} \lambda /$
100 U , may be a useful dimensionless parameter for representing the propulsion effort of
101 different fish species on a comparable basis. Extensive observations have shown that
102 maximum propulsive efficiency lies in the range $0.25 < St_{fish} < 0.35$ for a large range of fish
103 species (Triantafyllou et al., 1993; Eloy, 2012).

104 In this work, we study the behavior and tail beat kinematics of the native Chilean
105 species, *C. galusdae* and *B. microlepidotus* (juveniles), in the wake of vertical and bottom-
106 mounted cylinders in an open channel flow. The focus is on the variation in swimming
107 styles, and the potentially destabilizing effects of wake vortices in order to improve criteria
108 for hydraulic design of multispecific fishways, which urgently need to incorporate elements
109 promoting the passage of small body sized fish. This research contributes to the
110 conservation of non-sport fish species threatened due to pressures for hydropower
111 development.

112

113 **1. Methods**

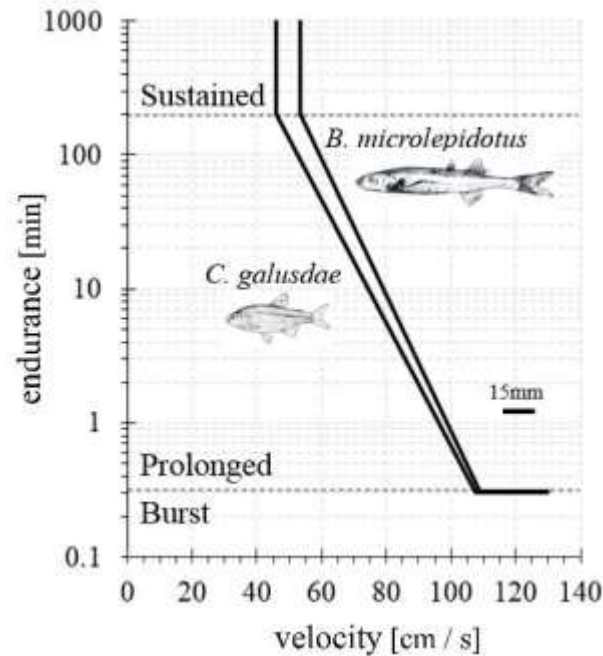
114 *2.1. Studied species*

115 *Basilichthys microlepidotus* inhabits the piedmont of the Andes and Central Valley
116 from 21 to 40° latitude south (Véliz et al., 2012). Maximum body size is 120 mm for
117 juveniles and 300 mm when adults. This species spawns and rears in floodplains during the
118 austral spring (egg laying from November to December and larvae from November to
119 February in the southern range of its distribution; Montoya et al., 2012). Diet varies from
120 planktivorous to omnivorous and bentophagous when adults (Acuña et al., 2005).
121 Swimming mode is carangiform (Link and Habit, 2015) and during the reproductive season
122 this species swims in schools (Vila et al., 1981). Genetic and mark-recapture data suggests
123 that this species exhibits extensive movements along rivers (Victoriano et al., 2012;
124 Piedra et al., 2012).

125 *Cheirodon galusdae* also inhabits the piedmont of the Andes and Central Valley
126 from 35 to 39° latitude south (Dyer, 2000). Maximum body size is 90 mm when adult, and
127 swimming mode is subcarangiform (Link and Habit, 2015). Its reproductive season occurs
128 from late spring to summer, but spawning and rearing habitats are unknown. *Cheirodon*
129 *galusdae* feeds on periphyton and epizoon communities and inhabit in lakes and shallow
130 vegetated ponds in rivers (Ruiz, 1993; Habit et al. 2006). There is no data about its
131 movement patterns.

132 Conservation status of both species is Vulnerable (Vila and Habit, 2015). Endurance
133 was described for both species by Laborde et al. (2016), finding that both species
134 performance was very similar (Figure 1).

135



136

137 **Fig. 1.** Endurance curves for *C. galusdae* and *B. microlepidotus* (after Laborde et al., 2016).

138

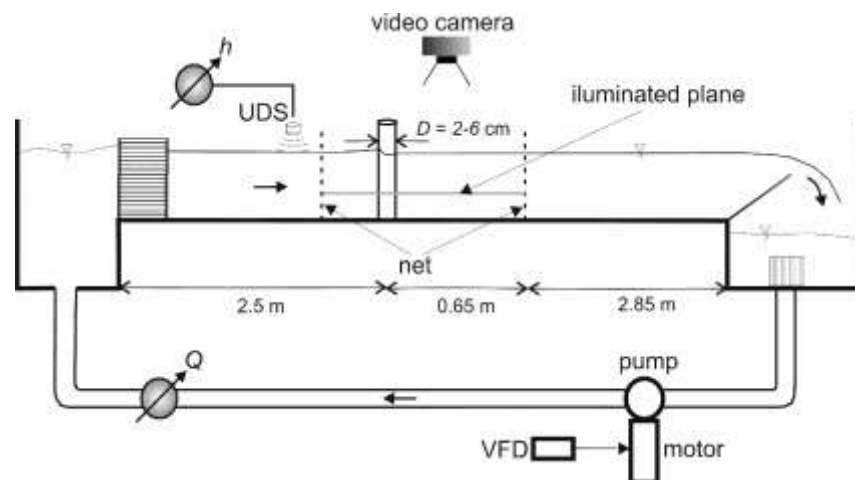
139 Fish were collected from the Itata River (at 36°45'30"S, 72°24'53"W) using a backpack
 140 electroshocker (Smith-Root LR24, Vancouver, WA, USA) and seine net (2-mm mesh). All
 141 collected fish were transported to glass aquariums at the Hydraulics and Environmental
 142 Engineering Laboratory of the University of Concepción. To avoid mortality, guidelines for
 143 fish transportation and successful maintenance in captivity of Chilean native fish were
 144 followed (Sobenes et al., 2012). Fish were kept for at least 15 days before experiments.
 145 Fish were fed *ad libitum* with live prey (macroinvertebrates from streams and *Enchitrea*
 146 sp., *Tenebrio molitor*, and *Eisenia foetida*) three or four times a week according to Sobenes
 147 et al. (2012) and García et al. (2012). Following Jobling (1982) feeding was interrupted 48
 148 h before each experiment. Water temperature was kept stable at 17±1°C for 1 week before
 149 the experiment. A total of 12 individuals (6 *C. galusdae* and 6 *B. microlepidotus*) of similar

150 body length (44.8 ± 1.5 mm for *C. galusdae* and 77.7 ± 5.9 mm for *B. microlepidotus*) were
 151 tested.

152

153 2.2 Experimental installation

154 Experiments were conducted in a laboratory flume 6 m length, 40 cm width, and 40 cm
 155 height located at the Hydraulic Engineering Laboratory of the University of Concepción. A
 156 honeycomb matrix was placed at the flume entrance to provide an aligned flow. An
 157 interrogation area of 0.65 m length, located 2.5 m downstream from the entrance was
 158 isolated with a net in order to keep fishes in the interrogation area. Vertical mounted
 159 cylinders with diameters of 2, 3, 4, 5 and 6 cm were placed at the upstream end of the
 160 interrogation area. The discharge Q was controlled by a variable frequency drive (VFD)
 161 and measured with an electromagnetic flow meter having an accuracy of $\pm 0.5\%$. The flow
 162 depth, h , was controlled by adjusting the tailgate at the end of the flume, and was measured
 163 with an ultrasonic distance sensor (UDS). (Figure 2).



164

165

Fig. 2. Scheme of the experimental installation.

166

167 2.3. Particle Image Velocimetry

168 The flow field was characterized using a two dimensional Particle Image Velocimetry
169 (PIV) measurement system in order to determine the vortex shedding frequencies f and
170 corresponding length scale, L_u at the cylinder wakes. Measurements were performed at a
171 horizontal plane located at a height of 40% of the flow depth. The particle seeding density
172 was carefully designed to allow the recommended minimum of ~ 5 particles in each
173 interrogation window (Adrian and Westerweel, 2011). A Sony Action Cam HDR-
174 AS100V® with a 32GB memory, 1280x720 pix resolution and acquisition frequency of
175 120 Hz was used to record the particle motion. For the flow conditions analyzed, the 120
176 Hz allowed displacements between frames larger than the particle diameter in the images,
177 thus errors produce by short displacements were minimized. These displacements were also
178 long enough to allow a good correlation peak magnitude in the correlation analysis. To
179 ensure statistical convergence, the flow field was measured during 7 minutes, i.e. 50400
180 frames.

181 Before the measurements, but using the same experimental conditions, a target
182 containing reference marks was placed in the flow channel at same position as the light
183 plane. Images of the target were used to correct the PIV images for typical barrel and
184 pincushion lens distortions, but also to correct optical deformations induced by the
185 experimental setup. After the PIV processing was completed, the displacements in camera
186 coordinates (pix) were converted to real world coordinates (cm) using also the information
187 provided by the calibration target. An enclosure around the flume was built to avoid the
188 recording of environmental light in the images. Analogously to the work by Gross et al.
189 (2010) two sources of light were used as the light density of a single one was not enough to

190 produce a good contrast level in the images. The light was collimated to illuminate a flow
191 region of 20 cm-long and 0.8 cm-wide. Polyamide-12 particles of 100 μm diameter and
192 1.06 g/cm^3 density were used as tracers. The size and density of these particles ensure that
193 they will respond to a wide range of flow structures of interest (Melling, 1997).

194 Tracer displacement was calculated using the toolbox for Matlab, PIVlab® developed
195 by Thielicke and Stamhuis (2014a,b). A multi-pass approach with final interrogation
196 windows of 32 x 32 Pix was used for the calculations. With the aim of improving the
197 velocity estimation in high shear regions, the image deformation technique was used
198 (Scarano, 2001). The displacement calculation was improved using a Gaussian subpixel
199 accuracy estimation (Adrian and Westerweel, 2011). The percentage of outlier vectors in
200 individual frames was always less than the 4~5% recommended (Adrian and Westerweel
201 2011). During the post processing of the estimated velocity fields, the universal outlier
202 filter of Westerweel and Scarano (2005) was used for outlier removal, while a cubic
203 interpolation technique was used for their estimation.

204

205 *2.3.1 Vortex shedding frequency*

206 Time series of the spanwise velocity component were extracted from the PIV
207 measurements and a Fourier analysis was performed for determination of the dominant
208 frequencies corresponding to shedding frequencies of the wake vortices. The power spectra
209 density, E_v was calculated for each experiment applying the Fourier transform to the
210 spanwise velocity autocorrelation function $R_v(\tau)$ of the velocity fluctuations v' :

211

$$212 \quad R_v(\tau) = \overline{v'(x,t)v'(x,t+\tau)} \quad (1)$$

$$213 \quad E_v = \frac{1}{2} \pi \int_{-\infty}^{\infty} e^{-if\tau} R_v(\tau) \partial\tau \quad (2)$$

214 The Fourier transform decompose the autocorrelation signal into a family of
 215 frequencies, where each frequency is associated with a different energy level. Peaks of the
 216 power spectra density correspond to dominant frequencies. In this case, the vortex shedding
 217 frequency correspond to the maximum spectral peak. The method of Welch (Welch, 1967)
 218 as implemented in the signal processing toolbox of Matlab was used for the calculations.

219

220 *2.3.2 Vortex length scale*

221 The integral vortex length scale is $L_u=D$, with D the cylinder diameter. With additional
 222 assumptions (Taylor, 1935), vortex length scale is given by $L_u = U / f$, where f is the
 223 shedding frequency.

224

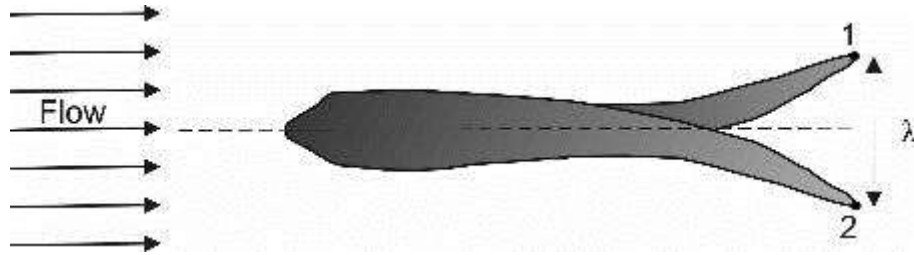
225 *2.4. Fish behavior and tail beat kinematics*

226 Video records of fish motion with 20 minutes duration were analyzed to characterize
 227 the fish behavior and the tail beat kinematics following the methodology by Oufiero et al.
 228 (2014). Fish were recorded dorsally at 120 fps using a Sony Action Cam HDR-AS100V®.
 229 The images obtained with this camera were also corrected for optical distortions.

230 For determination of tail beat amplitude (λ) and tail beat frequency (f_{TB}) videos were
 231 digitized using the software ImageJ (U.S. National Institutes of Health, Bethesda,
 232 Maryland, USA, <http://imagej.nih.gov/ij/>). The base of the caudal fin was digitized for

233 consecutive full tail beats taken from portions of the swimming trials with minimal
 234 movement of the fish centroid. This point was digitized when the tail was extended
 235 maximally laterally, on either side for each of the full tail beats (Fig. 3).

236



237

238 **Fig. 3.** Digitized points (1 and 2) for determination of the tail beat amplitude λ .

239

240 Horizontal and vertical coordinates for each video and trial were further processed to
 241 obtain the average tail beat amplitude and timing. Tail beat time was the time it took for
 242 one complete tail beat cycle, from maximal lateral position on the right side of the fish,
 243 through the center position, to the maximum lateral position on the left side of the fish, and
 244 back to the original starting position on the maximum lateral right side. From these two
 245 observations, tail beat frequency f_{TB} was calculated, i.e. the inverse of the tail beat time was
 246 calculated, giving an estimate of the number of tail beats per second. In order to quantify
 247 the propulsion effort in terms of tail beats the average tail beat frequency f_{TB}^{30}
 248 corresponding to 30 tail beats was analyzed. The fish Strouhal number, $St_{fish} = f_{TB}^{30} \lambda / U$,
 249 was then determined. U is the section averaged flow velocity.

250

251 *2.5. Experimental series*

252 Six individuals of each study species, having similar body length (BL) and critical
253 swimming speed, were tested with free flow, and with five cylinders having diameters of 2,
254 3, 4, 5, and 6 cm. S1 was the reference series with free flow experiments. Series S2 and S3
255 served to investigate behavior and tail beat kinematics of *C. galusdae* and *B.*
256 *microlepidotus* in the presence of cylinders, respectively. In series S2 and S3, individuals
257 were exposed to repeated tests, being exposed to wakes caused by the cylinder of 2, 3, 4, 5,
258 and 6 cm in diameter. Conditions for each of the 72 experiments are included as
259 supplementary material. Each trial began with 1.5 hours of acclimatization with a section
260 averaged velocity of 1 BL/s in order to decrease the stress produced on the fish.
261 Subsequently, flow velocity was slowly raised up to the tested condition. In order to avoid
262 fish fatigue, in all experiments the section averaged flow velocity was equal 0.7 times the
263 critical swimming speed of the individual, U_{cr} (Webb, 1971), which was reported by
264 Laborde et al. (2016). In order to confirm this assumption variation of tail beat frequency at
265 the beginning and end of the experiments was compared with the Wilcoxon Matched Pair
266 Test. The experiments spanned cylinder Reynolds number $Re_D = \rho U D / \mu$, where ρ is the
267 fluid density, U the section averaged flow velocity, D the cylinder diameter and μ the
268 dynamic viscosity of water, in the range of 3000 to 17000 and cylinder Strouhal number St
269 $= f D / U$, where f is the shedding frequency from 0.17 to 0.21.

270 Tail beat frequency, tail beat amplitude and fish Strouhal number were compared
271 between the two species with a one-way Analysis of Variance (ANOVA) prior verification
272 of variance and normality homogeneity tested by the Levene and the Kolmogorov-Smirnov
273 test, respectively. Significant differences of the tail beat kinematics and fish Strouhal in
274 wakes and free flow for each species were tested using a Friedman ANOVA χ^2 test.

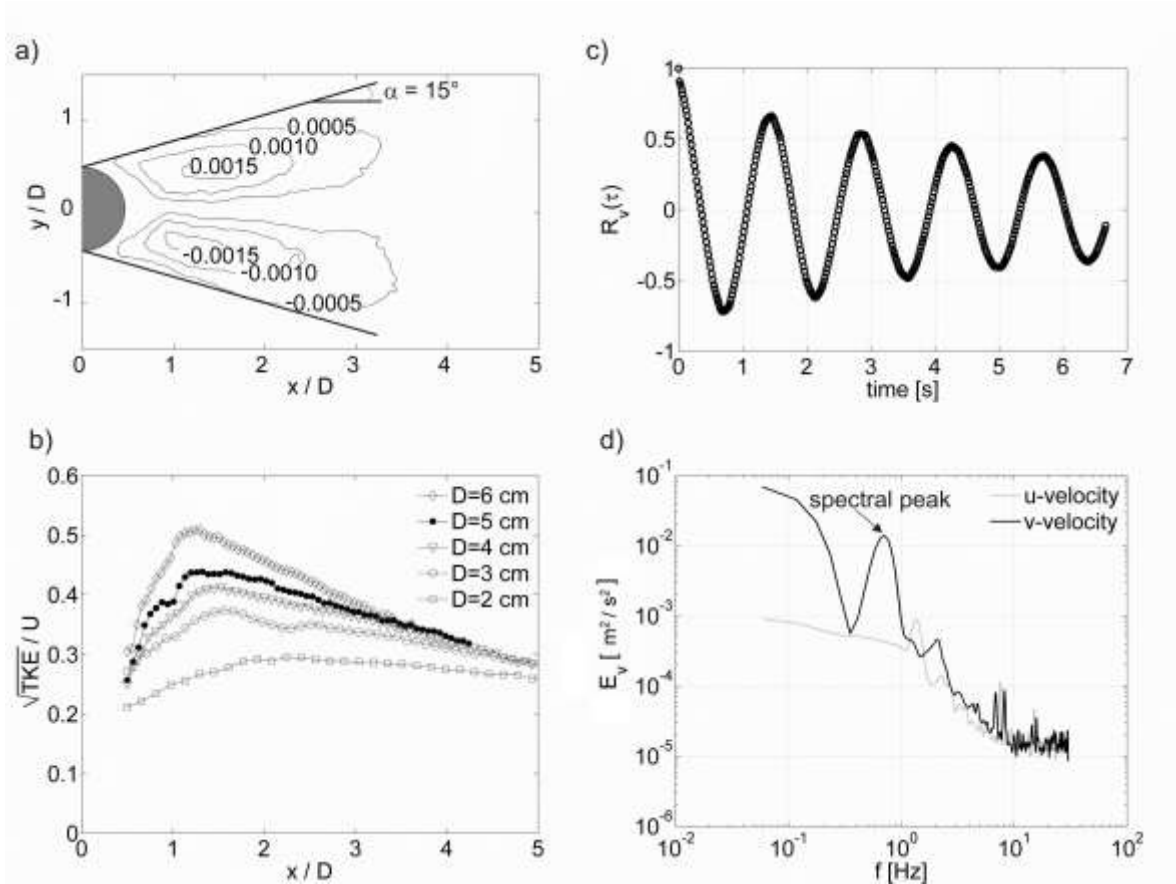
275 Tendencies of the aforementioned variables with flow properties such as the relative vortex
276 size and vortex shedding frequency were analyzed fitting linear or potential regressions.

277

278 **3. Results**

279 *3.1. Flow properties*

280 The angle of flow separation, α at the cylinder wakes was computed from the Reynolds
281 stress distributions as illustrated in Fig. 4 (a). In all cases $\alpha = 15^\circ \pm 1^\circ$. The point of merging
282 of the two separated shear layers in Fig. 4 (a) can be identified as the location of the peak of
283 the TKE profile at the longitudinal centerline position in Fig. 4 (b). For small diameters the
284 distance of the TKE peak to the cylinder slightly increases. After the TKE peak almost a
285 linear decay of the TKE with the downstream direction is observed, which occurs as a
286 consequence of the diffusion of the wake vortices, or in other words occurs as a
287 consequence of the processes responsible of recovering the channel flow condition. Figures
288 4 (c) and 4 (d) shows the autocorrelation function and corresponding spectral peak in
289 experiment S3-19 according to Eqs. (1) and (2). From the figure 4 (d) the dominant
290 frequency is 0.7 Hz.



291

292 **Fig. 4.** a) Normalized Reynolds stresses $\overline{v'u'}/U^2$, b) profiles of Turbulent Kinetic Energy
 293 along the centerline, c) spanwise velocity autocorrelation function, and d) power spectral
 294 density for experiment S3-19.

295 Table 1 in Suppl. Material includes frequency for each experiment. Cylinder wakes
 296 were found in the so-called shear-layer transition regime with Kelvin-Helmholtz
 297 instabilities which occurs in the range $1000 < Re_D < 100,000$ (Williamson 1996). The wake
 298 vortices were shed on a vertical axis at a dominant frequency described by the cylinder
 299 Strouhal number. In the experiments the observed relationship between Re_D and St
 300 followed the curve proposed by Fey et al. (1998):

$$St = \begin{cases} 0.2040 + \frac{0.3364}{\sqrt{Re_D}} & 1300 < Re_D < 5000 \\ 0.1776 + \frac{2.2023}{\sqrt{Re_D}} & 5000 < Re_D < 2 \cdot 10^5 \end{cases} \quad (3)$$

302

303 *3.2. Fish behavior*

304 Video records of fish motion during the experiments revealed that both studied species
 305 interacted with vortices with different consequences for swimming kinematics, i.e.
 306 propulsion effort associated with the movement of the caudal fin (see supplementary
 307 material). In the free flow condition, *C. galusdae* exhibited a burst-and-coast swimming
 308 style. In general, all analyzed individuals of this specie avoided the cylinder wakes,
 309 searching for more favorable flow conditions (i.e., less swimming effort) in the
 310 interrogation area. During the experiments with cylinders >2 cm in diameter, *C. galusdae*
 311 diminished the coast phase respect to the free flow, reducing it with the vortex length scale
 312 towards zero, and when entering in these wakes clear destabilization was observed (See
 313 Video 1 in supplementary material). In this context, destabilization was considered to have
 314 occurred when the fish was displaced downstream, accompanied by lateral displacement
 315 and loss of heading, despite increasing tail beat frequency (Tritico & Cotel, 2010; Maia et
 316 al., 2015).

317 In contrast, *Basilichthys microlepidotus* swam holding position in free flow, and in the
 318 cylinder wakes (See Video 2 in supplementary material). Its lateral body displacement in
 319 the cylinder wake was consistent with the width of the wake (Figure 4) as observed for

320 Kármán gaiting (Liao et al., 2003a; Liao et al., 2003b; Liao et al., 2007; Taguchi and Liao,
321 2011).

322

323 3.3. Tail beat kinematics

324 During experiments tail beat frequency did not show a trend of change with time
325 (See Figure 1 in Supplementary material). Additionally, no significant differences in
326 average tail beat frequency in free flow and wake were observed (Wilcoxon Matched Pair
327 Test was $Z = 0,943$, $p = 0,345$ for *C. galusdae*, and $Z = 1,153$, $p = 0,248$ for *B.*
328 *microlepidotus*). This results support that no time effect related to fatigue occurred in the
329 experiments. Detailed information is included as supplementary material.

330

331 3.3.1 Tail beat frequency, f_{TB}

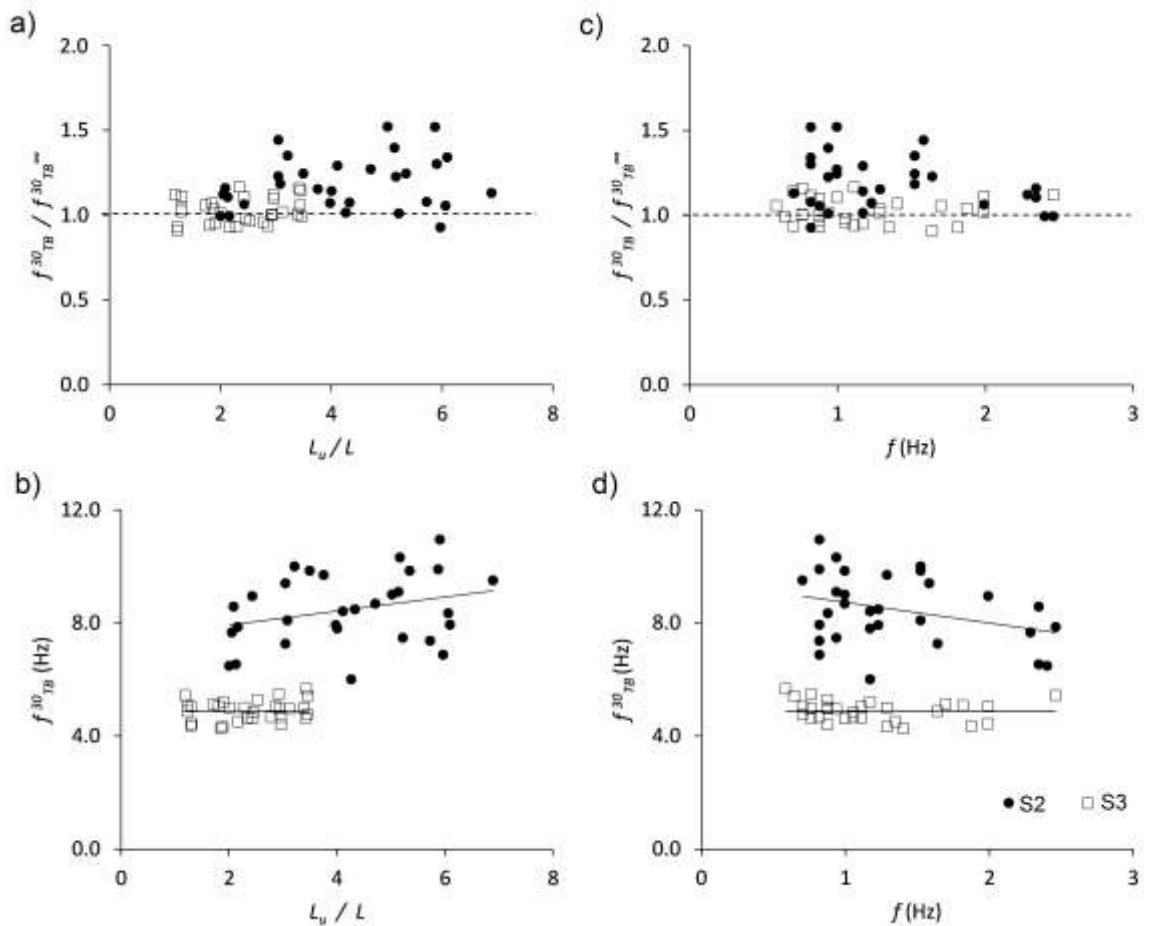
332 *Cheirodon galusdae* adopted a burst-and-coast swimming style. Typically, a burst
333 phase consisted of 5 to 20 tail beats, and thus for individuals of *C. galusdae* the average tail
334 beat frequency, f_{TB}^{30} included several burst and coast phases. *Basilichthys microlepidotus*
335 used the caudal fin for propulsion continuously and thus f_{TB}^{30} was constant. f_{TB}^{30} was
336 significantly higher in *C. galusdae* (8.18 ± 1.30 SD) than in *B. microlepidotus* (4.87 ± 0.41
337 SD) (one way ANOVA, $F_{(1,70)} = 77.35$, $p < 0.001$).

338 Different tendencies of f_{TB}^{30} with the relative vortex size L_u / L and with vortex
339 frequency f were observed for both species (Fig. 5). *Cheirodon galusdae* in cylinder wakes
340 presented higher values of f_{TB}^{30} than in the free flow case, up to 52% (ANOVA $\chi^2=19.37$,

341 $p < 0.001$). By the contrary, *B. microlepidotus* presented similar values of f_{TB}^{30} in free flow
 342 and in cylinder wakes (ANOVA $\chi^2 = 4.47$, $p = 0.48$).

343 The tail beat frequency of both species did not change significantly with the flow
 344 properties, i.e. relative vortex size ($R^2 = 0.084$, $p = 0.119$ for *C. galusdae* and $R^2 = 0.029$,
 345 $p = 0.365$ for *B. microlepidotus*) and vortex shedding frequency ($R^2 = 0.107$, $p = 0.077$ for *C.*
 346 *galusdae* and $R^2 = 0.021$, $p = 0.447$ for *B. microlepidotus*).

347



348

349 **Fig. 5.** a) Average tail beat frequency, f_{TB}^{30} divided by average tail beat frequency in the
 350 reference series S1 with free flow, $f_{TB}^{30\infty}$ over relative vortex size L_u / L . b) f_{TB}^{30} over relative

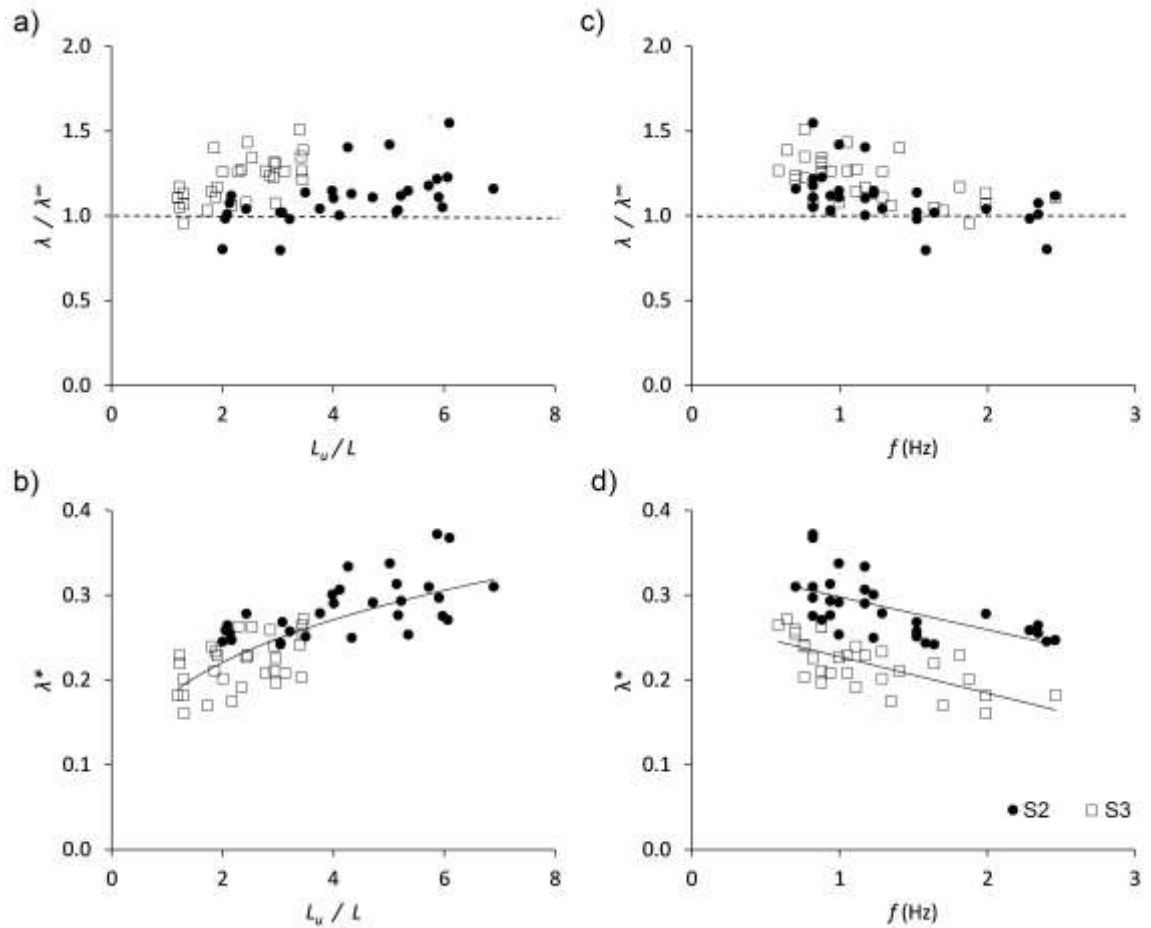
351 vortex size L_u / L . c) f_{TB}^{30} divided by f_{TB}^{∞} over vortex frequency f , and d) f_{TB}^{30} over f for
 352 experiments of series S2 (circles) and S3 (squares). Grey dashed lines indicate the free flow
 353 condition for reference. Black, solid lines show the observed tendencies.

354

355 3.3.2. Tail beat amplitude

356 Relative tail beat amplitude λ^* (normalized with the fish length, $\lambda^* = \lambda / L$) was
 357 significantly higher in *C. galusdae* (0.28 ± 0.03 SD, and 0.21 ± 0.03 SD for *B.*
 358 *microlepidotus*; one way ANOVA, $F_{(1,70)} = 72.41$, $p < 0.001$). The tail beat amplitude
 359 showed a significant increase for individuals of both species in the cylinder wake respect to
 360 the free flow case, up to 55% ($\chi^2=21.38$, $p<0.001$ for *C. galusdae*, and $\chi^2=22.26$, $p<0.001$
 361 for *B. microlepidotus*) (Figure 6). Tail beat amplitude ranged between 0.16 and 0.37 times
 362 the fish length with a mean value of $\lambda = 1.26 \pm 0.17$ SD for *C. galusdae* and $\lambda = 1.64 \pm 0.19$
 363 SD for *B. microlepidotus*. For both species λ^* increased with the relative vortex size L_u / L
 364 following a potential relationship $\lambda^* = a(L_u / L)^b$ ($a=0.180$, $b=0.296$, $R^2=0.561$, $p<0.001$),
 365 and decreased linearly with vortex frequency f , following $\lambda^* = m + nf$ ($m=0.337$, $n=-0.039$,
 366 $R^2=0.371$, $p<0.001$ for *C. galusdae*, and $m=0.271$, $n=-0.043$, $R^2=0.464$, $p<0.001$ for *B.*
 367 *microlepidotus*).

368



369

370 **Fig. 6.** Tail beat amplitude, λ divided by tail beat amplitude in reference series S1 with free371 flow, λ^∞ over relative vortex size L_u / L , (with $L_u = U / f$). b) Normalized tail beat amplitude372 λ^* (relative to the fish length, L) over L_u / L . c) Tail beat amplitude, λ divided by tail beat373 amplitude in reference series S1 with free flow, λ^∞ over vortex frequency f , and d)374 normalized tail beat amplitude λ^* over f for experiments of series S2 (circles) and S3

375 (squares). Grey dashed lines indicate the free flow condition for reference. Black, solid

376 lines show the observed tendencies.

377

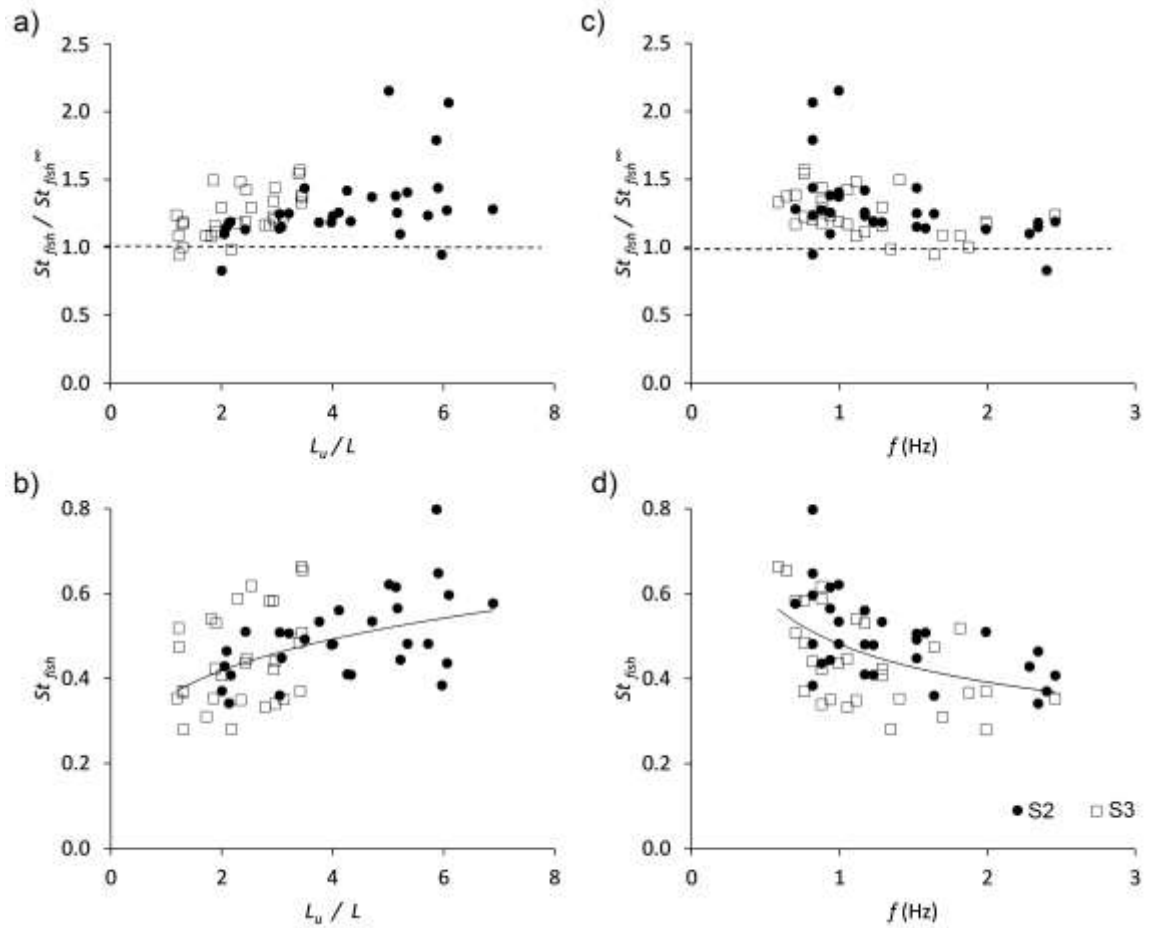
378 *3.4. Fish Strouhal number, St_{fish}*

379 St_{fish} showed no statistical differences between the two species (0.48 ± 0.10 for *C.*
 380 *galusdae* and 0.43 ± 0.11 for *B. microlepidotus*; one way ANOVA, $F_{(1,70)} = 3.30$, $p =$
 381 0.071).

382 In the free flow case fish Strouhal number St_{fish}^{∞} ranged from 0.29 to 0.50 with a value
 383 of 0.38 ± 0.08 SD, while in the cylinder wakes St_{fish} ranged from 0.28 to 0.80 with a $0.47 \pm$
 384 0.11 SD. The fish Strouhal number in cylinder wakes was significantly higher than in free
 385 flow ($\chi^2=17.90$, $p=0.003$ for *C. galusdae*, and $\chi^2=17.78$, $p=0.0014$ for *B. microlepidotus*)
 386 (Fig. 7).

387 For both species St_{fish} increased with the relative vortex size following a potential
 388 relationship $St_{fish} = a(L_u/L)^b$ ($a=0.356$, $b=0.235$, $R^2=0.232$, $p<0.001$), and decreased with
 389 vortex frequency f , following a potential relationship $St_{fish} = af^b$ ($a=0.481$, $b=-0.296$,
 390 $R^2=0.248$, $p<0.001$). Neither a significant correlation of St_{fish} with the cylinder Reynolds
 391 number Re_D nor with the flow Strouhal number St was observed ($p=0.147$ and $p=0.304$,
 392 respectively).

393



394

395 **Figure 7.** a) Fish Strouhal number, $St_{fish} = f_{TB}^{30} \lambda / U$ divided by the fish Strouhal number in
 396 the reference series S1, St_{fish}^{∞} , over relative vortex size L_u / L , b) St_{fish} over L_u / L , c)

397 $St_{fish} / St_{fish}^{\infty}$ over f , and d) St_{fish} over f , for experiments of series S2 (circles) and S3 (squares).

398 Grey dashed lines indicate the free flow condition for reference. Black, solid lines show the
 399 observed tendencies.

400

401 **4. Discussion**

402 Experiments on behavior and tail beat kinematics of fish swimming in a cylinder wake
403 were analyzed in the context of fishway design criteria. A total of six individuals of *C.*
404 *galusdae* and six individuals of *B. microlepidotus* (juveniles) were tested in a reference
405 condition with free flow, and in the wake of cylinders having 2, 3, 4, 5, and 6 cm diameter.
406 In all experiments, the average flow velocity was 0.7 times the critical swimming speed for
407 each species, avoiding fish fatigue. Individuals had lengths that correspond to the
408 standardized critical swimming speed and in this sense, they were representative of the
409 species (Laborde et al. 2016). Individuals of each study species were selected to have
410 similar body lengths, and thus they were considered replicates of the behavioral responses
411 to turbulent wakes.

412 Our results demonstrate the difficulties in establishing realistic hydraulic design criteria
413 for multispecies fishways based on critical swimming speed and endurance curves only,
414 due to the divergent swimming style and performance exhibited by the two species in the
415 altered flows, i.e. cylinder wakes. As currently guidelines for hydraulic design of fishways
416 are based on criteria suitable for relatively strong-swimming species with migratory
417 behavior, such as salmonids (Katopodis and Williams, 2012), further development of fish
418 passage technology is especially needed for non-sport fish (Link and Habit, 2015). The
419 main reasons are: (i) although many non-sport fish do not exhibit strong migration patterns,
420 they do need to perform local movements to complete their life cycles (Piedra et al., 2012)
421 and maintain idiosyncratic patterns of gene flow within river networks (Victoriano et al.,
422 2012); (ii) the small body length of non-sport fish limits absolute swimming speeds (i.e. not
423 relative to body length) (*e.g.* Mitchell, 1989; Nikora et al., 2003; Plew et al., 2007; Laborde
424 et al., 2016); and (iii) depending on turbulence swimming performance may be enhanced,

425 diminished or unaffected in altered flows (Lacey et al., 2012; Wilkes et al., 2013; Enders
426 and Boisclair, 2016).

427 In nature, *B. microlepidotus* juveniles inhabit shallow riparian zones and littoral zones
428 (Link and Habit, 2015), moving to the main current with maturity (Montoya et al., 2012).
429 This ontogenetic shift in habitat use might explain its high swimming capacity relative to
430 body length (Laborde et al., 2016). In our experiments, *B. microlepidotus* adopted a
431 distinctive swimming gait by attuning its body amplitude to match the structure of the
432 classic von Kármán vortex street found downstream of a bluff body. Tail beat amplitude
433 increased with vortex length scale, and the lateral movement of the fish centroid in the
434 wake was consistent the wake width. This indicates that *B. microlepidotus* was adopting a
435 Kármán gait-like swimming strategy, thus reducing swimming costs in the cylinder wake.
436 However, differently to rainbow trout (*Onchorhynchus mykiss*) (Liao et al., 2003a; Liao et
437 al., 2003b; Liao et al., 2007; Taguchi and Liao, 2011) in the presence of cylinders, *B.*
438 *microlepidotus* did not attune its tail beat frequency to the shedding frequency. One
439 possible reason is that vortex length scale to fish length ratio was too high (for *O. mykiss*
440 the special conditions required for Kármán gaiting may be limited to $0.25 < L_u / L < 0.5$,
441 while in our experiments $L_u / L > 1.2$). Even though *B. microlepidotus* in wakes did not
442 change the tail beat frequency respect to the free flow, it increased the tail beat amplitude
443 with the relative vortex length scale, evidencing a higher propulsion effort using the caudal
444 fin. Further research in order to investigate if *B. microlepidotus* can gain an energetic
445 advantage in the wake of a cylinder, by reducing muscle activity and oxygen consumption
446 in comparison to swimming in the free flow, is needed.

447 In our experiments mean flow velocity was equal to 70% of the critical swimming
448 speed of the individual. In nature, however, *C. galusdae* inhabits vegetated riparian zones
449 with lower flow velocities (Link and Habit, 2015), swimming intermittently to hold
450 position. Contrary to this behavior in nature, during experiments *C. galusdae* adopted a
451 burst-and-coast swimming strategy often observed in fish with a fineness ratio of 4–6.5
452 (Videler 1993). Studied individuals of *C. galusdae* presented fineness ratios of 4. In the
453 presence of cylinders >2 cm in diameter, *C. galusdae* reduced the coast phase dramatically,
454 swimming quasi-continuously and suffering destabilization and displacement. Average tail
455 beat frequency f_{TB}^{30} as well as tail beat amplitude increased with relative vortex length
456 scale. Even though the burst-and-coast swimming style has been shown to save up to 45%
457 of the energy due to drag reduction in the coast phases (Wu et al. 2007, Chung 2009) our
458 results suggest that, under the studied conditions, *C. galusdae* increased propulsion effort in
459 the cylinder wake due to coast phase reduction. It is not clear if the swimming behavior
460 observed in *C. galusdae* constitutes aerobic or anaerobic activity. Therefore, further work
461 on muscle activity and oxygen consumption is also required for this species.

462 The fish Strouhal number defined in terms of the average tail beat frequency f_{TB}^{30} , the
463 tail beat amplitude λ , and the section averaged flow velocity U can be interpreted as a
464 measure of the propulsion effort. Extensive observations have shown that maximum
465 propulsive efficiency lies in the range $0.25 < St_{fish} < 0.35$ for a diversity of fish species
466 (Triantafyllou et al., 1993; Eloy, 2012). In our study, both species converged towards this
467 range with decreasing relative vortex size and corresponding higher shedding frequencies,
468 following one tendency even when the two species adopted very different swimming

469 strategies, i.e. Kármán gait-like and burst-and-coast. This would support the idea that in the
470 sense of propulsion effort, *B. microlepidotus* in a wake is expending more effort than in a
471 free flow, similar to *C. galusdae*. Probably, the similar propulsive effort observed through
472 Strouhal number for both species is related to their similar swimming capacity, and thus
473 species with significantly different swimming capacity (critical swimming speed,
474 endurance) might be expected to exhibit different relations of St_{fish} with vortex length scale
475 and shedding frequency. Overall, the fish Strouhal number appears to be a suitable design
476 criterion, as it compiles the propulsion effort of fish in a flow (free and/or altered) and
477 could be limited to manage propulsion efficiency of different species in a fishway. Energy
478 saving mechanisms associated with Kármán gaiting could counteract the additional effort in
479 propulsion exhibited by *B. microlepidotus*, and should constitute additional/complementary
480 criteria for fishway design.

481 Fish behavior in wakes is species-specific. The intensity, periodicity, orientation and
482 scale of wake vortices are expected to influence fish behavior and swimming performance
483 since they are critical for fish maneuvering and swimming stability (Lacey et al., 2012;
484 Wilkes et al., 2013; Maia et al., 2015). Cylinder wakes represent a special case of
485 turbulence which is significantly different to the free flow turbulence due to the periodicity
486 and location of the vortices, it is a two-dimensional case with homogeneous properties
487 along the water column. In the present study, experiments were conducted under similar
488 flow conditions to those expected in real fishways, i.e. average flow velocity was 70% of
489 the critical velocity being in the sustained swimming mode (Webb, 1971). *Basilichthys*
490 *microlepidotus* appeared to be adapted to swimming in wakes, while *C. galusdae* did not.
491 Obstacles with different shapes however produce wakes with more complex vortices. In

492 fish ramps, submerged boulders produce wakes with a marked three-dimensional shape
493 (Bretón et al., 2013; Baki et al., 2014) and lower periodicity, i.e. predictability, than the
494 studied cylinder wakes. Therefore, in comparison to the cylinder case, a wake at a
495 submerged boulder is thought less predictable for a fish.

496

497 **5. Conclusions**

498 The behavior and tail beat kinematics of two non-sport fish species from Chile, *C.*
499 *galusdae* and *B. microlepidotus* (juveniles), was studied in the wake of vertical and bottom-
500 mounted cylinders in an open channel flow through Particle Image Velocimetry and
501 videography of fish motion.

502 *Cheirodon galusdae* was often destabilized in cylinder wakes and adopted an erratic
503 burst-and-coast like swimming style, decreasing the coast phase in the presence of
504 cylinders >2 cm in diameter. *Basilichthys microlepidotus* adopted a Kármán gait-like
505 swimming strategy, interacting with the wake vortices, but without attuning its tail beat
506 frequency to the shedding frequency, and increasing its tail beat amplitude with vortex
507 length scale. These findings suggest that *C. galusdae* and *B. microlepidotus* may increase
508 energetic costs when swimming in altered flows with vortex length scale to fish length
509 ratios as those in the present study.

510 The fish Strouhal number provided a good measure of propulsion effort and seems to
511 be a practical design criterion. Energy saving mechanisms (e.g. those associated with
512 Kármán gaiting) could counteract the additional propulsive effort, and should constitute
513 additional/complementary criteria.

514 Life histories provided a possible explanation to the main observed differences
515 between species behavior but further research is required in order to link the physiological
516 characteristics of non-sport fish with swimming performance in wakes.

517

518

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