Animal-mounted gyroscope/accelerometer/magnetometer: in situ measurement of the movement performance of fast-start behaviour in fish

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Abstract

A novel data logger incorporating a 3-axis gyroscope, a 3-axis accelerometer, and a 3-axis magnetometer was developed and externally attached to Japanese amberjacks, *Seriola quinqueradiata*, to investigate the possibility of using this device for monitoring the movement performance of the fast-start behaviour of fish in the field. Triggered escape behaviours were measured simultaneously by the data logger (500 Hz) and a high-speed camera (200 Hz) in a tank. By using a gyroscope, the data logger accurately reconstructed the gravity-based acceleration, 3-dimensional attitude, dynamic acceleration, and angular velocity of fish during the fast-start movement, which was impossible by previous methods using only an accelerometer and a magnetometer; these variables can therefore be used to assess the distance-

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related performance and manoeuvrability of fish. The escape movements can be categorised into two mechanical types (single- and double-bend) using the obtained locomotor variables, which showed significant differences between movement types. These results indicate the possibility of using this animal-mounted data logger to quantify the movement performance of the fast-start behaviour of fish in nature.

Keywords: data logger, gyroscope, accelerometer, magnetometer, fast-start, fish

1 **Introduction**

2 The ability to move with a sudden acceleration/velocity and a rapid turn-
3 ing rate is important for many animals in a predator-prey context (Domenici
4 and Blake, 1997; Higham, 2007). Kinematics and movement performance,
5 especially those of fast-start movements in fish, have received a significant
6 amount of attention and are usually investigated in laboratory-based settings
7 through the use of high-speed cameras (Harper and Blake, 1990; Domenici
8 and Blake, 1991; Hale, 2002; Lefrançois and Domenici, 2006). These studies
9 have identified various types of fast-start behaviours [C- and S-start (Hale,
10 2002), including single- and double-bend responses (Domenici and Blake,
11 1991; Kasapi et al., 1993; Jing et al., 2004; Lefrançois et al., 2005; Jing et al.,
12 2005), and slow and fast responses (Domenici et al., 2004)]. However, only
13 a small number of research approaches have investigated the movement per-
14 formance of fast-start behaviour of fish in their natural environment. In situ
15 measurement of the movement performance of fast-start behaviour should
16 reveal important insights into the physiological adaptations of animals to

17 different environments and their survival strategies in complex natural habi-
18 tats. This will in turn lead to an improved understanding of the relationship
19 between movement performance and fitness (Irschick, 2003; Higham, 2007).

20 Bio-logging methods, which utilise animal-mounted data loggers, have
21 been used effectively to measure the locomotion of animals in the field (Cooke
22 et al., 2004; Rutz and Hays, 2009). In particular, data loggers including a
23 3-axis accelerometer and, in some cases, a 3-axis magnetometer have been
24 used to monitor the attitude (pitch, roll, and yaw) and dynamic acceleration
25 of aquatic animals (Davis et al., 1999; Johnson and Tyack, 2003; Sato et
26 al., 2003; Wilson et al., 2008). Therefore, bio-logging methods should give
27 researchers the means to assess the movement performance of the fast-start
28 behaviours of fish in the wild. However, only a small number of studies have
29 focused on assessing the movement performance of fast-start behaviour using
30 data loggers (Bröell et al., 2013; Noda et al., 2013).

31 In laboratory-based studies, a number of variables, including maximum
32 acceleration, angular velocity (e.g., turning rate), and movement direction
33 (e.g., turning angle), have been found to be important for assessing the per-
34 formance of fast-start movements (Harper and Blake, 1990; Domenici and
35 Blake, 1991; Hale, 2002; Lefrançois and Domenici, 2006). Although many
36 studies have used accelerometers to monitor the activities of fish in the wild
37 (Kawabe et al., 2003; Tsuda et al., 2006; Wilson et al., 2008; Whitney et al.,
38 2010; Bröell et al., 2013), an accelerometer alone may not be sufficient for
39 obtaining accurate and detailed documentation of the 3D movements of the
40 fast-start behaviour of animals because it is difficult to differentiate gravity-
41 based acceleration (which can be converted to pitch and roll movements)

42 from the dynamic acceleration that is included in accelerometer measure-
43 ments (Fourati et al., 2010; Noda et al., 2012). Furthermore, rotational
44 information, such as the angular velocity and direction of the movement, is
45 lacking in these measurements.

46 Angular velocity can be directly measured with high temporal resolution
47 (e.g. 100 Hz to 1 kHz) by a gyroscope. Using the gyroscope, if the initial
48 attitude is known, any new attitude (hence, the gravity-based acceleration
49 that would be measured by the accelerometer) can be estimated using initial
50 attitude and the estimated attitude change calculated from the gyroscope
51 measurements. An accelerometer and a magnetometer can be used in ad-
52 dition to a gyroscope to determine initial attitude and to correct the error
53 when estimating attitude associated with the accumulation of noise from a
54 gyroscope. In fact, a novel gyroscope data logger (hereafter, gyro logger),
55 which incorporates a 3-axis gyroscope, a 3-axis accelerometer, and a 3-axis
56 magnetometer (for a total of 9 axes), was developed. This device can re-
57 construct the fine-scale dynamic acceleration, gravity-based acceleration and
58 attitude of animals (e.g. sea turtles), which have not been accurately mea-
59 sured in previous studies that only used an accelerometer (and occasionally
60 a magnetometer) (Noda et al., 2012). Therefore, a gyro logger may be more
61 suitable for monitoring the movement performance of fast-start behaviour in
62 fish.

63 Given the above considerations, a novel gyro logger was developed and
64 used in this study to investigate the possibility of using an animal-mounted
65 data logger to monitor the movement performance of the fast-start behaviour
66 of fish in the field. Specifically, the gyro logger was applied to measure the

67 fast-start movements of a fish, the Japanese amberjack *Seriola quinqueradi-*
68 *ata*, during escapes with a high sampling frequency (500 Hz). The link be-
69 tween escape movements and data logger measurements was thus explored.
70 Although most previous studies have used a relatively low sampling frequency
71 (≤ 32 Hz) (Kawabe et al., 2003; Tsuda et al., 2006; Whitney et al., 2010; Føre
72 et al., 2011), a higher sampling frequency was used in this study because fast-
73 start movements usually last only a fraction of a second. Our study focused
74 on three questions: 1) Is it possible to accurately define locomotor variables
75 from the gyro logger measurements? 2) Is it possible to define detailed vari-
76 ations in fast-start movements (e.g., single- vs. double-bend) from the gyro
77 logger measurements? and 3) What are the advantages and disadvantages of
78 using a gyro logger over a conventional accelerometer or high-speed imaging
79 for measuring locomotor variables?

80 **Materials**

81 *Study animals*

82 The escape movements of five Japanese amberjacks [fork length (FL): 65.9
83 ± 0.45 cm, body mass (BM): 4.08 ± 0.78 kg] (Table A1) were monitored in
84 tank experiments at the Institute for East China Sea Research at Nagasaki
85 University in Japan. The fish were obtained from a local fish hatchery (Na-
86 gasaki, Japan) and were maintained in a 300-cm-diameter outdoor tank with
87 flow-through seawater at a temperature of 19.05 ± 0.84 °C, a depth of 1 m,
88 and a dissolved oxygen level of 84.89 ± 3.88 %. The fish were acclimatised
89 to the tank for at least one week prior to the initiation of experiments; after
90 acclimatisation, the fish were tagged for the experiments.

91 *Data logger*

92 A gyro logger (LP-BLKU01, Biologging Solutions Inc., Kyoto, Japan) was
93 developed and used to record the 3-axial acceleration, 3-axial magnetism, and
94 3-axial angular velocity of the fish. This data logger was cylindrical in shape
95 (diameter: 3 cm, length: 17 cm) with a mass of 108 g in air, which includes
96 the attached CR123A battery. The measurement ranges were $\pm 16\text{ g}$, $\pm$
97 100000 nT , and $\pm 1500\text{ degree second}^{-1}$ for the acceleration, magnetic field,
98 and angular velocity, respectively. The resolution of the measurements was
99 16 bit ($-32768\sim+32768$): $4.88 \times 10^{-4}\text{ g}$, 3.05 nT , and $4.58 \times 10^{-2}\text{ degree}$
100 second^{-1} for the acceleration, magnetic field, and angular velocity, respec-
101 tively. The data logger measured and stored all of the sensor outputs in an
102 internal micro-SDHC memory ($\sim 32\text{ GB}$) at a sampling frequency of 500
103 Hz for a total sample time of 10 hours. Furthermore, this device allowed for
104 multiple-scheduled recordings (e.g., 2 hours of recording each day). The data
105 logger was covered with an alumite-treated case, which made it waterproof
106 and pressure-proof up to a depth of 300 m. The logger could also record tem-
107 perature of range of $-45 \sim 80\text{ }^{\circ}\text{C}$ and depth of up to 30 bar; however, only
108 acceleration, magnetic data, and angular velocity were used for the analysis.
109 A reflective marker was attached to the data logger for the video analysis
110 (see below).

111 *Measurement of escape responses*

112 One week prior to the escape response measurements, the length and mass
113 of the fish were measured under anaesthesia induced with phenoxyethanol ($<$
114 $0.05\text{ }\%$). A plastic plate ($3 \times 18\text{ cm}^2$) was sutured to the dorsal muscula-
115 ture just above the centre of mass (CM; $43\text{ }\%$ of the TL) using cable ties.

116 The plate formed the base of the data logger. The position of the CM was
117 determined by hanging a dead fish (different fish from those used for the
118 activity measurements, FL = 61.8 cm) using a suture and needle (Lefrançois
119 and Domenici, 2006). The temporary attachment of the gyro logger to the
120 plastic plate base was accomplished using cable ties; the fish were sedated
121 using anaesthesia during this procedure. The mass of the data logger was
122 less than 3 % of the body mass of the fish.

123 For the escape response measurements, gyro loggers were attached to five
124 fish, which were then transferred from the holding tank to an identical and
125 adjacent tank (300 cm in diameter). The water level in the experimental tank
126 was maintained at 0.44 m. The transfer and tagging time, which included
127 the anaesthetising time, was less than 5 min. None of the animals exhibited
128 any signs of stress, and they settled quickly into the experimental tank. The
129 fish were allowed to acclimate to the experimental tank for at least 12 hours
130 prior to the start of the escape measurements. The escape responses were
131 triggered by randomly and manually thrusting a PVC pole with a length of
132 100 cm and diameter of 4.0 cm to the bottom of the tank [thrusting speed =
133 0.80 (0.34) m s⁻¹ for the mean (s.d.), and N = 24] near the position of the
134 fish when the fish were at least one body length from the tank wall. These
135 responses were triggered at intervals of approximately 10 min. Overall, 4 to
136 11 escape responses were recorded for each fish (Table A1).

137 The responses were also recorded using two video cameras located 2.85 m
138 above the tank bottom: a 30-Hz standard USB webcam (HD C910, Logicoool
139 Co., Tokyo, Japan, with H264 Webcam 3.83 software, Timhillone software
140 Co. Ltd., Nanshan, China) and a 200-Hz high-speed camera (HAS-L1, DI-

TECT Co. Tokyo, Japan). The video cameras were controlled and manipulated using a connected PC. The high-speed camera was calibrated before the experiments by taking a picture of a checkerboard at the bottom of the tank. The relationship between the pixel size in the camera image and the actual distance was obtained by placing multiple markers at known interval distances along the bottom of the tank before the experiments. The clock times of the gyro loggers and the video recording were synchronised using the PC clock before the data loggers were attached to the fish. A reflective marker on the data loggers in the image sequences was digitised using Dipp-Motion PRO (DITECT Co. Tokyo, Japan). The acceleration and turning rate of the markers were derived using a five-point smoothing regression (Lanczos, 1956). The turning rate was obtained using two points: the snout of the fish and the marker on the data logger.

All experimental procedures were approved by the Animal Research Committee of Kyoto University (protocol number: Informatics 25-7).

Methods

The objective of this study was to reconstruct the locomotor variables of fast-start movements from the data logger measurements (Fig. 1). The estimation of the locomotor variables of the fast-start movements was divided into two parts:

- Reconstruction of the attitude and dynamic acceleration. Accelerometer measurements are usually modelled as a combination of linear, gravity-based, centripetal, and tangential accelerations. In this study, the acceleration components, including linear, centripetal and, tangen-

165 tial accelerations, are referred to as dynamic acceleration (i.e., all of
166 the components with the exception of gravity-based acceleration).

- 167 • Derivation of the locomotor variables (e.g., maximum acceleration,
168 turning rate, and turning angle) using the reconstructed attitude (pitch,
169 roll, and yaw), dynamic acceleration, and angular velocity. Dynamic
170 acceleration was considered a time-distance variable. Angular velocity
171 and attitude were considered angular variables.

172 *Reconstruction of attitude and dynamic acceleration*

173 The gyroscope measurements were used to determine the actual gravity-
174 based acceleration from the accelerometer measurements. An accelerome-
175 ter and a magnetometer were used to determine the initial attitude and to
176 correct for any errors in the attitude estimation associated with the accu-
177 mulation of gyroscope noise (e.g. Trawny and Roumeliotis, 2005; Sabatini,
178 2006; Fourati et al., 2010; Noda et al., 2012). The data logger was first
179 calibrated according to previously described algorithms (Fong et al., 2008)
180 for calibrating an accelerometer and a gyroscope and a two-step algorithm
181 developed for calibrating a magnetometer (Gebre-Egziabher et al., 2001).
182 To accurately estimate the attitude and dynamic acceleration by integrating
183 the accelerometer, magnetometer, and gyroscope measurements, a previously
184 described algorithm using an orientation filter (Madgwick et al., 2011) was
185 adopted (hereafter, the gyro method).

186 *Reconstruction of locomotor variables*

187 Four coordinate frames were assumed: the earth frame, camera frame,
188 fish frame and data logger frame (Fig. 2). The z-axis of the camera frame

189 (vertical) was assumed to coincide with the z-axis of the earth frame (the
190 x- and y-axes do not necessarily coincide). A vector in one frame can be
191 converted to a corresponding vector in another frame using a rotation matrix
192 derived from the angular differences in pitch, roll, and yaw between the two
193 frames (Titterton, 2005).

194 Ideally, the data logger frame should coincide with the fish frame; hence,
195 the axes of the data logger measurements should coincide with the axes of
196 the fish. However, in practice, it is sometimes difficult to attach a data logger
197 such that its axes coincide with those of the fish. Therefore, after the data log-
198 ger was attached, the fish was kept stationary and photographed on both its
199 anterior and lateral sides. The angular differences in pitch and roll between
200 the two frames were then calculated from these photos using a free image
201 calculation software program (Image J 1.45, <http://rsbweb.nih.gov/ij/>). The
202 yaw angle difference was assumed to be zero.

203 Because the fish frame and the earth frame change simultaneously as the
204 fish moves, it was assumed that the movement in the earth frame would pro-
205 vide little insight into the forces acting on each dimension of the fish (x-, y-,
206 and z-axes). Therefore, the locomotor variables were represented in the fish
207 frame after the appropriate coordinate conversions were made to more ac-
208 curately describe the motions experienced by the fish. However, to compare
209 the values of the locomotor variables obtained from the data logger measure-
210 ments with those of the high-speed video camera images (see the Analysis),
211 the locomotor variables obtained from the data logger measurements were
212 converted to their corresponding values in the earth frame.

213 *Time-distance variables*

214 Once attitude and dynamic acceleration were calculated, the dynamic
215 acceleration could be processed to obtain linear acceleration, velocity, and
216 displacement. Although dynamic acceleration usually includes tangential
217 and centripetal acceleration as well as linear acceleration during the quick
218 turning of escape movements, tangential and centripetal acceleration were
219 not removed because the turning radius, required for calculating the tangential
220 and centripetal acceleration, is not measurable by the current gyro logger
221 system alone. Note that turning rate and its derivative (angular acceleration)
222 can be measured by a gyroscope. In addition, although the fish usually
223 swim steadily before performing a fast-start movement (i.e., they do not
224 stop before making rapid changes in motion; camera measurements indicated
225 0.33 (0.04) m s⁻¹ for the mean velocity (s.e.m.), and N = 24), the initial
226 velocity was assumed to be zero because the current gyro logger cannot
227 directly measure velocities. Thus, the dynamic acceleration (including the
228 tangential and centripetal accelerations as well as the linear acceleration) was
229 time-integrated to calculate velocity and displacement, which were termed
230 relative velocity and relative displacement to distinguish these measurements
231 from the true velocity and displacement (Fig. 1). Although the relative
232 velocity and displacement are not the actual velocity and displacement of
233 the fish in a physical sense, these values should represent relative values of
234 the magnitude of the velocity and displacement as long as the onset of the
235 time integration is determined using the same criteria and assuming that the
236 fish swims at a similar speed before all fast-start movements.

237 *Angular variables*

238 In the escape events, the turning rate, angles and duration of stage 1 and 2
239 [hereafter, S1 and S2, respectively; reviewed by (Domenici and Blake, 1997)]
240 can be determined from the gyroscope measurements around the vertical axis
241 (z-direction, as illustrated in Fig. 2) and the yaw angles (Fig. 3). Similar
242 to Domenici and Blake (1997), it was defined that S1 begins at the first
243 detectable movement of the fish and is completed when the turning rate-
244 time curve crosses the (turning rate = 0) axis. The onset of S2 coincides
245 with the end of S1, and S2 ends when the turning rate-time curve crosses the
246 (turning rate = 0) axis again.

247 *Analysis*

248 The programs used for calibrating the data logger measurements, extract-
249 ing data for the fast-start events, and reconstructing locomotor variables from
250 the data logger measurements were all created in Igor Pro 6.3 (WaveMetrics,
251 Inc. Tigard, OR, USA). Statistical analyses were performed using R 2.15
252 (the R Foundation for Statistical Computing).

253 *Comparison of the locomotor variables of the data logger measurements and* 254 *high-speed video camera recordings*

255 In this analysis, the accuracy of the reconstructed locomotor variables
256 from the gyro logger measurements was examined. Assuming that the z-axis
257 of the earth frame coincides with the z-axis of the camera frame, the dynamic
258 acceleration of the combined x- and y-directions in the earth frame obtained
259 from the data logger measurements (see the Appendix for the calculation)
260 was compared with the acceleration measured by the video camera. The rel-

261 active velocity and cumulative distance of the combined x- and y-directions in
262 the earth frame obtained from the data logger measurements were also com-
263 pared with the velocity and cumulative distance obtained from the camera
264 measurements. Two dimensional trajectory (x-y surface) measured by the
265 data logger was compared with the trajectory measured by the camera. The
266 angular velocity and angle of the yaw direction in the earth frame obtained
267 from the data logger measurements were compared with the turning rate
268 and angle measured by the video camera. Specifically, a regression analysis
269 of the following variables between the two measurements was conducted for
270 the comparisons: maximum acceleration, maximum velocity, cumulative dis-
271 tance, turning rate, S1 and S2 angles, and S1 and S2 durations. Maximum
272 acceleration, maximum velocity, cumulative distance, and 2D trajectory were
273 measured for a fixed duration of 0.18 s from the onset of the escape move-
274 ments, which was chosen by calculating the mean of the (S1+S2) durations
275 of events that clearly showed the end of stage 2 [this occurred in 9 out of
276 24 events that were simultaneously recorded with the high-speed camera].
277 The turning rate was calculated as S1 angle / S1 duration (Domenici and
278 Blake, 1991). Mean Euclidean distance was calculated from the 2D trajectory
279 between the data logger and camera measurements.

280 *Variations in escape movements*

281 The escape movements were divided into different mechanical types (single-
282 and double-bend) using the film images following Domenici and Blake (1991).
283 Then, to investigate whether the gyro logger measurements can be used to
284 identify the variations in escape movements, the locomotor variables obtained
285 from the gyro logger measurements of escape events were compared between

286 the two types of escape movements. The following locomotor variables were
 287 then examined in detail: time-distance variables [maximum acceleration and
 288 relative velocity in the x-, y-, and z-directions; maximum of the MA and
 289 the magnitude of the relative velocity (MV, vector summation of the relative
 290 velocity along the x-, y- and, z-axes); relative cumulative distance], angu-
 291 lar variables (maximum angular velocity in the x-, y-, and z- directions; S1
 292 angle; range of pitch and roll), and time variables [S1 duration; difference
 293 in the time required to reach the maximum acceleration between the x- and
 294 y-positions ($T_x - T_y$) and between the x- and z-positions ($T_x - T_z$); time re-
 295 quired to reach the maximum MA and MV]. All of the variables except for
 296 the S1 angle were measured for a fixed duration of 0.18 s from the onset of
 297 the escape movements. The maximum acceleration was obtained from the
 298 absolute value of the acceleration in each direction because the sign of the
 299 accelerometer measurements is not important when considering the maxi-
 300 mum force acting on the fish. A repeated measure ANOVA (RM-ANOVA)
 301 was performed on each locomotor variable using the mechanical movement
 302 types as fixed factors and the individual fish as random factors.

303 *Comparison of the gyro and smoothing methods for deriving acceleration vari-* 304 *ables*

305 The advantages of using the gyro logger to derive locomotor variables
 306 were examined by comparing the locomotor variables obtained using a con-
 307 ventional accelerometer with those obtained using a gyro logger. If a gyro-
 308 scope is not available, it may be impossible to accurately derive acceleration
 309 variables such as the maximum dynamic acceleration because the value of
 310 the true gravity-based acceleration, which is included in the accelerometer

311 measurements, is not known. In previous works, the gravity-based acceler-
 312 ation has been determined by smoothing (Wilson et al., 2006; Shepard et
 313 al., 2008) or low-pass filtering (Sato et al., 2003; Tanaka et al., 2001) meth-
 314 ods. It is therefore useful to investigate whether smoothing the measurements
 315 obtained from an accelerometer is sufficient to assess the performance of fast-
 316 start movements. Because the smoothing and low-pass filtering methods are
 317 both based on the same principle, only the smoothing technique was exam-
 318 ined in this study. The effect of the extent of smoothing on the accuracy of
 319 the derived acceleration variables was determined through a comparison to
 320 the values derived from the gyro logger measurements. The investigated ac-
 321 celeration variables were the maximum, mean, standard deviation (s.d.), and
 322 root mean square (RMS) of the acceleration in the x-, y-, and z-directions,
 323 the overall dynamic body acceleration [ODBA, which combines the absolute
 324 dynamic acceleration values in the 3 axial directions (Wilson et al., 2006;
 325 Shepard et al., 2008)], and the time to maximum acceleration in the x-, y-,
 326 and z-directions. All of the variables were measured using data that were
 327 extracted such that the maximum peak of the MA was mapped to the centre
 328 of the duration (1 s).

329 **Results**

330 All of the escape movements ($N = 11, 8, 11, 4$, and 7 from 5 different
 331 fish, for a total of 41 events) were simultaneously recorded by a data logger
 332 and a normal 30-Hz video camera (Table A1). In addition, 24 of the escape
 333 events ($4, 5, 8, 3$, and 4 events for 5 different fish) were also simultaneously
 334 recorded with a 200-Hz high-speed video camera (Table A1).

335 *Comparison of the locomotor variables obtained from the data logger mea-*
336 *surements and from the high-speed video camera recording*

337 The cumulative distance, velocity, acceleration, turning rate, and turning
338 angle obtained from the gyro logger measurements typically exhibited similar
339 profiles to those from the video recordings (Fig. 4a). In the two escape events
340 of the camera recordings, the angular variables were not obtained because the
341 snout of the fish was not clearly visible in the film images due to low contrast
342 with the background. Because there were two types of movement in the
343 escape response (single- and double-bend; for the detail, see the next section),
344 S2 angle and duration were obtained only for the double-bend events. A
345 regression analysis of all of the variables except for the maximum acceleration
346 between the camera and data logger measurements indicated a statistically
347 linear relationship [(a) cumulative distance: Video = $1.08 \times \text{Logger} + 0.02$;
348 $R^2 = 0.85$; F value = 128.60 (1 and 22 Degree of Freedom (D.F.)); $p < 0.0001$;
349 N = 24, (b) maximum velocity: Video = $0.85 \times \text{Logger} + 0.21$; $R^2 = 0.56$; F
350 value = 28.47 (1 and 22 D.F.); $p < 0.0001$; N = 24, (c) maximum acceleration:
351 $R^2 = 0.01$; F value = 0.13 (1 and 22 D.F.); $p = 0.73$; N = 24, (d) turning rate:
352 Video = $0.78 \times \text{Logger} + 102.98$; $R^2 = 0.53$; F value = 22.36 (1 and 20 D.F.);
353 $p < 0.001$; N = 22, (e) S1 angle: Video = $0.95 \times \text{Logger} + 6.86$; $R^2 = 0.41$; F
354 value = 13.95 (1 and 20 D.F.); $p < 0.01$; N = 22, (f) S2 angle: Video = 0.97
355 $\times \text{Logger} - 2.20$; $R^2 = 0.93$; F value = 108.6 (1 and 8 D.F.); $p < 0.0001$; N =
356 10, (g) S1 duration: Video = $1.02 \times \text{Logger} - 0.00$; $R^2 = 0.99$; F value = 2785
357 (1 and 20 D.F.); $p < 0.0001$; N = 24, (h) S2 duration: Video = $0.98 \times \text{Logger}$
358 $+ 0.00$; $R^2 = 0.97$; F value = 263.2 (1 and 8 D.F.); $p < 0.0001$; N = 10] (Fig.
359 5). There were larger variations in the maximum acceleration between the

360 camera and data logger measurements (Fig. 5). Compared to the S2 angle
361 and S1 and S2 durations, the S1 angle and turning rate exhibited greater
362 variability between the camera and data logger measurements (Fig. 5). The
363 2D trajectory obtained from the data logger also exhibited similar profiles
364 to the trajectory from the video recordings (Fig. 4b); the mean Euclidean
365 distance was 0.032 (0.017) m for the mean (s.e.m.).

366 *Variations in escaping movements*

367 Image sequences of the escape events captured by the high-speed camera
368 were used to categorise the fast-start movements into two types of escape
369 movements based on the bending (Domenici and Blake, 1997): single-bend
370 ($N = 3, 2, 4, 3$, and 1 for the 5 fish, for a total of 13 events) and double-bend
371 ($N = 1, 3, 4, 0$, and 3 for the 5 fish, for a total of 11 events). In the single-bend
372 escape movement, the fish bends into a C shape and subsequently straightens
373 without bending in the opposite direction (Fig. A1a). In the double-bend
374 escape movement, the fish performs a full return flip of the tail after the ini-
375 tial contraction (Fig. A1b). The differences in these movements were clear in
376 the sensor-derived locomotor variables. The fish bent at significantly larger
377 angles and exhibited larger S1 angles in the single-bend response than in
378 the double-bend response (Fig. 6, Table 1). The maximum acceleration and
379 angular velocity were significantly lower in the single-bend response move-
380 ments than in double-bend responses (Fig. 6, Table 1). In addition, the fish
381 moved a significantly shorter cumulative distance in the single-bend response
382 (Fig. 6, Table 1). In the single-bend response, the maximum acceleration
383 in the lateral direction was reached before the maximum acceleration in the
384 forward direction was achieved, whereas in the double-bend movements, the

385 maximum acceleration in the lateral direction was reached after the maxi-
386 mum acceleration in the forward direction was obtained; these results were
387 found to be significantly different (Fig. 6, 7, Table 1).

388 *Comparison of the gyro and smoothing methods for deriving acceleration vari-* 389 *ables*

390 The effect of the extent of smoothing employed to determine the gravity-
391 based acceleration on the accuracy of the derived acceleration variables was
392 assessed. The percent changes in the maximum, s.d., and RMS of the dy-
393 namic acceleration and the ODBA decreased and appeared to stabilise when
394 the running-mean duration increased; in fact, this change was small and
395 nearly stable (less than 10 %; the ODBA obtained from the gyro method
396 was 1.23 *g*) when the running-mean duration was more than approximately
397 0.3 s (Fig.8, Table 2). However, the percent change of the mean dynamic
398 acceleration was more than 95 % regardless of the running-mean duration
399 (Table 2). Note that the smoothing technique was not capable of estimating
400 the true values of the acceleration variables, the gravity-based acceleration or
401 the dynamic acceleration (Fig. 9, Table 2). For example, the RMS values of
402 the difference in the gravity-based accelerations determined using the gyro
403 and smoothing methods with a running-mean duration of 0.3 s for 1 s of
404 measurement data were 0.211 (0.019), 0.274 (0.021) and 0.151 (0.008) *g* for
405 the mean (s.e.m.), respectively for the x-, y-, and z-directions in the escape
406 events, which are significantly larger than the values of 0.021 (0.004), 0.013
407 (0.002) and 0.017 (0.002) *g* measured in routine movements [paired t-test (*N*
408 = 41); $p < 0.001$, $p < 0.001$, and $p < 0.001$ for the x-, y-, and z-directions,
409 respectively]. The percent change in the time required to reach the maximum

dynamic acceleration was small (less than 2 %) and stable regardless of the running-mean duration (Table 2).

Discussion

Accuracy of the gyro logger for monitoring the locomotor variables of fast-start movements

Cumulative distance, velocity, acceleration, turning rate and turning angle have been important variables with which to assess the movement performance of fast-start fish (Harper and Blake, 1990; Domenici and Blake, 1991; Hale, 2002; Lefrançois and Domenici, 2006). In addition to the similar profiles of the graphed variables between the camera and data logger measurements, the statistically significant linear relationships between most of the locomotor variables (cumulative distance, maximum velocity, turning rate, S1 and S2 angles, and S1 and S2 durations) obtained from the gyro logger measurements and the camera recordings indicate that the gyro logger measurements can be used to assess movement performance. The statistically significant linear relationships even from the relative values of the cumulative distance and velocity obtained by the gyro logger may indicate that those values can also be used as a performance measure. This may be also supported by the similar profiles of the 2D trajectory and small mean Euclidean distance between the data logger and camera measurements. Although there was large variability and no significant relationship was found between the data logger and camera measurements for maximum acceleration, considering that the accelerometer itself produces a high accuracy for measuring acceleration, the variability may mostly result from the digitisation error of the camera record-

434 ings: the acceleration in the camera recordings is derived from the second
435 differential of the digitised points, whereas the acceleration in the accelerom-
436 eter is directly measured. This may be supported by the fact that velocity
437 and cumulative distance, which are the first and second integrals of acceler-
438 ation and can thus accumulate a large error from any misdetermination of
439 the dynamic acceleration, exhibited more similar values to those obtained by
440 the camera recordings than the accelerations. Although a common method
441 was utilised for smoothing the digitised points [a five-point smoothing re-
442 gression (Domenici and Blake, 1991; Domenici et al., 2004; Lefrançois et al.,
443 2005)], it is possible that the image magnification and the film rate were not
444 high enough to obtain accurate estimates of maximum acceleration from the
445 digitised points (Harper and Blake, 1989). Not removing tangential and cen-
446 tripetal acceleration from the accelerometer measurements may also result in
447 the error between the data logger and camera measurements, although max-
448 imum acceleration would be much less influenced by tangential acceleration
449 (Harper and Blake, 1990).

450 The error in the angular variables between the two measurements, es-
451 pecially in the turning rate and S1 angle, may result from the difference in
452 the places where the turning rate and angles were measured. In the camera
453 recordings, the turning rate and angle were obtained using two points: the
454 snout of the fish and the marker on the data logger attached to the dorsal
455 musculature approximately above the fishs CM, following previous research
456 (Domenici and Blake, 1991; Domenici et al., 2004; Hale, 2002). On the other
457 hand, the turning rate and angle measured by the gyro logger should corre-
458 spond with those obtained from the camera recordings using two points on

the data logger along the longitudinal direction (e.g., tip and centre). Therefore, when the fish bends deeply, typically during a single-bend response, the line between the snout and the marker on the data logger would produce a larger angle than that between the two points on the data logger along the longitudinal direction. During a double-bend response, the error would be smaller because the bending of the fish is shallower. However, the difference between the camera and the gyro logger in the place where the turning rate was measured produced little effect on the S1 and S2 durations, possibly because the timing of the movement change is almost the same between the two lines.

Overall, these results suggest that it is possible to use the data logger measurements for assessing movement performance, although care must be taken when interpreting and comparing the locomotor variables obtained by the data logger measurements with those obtained from camera recordings in previous research. The error of the 2D trajectory, cumulative distance and velocity between the data logger and camera measurements will be mitigated using a speed sensor (such as a propella) additionally.

Variation in escape movements

It was possible to identify the variation in escape movements using the data logger measurements. In this study, escape movements were classified into two distinct mechanical types (single- and double-bend), consistent with previous results for other fish (Domenici and Blake, 1991; Kasapi et al., 1993; Jing et al., 2004; Lefrançois et al., 2005; Jing et al., 2005). The different mechanical types of escape movements were clearly reflected in the timing of maximum acceleration in the lateral and forward directions as well as other

locomotor variables: the timing difference has not reported in the previous research. In the single-bend movements, maximum acceleration in the lateral direction occurs before maximum acceleration in the forward direction. This result is reasonable considering that, in the single-bend movements, the fish turns away from an offending stimulus by bending into a C-shape in stage 1, which results in the occurrence of a lateral movement prior to forward propulsion (forward direction). In the double-bend movements, maximum acceleration in the lateral direction occurs after maximum acceleration in the forward direction. This result is also reasonable because, although strong forward acceleration occurs after an initial bend with a small turning angle, the second bend that occurs later in the double-bend movement may exhibit a stronger lateral acceleration than the initial bend to maintain or increase the forward velocity and the distance covered. Therefore, the difference in the timing of maximum acceleration along these two axes may be a simple yet powerful parameter for distinguishing between these two types of movement.

Advantages and disadvantages of using a gyro logger over conventional methods

Comparison with an accelerometer

Although smoothing (Wilson et al., 2006; Shepard et al., 2008) is commonly used to determine gravity-based acceleration from accelerometer measurements, the acceleration variables can be affected by the extent of smoothing used. This study indicated that the percent change of the measured variables (the ODBA, maximum, s.d., and RMS of acceleration, and the time required to reach maximum acceleration) obtained from the smoothing method decreased (less than 10 % using a duration of 0.3 s) compared to

509 that obtained using the gyro method and became nearly stable when the
 510 running-mean duration increased. This result indicates that if the appro-
 511 priate running-mean duration is set, the acceleration variables determined
 512 through the smoothing method may become stable and thus less prone to
 513 error (in this case, a duration of more than 0.3 s to decrease the error rate
 514 less than 10 %). Although previous studies (Shepard et al., 2008; Halsey
 515 et al., 2009) have used steady swimming and walking behaviour to examine
 516 the variability of the ODBA as a function of the extent of smoothing, the
 517 variability of the ODBA in fast-start movements has not yet been assessed.
 518 This study showed that the ODBA was stable with a smaller running-mean
 519 duration (0.3 s) for the fast-start movements of this fish species in compar-
 520 ison to the duration obtained for the steady swimming of other animals [3
 521 s (Shepard et al., 2008)]. This difference may arise because fast-start move-
 522 ments occur within a fraction of a second, a duration that is generally shorter
 523 than the duration of 1 cycle of propulsion during steady swimming. In addi-
 524 tion, because the scale of the ODBA is much larger in fast-start movements
 525 (more than 1.2 g), the small error caused by the extent of smoothing may be
 526 negligible.

527 The percent change in the time required to reach maximum acceleration
 528 was less than 1 %, which indicates that this parameter may be stable re-
 529 gardless of the extent of smoothing used. Because the timing of maximum
 530 acceleration in the x- and y-directions was found to be a powerful parame-
 531 ter (as described above) for distinguishing between the different mechanical
 532 types of movements, this variable may also be used to categorise movement
 533 types regardless of the extent of smoothing. However, the mean acceleration

534 changed significantly (more than 90 %) regardless of the extent of smoothing,
535 which indicates that mean acceleration cannot be assessed from the values
536 obtained through the smoothing method. It is possible that the smoothing
537 method is not capable of accurately reconstructing dynamic acceleration; in
538 addition, mean acceleration is significantly affected by the accuracy of the
539 dynamic acceleration estimate compared to other acceleration metrics (i.e.,
540 the ODBA, maximum, s.d., and RMS of acceleration and the time required
541 to reach maximum acceleration).

542 The extent to which the misdetermination of gravity-based acceleration
543 based on the smoothing method affects the accuracy of estimated accelera-
544 tion variables may depend on the intensity and range of the acceleration. In
545 the fast-start movements of the fish studied herein, the mean maximum ac-
546 celeration was approximately 5~10 g . Because the range of gravity-based ac-
547 celeration was -1~1 g , the error of the gravity-based acceleration determined
548 by the smoothing method is at most 2 g . Therefore, if the intensity and range
549 of the acceleration are small, the error in the gravity-based acceleration due
550 to the smoothing process may result in a significant under- or over-estimation
551 of the acceleration variables, whereas the error may be negligible if the inten-
552 sity and range of the acceleration are large. The intensity and range of the
553 acceleration will vary depending on the species, context (temperature, moti-
554 vation, etc.) (Lefrançois and Domenici, 2006; Marras et al., 2011), and even
555 the position at which the data logger is attached to the fish. However, be-
556 cause the error rate becomes stable after a sufficient running-mean duration
557 in the fast-start context, it might be possible to obtain reasonably accurate
558 acceleration variables by smoothing the measurements obtained from an ac-

559 celerometer (without a gyroscope) once the error rate is estimated; this is
560 only possible if the accelerometer is applied to the same species at a similar
561 attachment location and if acceleration variables similar to those examined
562 in this study are obtained (except for the mean acceleration).

563 The advantage of using measurements from a gyro logger over those ob-
564 tained from an accelerometer is that gravity-based acceleration can be easily
565 and clearly removed from the measurements, which means that the accel-
566 eration variables can be accurately derived. In addition, gyro logger mea-
567 surements can be used to calculate additional data, such as attitude, angular
568 velocity, relative velocity, and relative cumulative distance (displacement),
569 which cannot be obtained from an accelerometer alone. Although most of the
570 acceleration variables calculated in this study became stable once an appro-
571 priate running-mean duration had been set, the smoothing procedure could
572 not be used to accurately estimate gravity-based acceleration in fast-start
573 movements in which dynamic acceleration and attitude (hence, gravity-based
574 acceleration) change rapidly and exhibit a stronger intensity in comparison
575 to steady swimming movements. A previous study (Noda et al., 2012) found
576 that the error of the gravity-based acceleration RMS produced by smoothing
577 data obtained for the steady swimming of green sea turtles was less than
578 0.1 *g*. However, the error in the RMS was much larger (greater than 0.15 *g*)
579 in the fast-start movements examined in this study. Thus, the gyro logger
580 can be used to accurately gain information on distance-related performance
581 and manoeuvrability parameters, which will prove effective in the analysis of
582 fast-start movements involving a rapid change in motion.

583 *Comparison with high-speed imaging*

584 The most important advantage of a data logger is that it can measure
585 the locomotion of animals in the field. High-speed imaging with a camera
586 has an advantage over data logger methods because it does not require at-
587 tachment to an animal. Furthermore, high-speed imaging can be used to
588 simultaneously track multiple individuals (Kane et al., 2004; Lochmatter et
589 al., 2008). Kinematics and mechanics information can be obtained from the
590 images to interpret fast-start movements and to assess the performance of
591 the movements. The latency and prey reaction distance, as defined in the
592 predator-prey relationship, can also be measured. Although many previous
593 studies have studied the 2D locomotion of fast-start movements, high-speed
594 imaging-based methods have recently been developed for monitoring the 3D
595 locomotion of fast-start movements (Butail and Paley, 2011). However, high-
596 speed imaging is very difficult to implement in the field, especially for mon-
597 itoring highly migratory or elusive animals. As described in this study, a
598 gyro logger can be used to directly monitor all of the 3D forces acting on the
599 body of an animal. Although the data logger must be attached to the body
600 of the animal and recovered at the end of the measurement period to obtain
601 the data stored in the internal memory of the device, this instrument can be
602 used to measure the movement of animals in the wild. Although data log-
603 ger measurements can only partially capture the movement of the body and
604 although some of the movements, such as the movement of an appendage,
605 are not measurable, once links between data logger measurements and the
606 mechanical types of movements are established, we may be able to obtain a
607 clearer picture of the movements of animals, as shown in this study.

608 *Application of the developed method*

609 The method developed in this study can be used for assessing the move-
610 ment performance of the fast-start behaviour of fish in the field. Although
611 laboratory settings enable controlled experiments, measuring locomotion in
612 natural settings is also important. For example, to understand animals ener-
613 getic strategies, it is important to know when and under what type of envi-
614 ronmental conditions they conduct escape behaviours and how much power
615 they use for their escape, as it is not always necessary for animals to use
616 maximum performance (Irschick, 2003), and fast-start behaviour typically
617 involves a high energy requirement (Domenici and Blake, 1997).

618 The limitations of this method include the data logging duration. Al-
619 though most studies have used a relatively low sampling frequency (≤ 32
620 Hz) (Kawabe et al., 2003; Tsuda et al., 2006; Whitney et al., 2010; Føre
621 et al., 2011), this study used a high frequency (500 Hz) because fast-start
622 movements usually last only a fraction of a second (reviewed by Domenici
623 and Blake, 1997). Consequently, a sufficiently high sampling frequency is
624 required to monitor these behaviours. However, high-frequency sampling re-
625 quires more battery power and thus the total recording duration is limited. If
626 the battery size, and thus the total recording duration, increases, the size of
627 the data logger also has to be increased, which limits the size range of the an-
628 imals for which the data logger is applicable. The addition of a gyroscope to
629 the conventional sensors such as an accelerometer and a magnetometer also
630 requires more battery power. Although this study cannot solve the techno-
631 logical issues around the batteries, sampling frequencies, and sensor types, it
632 does address the possibility of using animal-mounted data loggers for mea-

633 suring the movement performance of fast-start behaviour in the wild. Future
 634 technological developments may give researchers access to smaller and more
 635 energy-efficient data loggers. Multi-schedule systems (e.g., 2 h of recording
 636 per day for multiple days) will increase the total number of recording days
 637 despite the short recording period that is used during each day; hence, these
 638 systems could be used for the sampling of long-term behaviours in animals.
 639 On-board processing for the storage of only important information may also
 640 improve the total recording duration (Murchie et al., 2011; Føre et al., 2011).

641 **List of symbols and abbreviations**

642 g : gravitational acceleration constant ($= 9.81 \text{ m s}^{-2}$)

643 MA: magnitude of acceleration: vector summation of the dynamic accelera-
 644 tion in the x- y- and z-directions

645 MV: magnitude of velocity: vector summation of the relative velocity in the
 646 x- y- and z-directions

647 ODBA: overall dynamic body acceleration

648 RMS: root mean square

649 S1: stage 1

650 S2: stage 2

651 T_x : the time required to reach the maximum acceleration in the x axis

652 T_y : the time required to reach the maximum acceleration in the y axis

653 T_z : the time required to reach the maximum acceleration in the z axis

654 Appendix

655 *Calculation of the dynamic acceleration of the combined x- and y-directions*

656 The acceleration obtained by video tracking is defined in the coordinate
657 fixed to the tank (camera frame), whereas the acceleration obtained by the
658 accelerometer is defined in the coordinate fixed to the data logger (logger
659 frame) (Fig. 1). Because, from the view of the camera frame, the logger
660 frame always changes when the data logger moves with the body of the fish,
661 it is necessary to transform the acceleration obtained by the accelerometer
662 to the acceleration that would be sensed in the camera frame to compare the
663 two accelerations. To achieve that transformation, the following calculation
664 was performed:

665 It was assumed that the logger frame coordinate is defined as a coordinate
666 composed of two vectors, one of which is the vector (Y_A axis) connecting the
667 two markers on the accelerometer in the longitudinal direction and the other
668 is the vector (X_A axis) perpendicular to the Y_A axis going through the centre
669 of the two markers. Assume M_t , M_{t+1} , and M_{t+2} to be the 2D points of the
670 centre of the two markers obtained by the video tracking at time t , $t + 1$,
671 and $t + 2$, respectively, in the camera frame coordinates. The acceleration
672 obtained by video tracking at time t should be defined as the acceleration
673 measured in terms of the change in the points M_t , M_{t+1} , and M_{t+2} with the
674 direction $\vec{\mu}$ from M_t to M_{t+2} . On the other hand, the acceleration obtained by
675 the accelerometer at time t is defined as the acceleration in the two directions
676 $\vec{\mu}_x$ and $\vec{\mu}_y$, respectively, in the X_A axis and the Y_A axis direction in the logger
677 frame coordinate. Therefore, two accelerations, Ax_t and Ay_t , measured by
678 the accelerometer can be transformed to the combined acceleration Av_t in

679 the $\vec{\mu}$ direction that would be measured in the camera frame by the vector
680 summation of $\vec{\mu}_x$ and $\vec{\mu}_y$ with the scalar of $\sqrt{Ax_t^2 + Ay_t^2}$.

681 **Table A1**

682 Summary of the total (TL) and fork (FL) lengths, body mass (BM), and
683 number of observed escape (N_e) activities identified using the video images
684 for 5 (A-E) different Japanese amberjacks. The N_e number in parentheses
685 indicates the number of escape responses that were simultaneously recorded
686 with a high-speed camera.

687 **Figure A1**

688 Image sequences of a) single- and b) double-bend escape movements.

689

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695 **Author Contributions**

696 T.N., N.A. and H.M. designed and developed a gyro logger. T.N., Y.K.,
697 N.A., and H.M. contributed to the design of the experimental study. T.N.,
698 Y.K. and S.W. contributed to the execution of the experiments. T.N. ana-
699 lyzed the data and wrote the manuscript. All authors provided critiques on
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852 **Figure Legends**

853 **Figure 1**

854 Diagram demonstrating the extraction of angular and time-distance variables
855 from the gyro logger measurements. An orientation filter (Madgwick et al.,
856 2011) was implemented to integrate the gyro logger measurements.

857

858 **Figure 2**

859 Four coordinate frames were assumed; the earth frame (X_E, Y_E, Z_E), camera
860 frame (X_C, Y_C, Z_C), fish frame (X_F, Y_F, Z_F), and data logger frame ($X_L,$
861 Y_L, Z_L).

862

863 **Figure 3**

864 a) Angular velocity in the z-direction (turning rate), as obtained from the
865 gyroscope measurements, and b) the calculated yaw angle, which shows the
866 S1 and S2 durations and angles.

867

868 **Figure 4**

869 A typical profile of the comparison of a) cumulative distance, velocity, accel-
870 eration, turning rate and turning angle (yaw angle), and b) 2D trajectory for
871 a fixed duration of 0.18 between the gyro logger measurements (solid line)
872 and the camera recordings (dashed line) during an escape event.

873

874 **Figure 5**

875 Regression analysis of the locomotor variables estimated from the gyro logger
876 (x-axis) and from the camera recordings (y-axis) showing a linear regression

877 line (solid line) and the lower and upper 95 % confidence interval (dotted
 878 line). The locomotor variables examined included (a) cumulative distance:
 879 $\text{Video} = 1.08 \times \text{Logger} + 0.02$; $R^2 = 0.85$; F value = 128.60 (1 and 22 Degree
 880 of Freedom (D.F.)); $p < 0.0001$; $N = 24$, (b) maximum velocity: $\text{Video} =$
 881 $0.85 \times \text{Logger} + 0.21$; $R^2 = 0.56$; F value = 28.47 (1 and 22 D.F.); $p <$
 882 0.0001 ; $N = 24$, (c) maximum acceleration: $R^2 = 0.01$; F value = 0.13 (1
 883 and 22 D.F.); $p = 0.73$; $N = 24$, (d) turning rate: $\text{Video} = 0.78 \times \text{Logger}$
 884 $+ 102.98$; $R^2 = 0.53$; F value = 22.36 (1 and 20 D.F.); $p < 0.001$; $N = 22$,
 885 (e) S1 angle: $\text{Video} = 0.95 \times \text{Logger} + 6.86$; $R^2 = 0.41$; F value = 13.95
 886 (1 and 20 D.F.); $p < 0.01$; $N = 22$, (f) S2 angle: $\text{Video} = 0.97 \times \text{Logger} -$
 887 2.20 ; $R^2 = 0.93$; F value = 108.6 (1 and 8 D.F.); $p < 0.0001$; $N = 10$, (g)
 888 S1 duration: $\text{Video} = 1.02 \times \text{Logger} - 0.00$; $R^2 = 0.99$; F value = 2785 (1
 889 and 20 D.F.); $p < 0.0001$; $N = 24$, and (h) S2 duration: $\text{Video} = 0.98 \times$
 890 $\text{Logger} + 0.00$; $R^2 = 0.97$; F value = 263.2 (1 and 8 D.F.); $p < 0.0001$; $N = 10$.

891

892 **Figure 6**

893 Typical profile of locomotor variables in a single- (solid line) and double-bend
 894 (dashed line) escape movement. Timing difference of maximum acceleration
 895 along the x- and y-axes are also shown. Turning rate corresponds to the
 896 angular velocity in the z-direction.

897

898 **Figure 7**

899 Box plot showing the difference in the timing of maximum acceleration along
 900 the x- and y-axes for the two types of escape movements (single-bend; N
 901 $= 11$, double-bend; $N = 13$). The timing difference indicates the difference

902 in the time required to reach maximum acceleration between the x- and y-
903 positions ($T_x - T_y$).

904

905 **Figure 8**

906 Variation in the ODBA (mean $\pm$ s.e.m.) for different running-mean dura-
907 tions for smoothing ($N = 41$). The acceleration is presented in g units as
908 previously described (Shepard et al., 2008).

909

910 **Figure 9**

911 Example of raw accelerometer measurements (gray line) and gravity-based
912 accelerations determined using the gyro (black line) or the smoothing method
913 with a running mean duration of 0.1 s (dotted black line) or 0.3 s (dotted
914 gray line) in the x-, y- and z-directions. Although the acceleration in escape
915 events is usually higher than $\pm 1 g$, accelerations within the range of $-1 \sim 1 g$
916 are displayed.

917

Table 1: Summary of the mean (s.e.m.) values of the locomotor variables in escape movements (single- and double-bend responses). The significant differences between the variables for the two types of escape movements ($N = 24$) are also shown.

	single-bend	double-bend	all	RM-ANOVA		
variable	mean (s.e.m.)	mean (s.e.m.)	mean (s.e.m.)	df	F value	p
A_{max} in x (m s^{-2}) ^a	82.73 (4.54)	106.38 (6.62)	93.57 (4.59)	1	8.34	<0.01 **
A_{max} in y (m s^{-2})	37.09 (3.29)	62.31 (4.71)	48.65 (3.80)	1	18.50	<0.001 ***
A_{max} in z (m s^{-2})	55.57 (4.81)	83.85 (4.41)	68.53 (4.37)	1	17.67	<0.001 ***
MA_{max} (m s^{-2}) ^b	85.87 (4.50)	121.25 (7.11)	102.09 (5.43)	1	17.18	<0.001 ***
MV_{max} (m s^{-1}) ^c	1.27 (0.08)	1.52 (0.08)	1.38 (0.06)	1	4.21	0.05
Cum Dist (m s^{-1}) ^d	0.11 (0.01)	0.17 (0.01)	0.14 (0.01)	1	16.95	<0.001 ***
ω_{max} in x (deg s^{-1}) ^e	369.04 (45.76)	708.13 (58.14)	524.46 (50.14)	1	30.07	<0.001 ***
ω_{max} in y (deg s^{-1})	1047.36 (81.37)	1759.25 (79.71)	1373.64 (92.30)	1	36.36	<0.001 ***
ω_{max} in z (deg s^{-1})	796.23 (48.28)	844.62 (52.48)	818.41 (35.87)	1	2.62	0.12
S1 angle (deg)	45.27 (2.60)	33.91 (3.42)	40.06 (2.37)	1	7.23	<0.05 *
range of pitch (deg)	33.74 (4.02)	28.01 (2.09)	31.11 (2.45)	1	0.20	0.66
range of roll (deg)	23.54 (2.21)	24.49 (1.88)	23.97 (1.48)	1	0.03	0.86
S1 duration (ms)	175.23 (23.25)	92.18 (7.28)	137.17 (15.42)	1	10.02	<0.01 **
$T_y - T_x$ (ms) ^f	37.69 (3.76)	-11.64 (2.40)	15.08 (5.53)	1	116.07	<0.001 ***
$T_z - T_x$ (ms) ^g	3.23 (5.38)	-5.27 (6.76)	-0.67 (4.34)	1	1.45	0.24
time to MA_{max} (ms)	16.62 (4.69)	50.00 (6.97)	31.92 (5.31)	1	16.26	<0.001 ***
time to MV_{max} (ms)	38.77 (2.55)	82.91 (18.06)	59.00 (9.52)	1	6.66	<0.05 *

^a A_{max} refers to maximum acceleration

^b maximum value of the magnitude of acceleration

^c maximum value of the magnitude of velocity

^d cumulative distance

^e ω_{max} refers to maximum angular velocity

^f timing difference in A_{max} between x and y

^g timing difference in A_{max} between x and z

Table 2: Percent change [mean (s.e.m.; standard error of mean)] in the maximum, mean, s.d., and RMS of the dynamic acceleration, the ODBA, and the time required to reach maximum dynamic acceleration for different running-mean durations of smoothing as obtained from escape events ($N = 41$). The values from the smoothing procedure were compared with those obtained using the gyro method.

	max acceleration			mean acceleration			s.d. of acceleration			RMS			ODBA	time to max acceleration		
duration (s)	x	y	z	x	y	z	x	y	z	x	y	z	x	y	z	
0.10	-8.53 (1.04)	-17.44 (2.25)	-1.11 (1.12)	-103.96 (4.22)	-99.76 (0.25)	-105.31 (5.66)	-7.72 (1.01)	-20.35 (1.72)	-0.21 (0.92)	-8.10 (1.05)	-21.78 (1.75)	-0.32 (0.93)	-10.53 (1.24)	-0.29 (0.17)	-0.53 (0.39)	-0.30 (0.14)
0.20	-1.75 (0.77)	-11.38 (1.47)	2.62 (0.60)	-99.46 (0.39)	-109.89 (10.31)	0.47 (0.62)	-10.90 (0.93)	4.13 (0.56)	0.03 (0.57)	-12.52 (1.00)	4.01 (0.57)	-1.47 (1.05)	0.05 (0.25)	-0.37 (0.40)	-0.29 (0.14)	-115.55 (9.86)
0.30	-1.31 (0.56)	-8.15 (1.28)	2.19 (0.42)	-129.26 (17.04)	-99.17 (0.60)	-107.14 (8.37)	0.30 (0.36)	-6.63 (0.61)	2.61 (0.31)	-0.13 (0.38)	-8.34 (0.70)	2.49 (0.31)	4.27 (0.81)	0.05 (0.28)	-0.36 (0.39)	-0.08 (0.08)
0.40	-1.07 (0.48)	-6.49 (1.12)	2.33 (0.40)	-138.37 (23.11)	-98.87 (0.84)	-105.10 (7.01)	0.55 (0.28)	-4.07 (0.58)	2.93 (0.28)	0.12 (0.29)	-5.83 (0.65)	2.82 (0.28)	6.72 (0.76)	-0.19 (0.13)	-0.27 (0.39)	-0.08 (0.08)
0.50	-0.64 (0.40)	-5.01 (0.99)	2.40 (0.38)	-149.89 (31.02)	-98.38 (1.07)	-101.41 (6.23)	0.87 (0.30)	-2.05 (0.66)	3.06 (0.26)	0.43 (0.30)	-3.86 (0.69)	2.94 (0.26)	8.73 (0.75)	-0.08 (0.08)	0.20 (0.14)	-0.08 (0.08)
0.60	-0.46 (0.37)	-3.96 (0.90)	2.40 (0.35)	-165.43 (43.39)	-97.55 (1.26)	-97.16 (9.59)	1.12 (0.32)	-0.75 (0.71)	3.08 (0.25)	0.69 (0.32)	-5.59 (0.73)	2.97 (0.25)	10.14 (0.73)	-0.08 (0.08)	0.20 (0.14)	-0.08 (0.08)

Table A1: Summary of the total (TL) and fork (FL) lengths, body mass (BM), and number of observed escape (N_e) activities identified using the video images for 5 (A-E) different Japanese amberjacks. The N_e number in parentheses indicates the number of escape responses that were simultaneously recorded with a high-speed camera.

fish ID	TL (cm)	FL (cm)	BM (kg)	N_e
A	71.6	66.8	3.2	11 (4)
B	66.6	60.9	4.1	8 (5)
C	69.8	63.9	3.8	11 (8)
D	77.8	73.1	5.3	4 (3)
E	67.8	65.0	3.9	7 (4)
			total	41 (24)

Figure 1: Diagram demonstrating the extraction of angular and time-distance variables from the gyro logger measurements. An orientation filter (Madgwick et al., 2011) was implemented to integrate the gyro logger measurements.

Figure 2: Four coordinate frames were assumed; the earth frame (X_E, Y_E, Z_E), camera frame (X_C, Y_C, Z_C), fish frame (X_F, Y_F, Z_F), and data logger frame (X_L, Y_L, Z_L).

Figure 3: a) Angular velocity in the z-direction (turning rate), as obtained from the gyroscope measurements, and b) the calculated yaw angle, which shows the S1 and S2 durations and angles.

Figure 4: A typical profile of the comparison of a) cumulative distance, velocity, acceleration, turning rate and turning angle (yaw angle), and b) 2D trajectory for a fixed duration of 0.18 between the gyro logger measurements (solid line) and the camera recordings (dashed line) during an escape event.

Figure 5: Regression analysis of the locomotor variables estimated from the gyro logger (x-axis) and from the camera recordings (y-axis) showing a linear regression line (solid line) and the lower and upper 95 % confidence interval (dotted line). The locomotor variables examined included (a) cumulative distance: Video = $1.08 \times \text{Logger} + 0.02$; $R^2 = 0.85$; F value = 128.60 (1 and 22 Degree of Freedom (D.F.)); $p < 0.0001$; N = 24, (b) maximum velocity: Video = $0.85 \times \text{Logger} + 0.21$; $R^2 = 0.56$; F value = 28.47 (1 and 22 D.F.); $p < 0.0001$; N = 24, (c) maximum acceleration: $R^2 = 0.01$; F value = 0.13 (1 and 22 D.F.); $p = 0.73$; N = 24, (d) turning rate: Video = $0.78 \times \text{Logger} + 102.98$; $R^2 = 0.53$; F value = 22.36 (1 and 20 D.F.); $p < 0.001$; N = 22, (e) S1 angle: Video = $0.95 \times \text{Logger} + 6.86$; $R^2 = 0.41$; F value = 13.95 (1 and 20 D.F.); $p < 0.01$; N = 22, (f) S2 angle: Video = $0.97 \times \text{Logger} - 2.20$; $R^2 = 0.93$; F value = 108.6 (1 and 8 D.F.); $p < 0.0001$; N = 10, (g) S1 duration: Video = $1.02 \times \text{Logger} - 0.00$; $R^2 = 0.99$; F value = 2785 (1 and 20 D.F.); $p < 0.0001$; N = 24, and (h) S2 duration: Video = $0.98 \times \text{Logger} + 0.00$; $R^2 = 0.97$; F value = 263.2 (1 and 8 D.F.); $p < 0.0001$; N = 10.

Figure 6: Typical profile of locomotor variables in a single- (solid line) and double-bend (dashed line) escape movement. Timing difference of maximum acceleration along the x- and y-axes are also shown. Turning rate corresponds to the angular velocity in the z-direction.

Figure 7: Box plot showing the difference in the timing of maximum acceleration along the x- and y-axes for the two types of escape movements (single-bend; $N = 11$, double-bend; $N = 13$). The timing difference indicates the difference in the time required to reach maximum acceleration between the x- and y-positions ($T_x - T_y$).

Figure 8: Variation in the ODBA (mean $\pm$ s.e.m.) for different running-mean durations for smoothing ($N = 41$). The acceleration is presented in g units as previously described (Shepard et al., 2008).

Figure 9: Example of raw accelerometer measurements (gray line) and gravity-based accelerations determined using the gyro (black line) or the smoothing method with a running mean duration of 0.1 s (dotted black line) or 0.3 s (dotted gray line) in the x-, y- and z-directions. Although the acceleration in escape events is usually higher than ± 1 g , accelerations within the range of $-1 \sim 1$ g are displayed.

Figure A1: Image sequences of a) single- and b) double-bend escape movements.