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Samuel Westrelin, Stéphanie Boulêtreau, Frédéric Santoul

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13 **European catfish *Silurus glanis* behaviour in response to a strong summer**
14 **hypoxic event in a shallow lake**

15
16 Westrelin Samuel⁽¹⁾, Boulêtreau Stéphanie⁽²⁾, Santoul Frédéric⁽³⁾

17
18 (1) INRAE, Aix Marseille Univ, Pôle R&D ECLA, RECOVER, 3275 Route de Cézanne - CS
19 40061, F-13182 Aix-en-Provence Cedex 5, FRANCE.

20 <https://orcid.org/0000-0002-0169-1363>

21 (2) Laboratoire Ecologie Fonctionnelle et Environnement, Université de Toulouse, CNRS,
22 Toulouse, FRANCE.

23 <https://orcid.org/0000-0002-0094-0196>

24 (3) Laboratoire Evolution & Diversité Biologique, Université Paul Sabatier, CNRS, ENFA,

25 UMR5174 EDB, 118 route de Narbonne, 31062 Toulouse, FRANCE. <https://orcid.org/0000->

26 [0002-2932-2172](https://orcid.org/0000-0002-2932-2172)

27
28 **Corresponding author**

29 Samuel Westrelin

30 INRAE

31 3275 Route de Cézanne - CS 40061

32 F-13182 Aix-en-Provence Cedex 5

33 France

34 samuel.westrelin@inrae.fr

35 +33 (0)4 42 66 69 71

36

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48

49

50 Abstract

51 Hypoxic events have always naturally occurred in freshwater ecosystems but are worsening due to
52 anthropogenic activities. Hypoxia tolerance greatly varies among fish species and is difficult to
53 quantify in nature in large fish species. We analysed the movements of 40 subadult and adult
54 European catfish *Silurus glanis* ([727; 2150] mm) exposed to a natural summer hypoxic event in a
55 shallow lake of southeastern France. Catfish could withstand very low dissolved oxygen
56 concentrations (DOC), down to 1.3 mg/L in the upper half of the water column (corresponding to a
57 mean dissolved oxygen saturation rate of 16%), when their preferred benthic habitats were anoxic.
58 While hypoxia was becoming more severe, individuals significantly increased their activity and the
59 surface area they visited, whatever their size. This led them to a refuge zone where they aggregated or
60 stayed in close vicinity, very little mobile, over one and a half day during the overall anoxia of the
61 lake. This zone, located very close to the well oxygenated water inflow, was probably one of the most
62 oxygenated accessible zone. During this aggregation, the smallest individuals were however more
63 active than the largest ones. This was probably because they more often needed to move to better
64 oxygenated places within the gathering area, compared to larger dominant fish that occupied the best
65 places. The ability of catfish to withstand very low DOC, along with its high optimum temperature
66 range, could give it a competitive advantage over other predatory species in the context of global
67 change.

68 Key Words

69 Aggregation, escape response, fish, hypoxia, lake

70

71 Introduction

72 Low dissolved oxygen conditions, so called hypoxic events, occur in a wide range of marine and
73 freshwater ecosystems (Diaz & Rosenberg, 2011). They happen when oxygen consumption, primarily
74 by decomposing organic matter, exceeds oxygen supply by photosynthetic production and diffusion
75 from the atmosphere. Hypoxic events have always naturally occurred in aquatic ecosystems but the
76 gradual rise in nutrient and organic enrichment due to human activities (sewage, industrial and land

77 runoff) has resulted in the increase in their frequency and seriousness, sometimes leading to anoxia
78 (Druon et al., 2004; Hagy et al., 2004). Increasing hypoxia is now recognized as an environmental
79 issue of global importance for fresh, coastal and oceanic waters (Breitburg et al., 2009; Diaz &
80 Rosenberg, 2011; Jenny et al., 2016). In lentic and lotic freshwater systems, hypoxia varies in
81 seasonality, frequency and persistence, depending on many factors, including eutrophication, inflow of
82 industrial waste, reduced mixing due to depth or wind conditions, thermal variations and ice cover
83 (Poff et al., 2002; Ficke et al., 2007).

84 Compared with most birds and mammals, ectothermic vertebrates (fish, amphibian, and
85 reptile) are tolerant of variable oxygen availability (Bickler & Buck, 2007). In fish, hypoxia tolerance
86 greatly varies among the 20,000 species. Species such as trout (*Oncorhynchus mykiss*) and tuna
87 (*Katsuwonus pelamis*, *Thunnus albacares*, *Thunnus obesus*), that extensively depend on aerobic
88 metabolism for rapid and sustained swimming, are moderately to extremely sensitive to hypoxia
89 (Gesser, 1977; Bushnell et al., 1990; Gamperl & Driedzic, 2009). Carp (*Cyprinus carpio*), eel
90 (*Anguilla anguilla*), catfish (*Silurus glanis*) and hagfish (*Myxine glutinosa*) can manage with low
91 oxygen concentrations (Weber et al., 1976; Gesser, 1977; Axelsson et al., 1990; Massabuau & Forgeue,
92 1995). At the extreme, the crucian carp (*Carassius carassius*) is able to endure months of hypoxia at
93 low temperature (Nilsson & Renshaw, 2004; Stecyk et al., 2004). Such hypoxia tolerance involves
94 metabolic adjustments, including metabolism depression, tolerance of metabolic products during
95 anaerobiosis, and strategies for avoiding or repairing cellular injuries during reoxygenation (Brauner et
96 al., 2004; Wells, 2009).

97 Behavioural responses can provide additional flexibility to mitigate exposure to hypoxic
98 stress. Changes in spontaneous swimming activity have been described in a wide range of fish species
99 when exposed to hypoxia (Schurmann & Steffensen, 1994; Chapman & McKenzie, 2009). Domenici
100 et al. (2000) found that the lower was the spontaneous speed in Atlantic herring (*Clupeus harengus*) in
101 normoxia, the greater was the increase in speed in hypoxia. Some fish up-regulate their speed,
102 performing an escape response, defined as a type of fast start characterized by a brief and sudden
103 acceleration (Domenici & Blake, 1997). Alternatively, others down-regulate their speed, they show
104 freezing behaviour by adopting a fixed and immobile posture through which they become less

105 susceptible to detection by predators. It has also been suggested that species that reduce their activity
106 in hypoxia tend to be demersal or benthopelagic, with a relatively sedentary lifestyle during which
107 they may often encounter hypoxia in their habitat; whereas species that increase activity in case of
108 hypoxia tend to be active pelagic schooling fishes (Domenici et al., 2000; Herbert & Steffensen, 2005;
109 Herbert & Steffensen, 2006). Therefore, changes in swimming activity as behavioural responses to
110 mitigate exposure to hypoxia are difficult to predict since they largely depend on fish species and
111 context (Chapman & McKenzie, 2009). Moreover, such behaviours are difficult to describe and
112 quantify in nature, and also in laboratory conditions for very large species.

113 The European catfish (*Silurus glanis*) is the largest fish species inhabiting European
114 freshwaters (up to 2.7 m in body length and 130 kg of weight, Boulêtreau & Santoul, 2016). The
115 species is native from Eastern Europe and has been introduced in Southwestern Europe during the 19th
116 Century for sport fishing and aquaculture (Copp et al., 2009). It has successfully established in most of
117 the large Southwest European watersheds (Boulêtreau et al., 2020). Several features could explain its
118 colonization and expansion success. The range of temperatures within which adults do not show any
119 sign of abnormal behaviour is quite large and falls between 12 °C and 28 °C, but reproduction
120 optimally occurs above 20 °C (Souchon & Tissot, 2012). It is also tolerant to water pollution, partly
121 due to low oxygen requirements as little as 1-1.5 mg/L depending on the temperature (Massabuau &
122 Forgue, 1995). The species is considered to use oxygen very efficiently, partly thanks to a high
123 haematocrit (35-38%, Mihalik, 1995). Nevertheless, such physiological capacities have only been
124 measured on young individuals in laboratory conditions. In natural conditions, one study has reported
125 the displacements of 19 juvenile catfish (total length less than 400 mm) in response to a winter
126 hypoxia in one oxbow lake of the river Elbe (Czech Republic). Fish were shown to exhibit unexpected
127 high activity and displacements (Daněk et al., 2014). But no behavioural response to hypoxia has ever
128 been studied on adult European catfish in natural conditions.

129 In an experiment set up to assess the space use and activity cycles of the European catfish, 40
130 large individuals (subadults and adults whose body length ranged in 727 - 2150 mm) have been
131 tracked by acoustic telemetry for three years in a 104-ha shallow eutrophic lake located in South-
132 Eastern France. Within this period, the lake experienced a severe hypoxia, leading to the mortality of

133 many fish from different species, including carp, eel and some small European catfish. However,
134 fourteen months later, our telemetry tracking data revealed that all the 40 tagged catfish were still
135 alive. Therefore, we aimed to analyse how large European catfish individuals could have resisted to
136 hypoxia in natural conditions. More specifically, we examined how telemetry data could provide
137 valuable information to highlight catfish individual tolerance and behaviour changes in response to
138 hypoxia depending on catfish body size.

139

140 **Material and methods**

141 **Study site**

142 “Etang des Aulnes” is a shallow natural lake, mean depth 3.8 m, maximum depth 6 m, 104 ha area,
143 located in South-Eastern France in a protected natural area. A primary canal and a secondary one
144 collect irrigation waters that feed the lake. The lake then outflows in another canal (Figure 1). The lake
145 water residence time is 300 days. The outflow is regulated to get high water levels in winter and low
146 water levels in summer (maximal difference of 0.6 m).
147 The fish assemblage, determined by fyke nets, fishing traps and electro fishing in October 2017, 2018
148 and 2019 was composed of 16 species. The most dominant species were bream (*Abramis brama*,
149 relative abundance 65%), European perch (*Perca fluviatilis*, 13%), pumpkinseed (*Lepomis gibbosus*,
150 8%), tench (*Tinca tinca*, 4%), pikeperch (*Sander lucioperca*, 4%), European catfish (*Silurus glanis*,
151 3%) and Northern pike (*Esox lucius*, 2%). In addition, two crayfishes were present: *Procambarus*
152 *clarkii* and *Faxonius limosus*. Fishing is allowed but only during daytime from the eastern bank of the
153 lake and no other activity is authorised.

154

155 **Physical and chemical lake conditions**

156 Hourly vertical profiles of water temperature (0.5, 3 and 5 m above the bottom) and dissolved oxygen
157 concentration (DOC) (0.5, 1.5, 2.5 and 3.5 m above the bottom) were recorded at the deepest point in
158 the lake (location 42 on Figure 1). HOBO data loggers U22 were used for temperature and U26 for
159 DOC. The dissolved oxygen saturation rate (DOS) was calculated from DOC and temperature values.
160 At 0.5 m above the bottom, there were no records from 09-02 03:00 to 09-04 12:00, because of a

161 sensor failure. 0.5-1.5 m, 2.5-3 m and 3.5-5 m heights of measurements above the bottom are named
162 bottom, middle and surface, respectively, in the following text. In addition, vertical profiles of
163 temperature and DOC were recorded on 09-04 with a YSI Exo2 multiparameter sonde at different
164 locations in the lake to get a spatial picture of what happened all over the lake at different depths
165 (Figure 1).

166 The mean hourly wind speed at a standard height of 10 meters above ground (10-m wind) was
167 measured at the meteorological station of Salon-de-Provence, located 24 km east of the lake and
168 representative of the weather conditions on the lake. The meteorological data were provided by
169 Météo-France, the French meteorological institute, and available from the INRAE CLIMATIK
170 platform (<https://intranet.inrae.fr/climatik/>, in French) managed by the AgroClim laboratory of
171 Avignon, France.

172

173 **Fish tagging**

174 A total of 40 European catfish were caught by fyke nets, angling or electrofishing over two sampling
175 campaigns: 10 in October 2017 and 30 in October 2018. Different techniques were used to sample the
176 whole range of sizes among subadults and adults and individual behaviours (Harkonen et al., 2016).
177 Once captured, catfish were stocked for a few hours in large aerated basins (2x1.25x0.5 m³) filled with
178 regularly changed lake water to check their condition. Fish were then individually anaesthetised, which
179 took 5-6 minutes, by immersion in a smooth and smaller tank 1.8x0.5x0.7 m³ containing an aerated
180 solution of benzocaine (80 mg/L). Once the fish had lost its balance (ventral side up), did not respond
181 to stimuli anymore and had a very slow and steady operculum rate, it was weighed, measured and
182 placed ventral side up in an identical tank containing an aerated solution of benzocaine (40 mg/L) to
183 irrigate the gills during surgery. A 15 to 20 mm long incision was made with a scalpel in the middle of
184 an imaginary line that would join the basis of the pectoral fin to the pelvic fin. An acoustic transmitter
185 sterilised in surgical spirit and rinsed with physiological liquid was inserted into the peritoneal cavity.
186 Vemco V13-1L acoustic transmitters (30.5 mm long, 9.2 g in the air, mean battery life 1825 days, 180
187 s - range 120-240s - mean burst interval for the 12 used in 2017 and 320 s - range 260-380s - in 2018)
188 were used. The transmitter weight in the air did not exceed 2% of the fish body weight (Winter, 1996;

189 Snobl et al., 2015). The incision was closed using 2 to 3 simple surgical sutures (3-0 Polydioxanon
190 resorbable monofilament) placed 5 mm apart. An antiseptic and antibiotic dressing was applied on the
191 incision wound to help healing and limit the risk of infection. Two surgeons took turn every four fish
192 to operate, one fish surgery taking 5-6 min. Fish were then put in large, aerated recovery basins
193 ($2 \times 1.25 \times 0.5 \text{ m}^3$), where they were continually observed until they recovered normal opercular activity,
194 swimming ability, balance and behavioural response to stimuli, usually after 10 min. Fish spent 3 to 6
195 hours in this recovery basin before being released to their capture site. All individuals could be
196 released in good shape.

197 At the time they were tagged, total length of the 40 tracked European catfish ranged in [727; 2 150]
198 mm (mean 1 033 mm) and weight in [2 301; 64 380] g (mean 9 658 g) (Table 1).

199

200 Fish tracking

201 An array of 52 underwater omnidirectional Vemco acoustic receivers (20 VR2W 69kHz and 32
202 VR2Tx 69kHz) with their associated synchronisation tag (additional V16-1L transmitter for VR2W
203 and built in V16-like transmitter for VR2Tx, 500-700 s, used to correct for receiver internal clock
204 drift) were anchored to the bottom throughout the lake from December 2017 (Figure 1). Seven
205 reference tags (V13-1L, 840-960s) were added to detect anomalies in the tracking system. On average,
206 neighbouring receivers were positioned 155 m from each other (range, 100-209 m), in 3.9 m water
207 depth (range, 1.5 - 6 m), 0.5 m above the bottom. Receivers were removed roughly every 6 months to
208 download fish detections. From these detections, fish 2D positions were calculated with the Vemco
209 Positioning System (VPS) (Smith, 2013). The horizontal position error, a dimensionless parameter
210 calculated by the VPS for each position, gives information on the quality of the position estimate, and
211 was used to filter the data set (Espinoza et al., 2011). Here, we retained only positions with horizontal
212 position error not exceeding 100; this limit represented a good compromise between the mean position
213 error (7.4 m) and the percentage of positions kept (87%).

214

215 **Space use metrics**

216 Fish have been continuously tracked from December 2017 but, here, we focused on ten days
217 throughout August-September of 2019, when a severe hypoxic event occurred. Individual raw
218 positions were interpolated using the R package *trajr* (McLean & Skowron Volponi, 2018) for each
219 quarter hour between the first and the last position to get synchronised individual tracks. Interpolated
220 positions from gaps in raw positions longer than 1 hour were discarded. These tracks were all together
221 plotted on the lake map to create a video of the catfish displacements, useful to get insights on catfish
222 space use (Online Resource 1). Distances between consecutive positions were computed and set to
223 zero if less than the telemetry system mean position error (7.4 m). To represent fish swimming
224 activity, for each individual and each hour, the mean speed (m/h) was calculated. A mean daily speed
225 (m/h) was calculated for each individual if at least seven hourly mean speeds were available in a day.
226 The mean distance of each individual to all others was calculated using the R package *spatstat*
227 (Baddeley et al., 2015). The distance to shore of each individual was calculated using the R package
228 *rgeos* (Bivand & Rundel, 2019). These distances were calculated for every quarter hour and averaged
229 over every hour and every day. The individual daily home ranges were estimated with an
230 Epanechnikov kernel as the utilization distribution with probability levels of 95% and 50%; the home
231 range 50% is often referred to as the core area (Powell, 2000). These both metrics were also estimated
232 for all pooled individuals over different periods of the ten days to map the areas used by the fish.
233 These spatial analyses were conducted using the R package *adehabitatHR* (Calenge, 2006).

234 The video (Online Resource 1) showed an attractive location where individuals gathered. To identify
235 possible differences in individual behaviours during the aggregation dynamics, we analysed input-
236 output movements of every fish when they could be identified on video recording. We could extract
237 the time when the fish reached the aggregation and stayed inside for 34 among 40 fish and the time
238 when it definitively left (i.e. it did never swim back to the aggregation location) for 30 among 40 fish.

239

240 **Statistical analyses**

241 We applied an algorithm to detect possible breakpoints corresponding to structural changes in the 2-
242 month time series of DOC and of the average hourly speed of all 40 individuals (Zeileis et al., 2003).

243 This was done with the *strucchange* R package (Zeileis et al., 2002). Then, we compared the
244 statistically detected breakpoints in each time series to identify potential concomitance between
245 changes in fish swimming activity and DOC dynamics. Among these periods bounded by the
246 breakpoints, one comprised the severe hypoxia. The same algorithm was re-run on the mean hourly
247 speed within this period to detect possible different levels of catfish activity depending on the hypoxia
248 severity. DOC was compared among these different periods of activity by Kruskal-Wallis tests and
249 pairwise comparisons by Fisher's least significant difference (R package *agricolae*, de Mendiburu,
250 2020).

251 To assess relationships between fish behaviour (characterised by speed, distance to shore, distance to
252 others and home ranges) and DOC, generalized linear mixed-effects models (Zuur et al., 2009) were
253 used by focusing on this hypoxic period. To get rid of temporal correlation that impeded the model
254 robustness, daily means of the different variables were used. After preliminary trials, fish size class
255 and day gave from far the best model adjustments compared to size in mm and DOC, very probably
256 because of threshold effects of DOC on the behaviour. Fish size was defined from body length
257 measured during fish tagging, i.e. up to 22 months before the anoxic period, and was classified into
258 three classes: “small”, “large” and “medium” corresponding to total length < 850 mm, ≥1100 mm and
259 in-between, respectively (Table 1). The two extreme classes were considered in order to maximise the
260 chances that the size of individuals from these both classes still differed in August-September 2019.
261 The fish identity was considered as a random effect to explicitly account for individual variability. To
262 take into account the skewed distribution of mean individual daily speed or distance to shore towards
263 zero, a Tweedie family function with a log-link was used (Gilman et al., 2012).

264 The model could be written as follows:

$$265 \quad \log(\overline{\text{METRICS}}_{\text{ind}}) = \alpha + \text{SIZE} * \text{DAY} + s(\text{ind}) + \varepsilon$$

266

267 where $\overline{\text{METRICS}}_{\text{ind}}$ is the expected daily mean individual speed, distance to the shore or home range, α
268 is the overall intercept, SIZE is the size class (Table 1), $s(\text{ind})$ is a smoothing function modeling the
269 individual effects (Wood, 2008), and " ε " is the error term following a normal distribution with zero

270 mean. Means among days and among sizes by day were pairwise compared by using the *emmeans* R
271 package (Lenth, 2016). The model fitting was assessed with regards to the homogeneity and normality
272 of the residuals (Zuur et al., 2009) and to the percentage of explained variance (Hastie & Tibshirani,
273 1990). For mean individual distance to others, as we could not find a reliable model, we compared the
274 distributions between days and between size classes among days by using Kruskal-Wallis tests and, if
275 significantly different, we made pairwise comparisons by Fisher's least significant difference (R
276 package *agricolae*, de Mendiburu, 2020).
277 All statistical analyses were made with R version 3.6.3 (R Core Team, 2020).

278

279 Results

280 DOC dynamics

281 The surface DOC showed large variations over August-September 2019 (Figure 2). A striking event
282 occurred at the end of August when the surface DOC collapsed and, during several days, reached very
283 low values (mean surface DOC was 1.2 mg/L over 08-29 – 09-04), even becoming null for 52 hours.
284 This corresponded to a full anoxia which first appeared at the bottom on 08-26 and propagated at the
285 surface to make the whole water column anoxic on 08-30 03:00 (Online Resource 2). At this time,
286 water temperatures were stratified and ranged from 22.8 °C at the bottom to 26.7 °C at the surface
287 (Online Resource 2). The anoxia ended on 09-02 16:00 when surface DOC raised up to 1.6 mg/L and
288 the oxygenation was homogeneous over the whole water column (middle and bottom DOC
289 respectively at 1.6, mg/L and 1.5 mg/L). One hour before, DOC was 0, 0.2 and 0.2 mg/L, at the
290 surface, in the middle and at the bottom respectively. In parallel, water temperatures started to
291 homogenize from 09-01 14:00 to be mixed on 09-02 04:00 (24.7 °C at the bottom and 24.8 °C at the
292 surface). This was very linked to the wind that strengthened from 09-01 09:00 (greater than 3 m/s,
293 Online Resource 2).

294

295 DOC dynamics and fish activity

296 Several structural change points were found in the hourly mean speed and DOC time series (Figure 2).
297 The corresponding dates for 2-month speed time series matched well those of surface DOC. Worthy of

298 note, they did not match with dates of changes of deeper DOC (Online Resource 3). In the next, we
299 focus on surface DOC.

300 The 08-27 23:00 to 09-06 06:00 period, that comprises the full anoxia, shows very large variations of
301 hourly speed that appear different from the diel cycle that could be observed outside of this period
302 (Figure 2b). Within this period, four subperiods were detected: at the beginning, fish activity appeared
303 quite similar to the previous period; then, speed sharply increased for 32 hours before fish suddenly
304 stopped and performed very few movements during one and a half day, after which they started to
305 progressively move again. The surface DOC was different between all four speed subperiods
306 (Kruskal-Wallis test, $\chi^2=94.010$, 3 d.f., $p<0.001$): the surface DOC was 1.1 mg/L in average (DOS
307 13%) during the highest activity subperiod and 0.1 mg/L (DOS 1%) during the lowest. The daily
308 analysis also showed that the speed increase (on 08-30) and decrease (on 08-31 and 09-01) were
309 significant (Table 2a, Figure 3b). This enhanced activity corresponded to higher individual home
310 ranges (Tables 2c, 2d, Figures 3e, 3f) and to larger areas visited by the pool of individuals (Figure 4b).
311 Conversely, the home range 95% as well as the core area were considerably reduced when the activity
312 was the lowest (Figures 3e, 3f) and most of individuals gathered in a tiny area (Figure 4c) where they
313 aggregated (Figure 3d). On 09-02, when fish recovered their activity, the areas they travelled over
314 were still reduced (Figure 3f) and nearby the area where they had aggregated (Figure 4d).
315 The highest activity subperiod started when surface DOC dropped down to 1.3 mg/L (DOS 16%) and
316 ceased when the whole water column became anoxic. After the reduced activity subperiod, fish started
317 to progressively move again when surface DOC raised up to 0.7 mg/L (DOS 8%) whereas the half
318 lower of the water column was still anoxic (Online Resource 2).

319

320 [Aggregation location and dynamics](#)

321 From 08-31 to 09-01, catfish were almost inactive, closer to each other, closer to the bank and
322 gathered in a same tiny area (Figures 3b, 3c, 3d, 4c). They aggregated where the main tributary flows
323 into the pond. This was among the places that exhibited the highest DOC values recorded on 09-04 in
324 the whole lake, a few days after the full anoxia (Figure 5). At the main inflow location (points 91 and

325 93), 1-m deep, DOC was near 8 mg/L (DOS 85%) and temperatures much cooler, 18°C against 23 -
326 24°C everywhere else (not shown).

327 The time span between the first fish to join the aggregation location and the last one was 26 hours 15
328 min (from 08-30 16:45 to 08-31 19:00), but 27 individuals joined the location in a short time, 4 hours
329 45 min (from 08-30 20:30 to 08-31 01:15). The dates at which individuals definitively left the
330 aggregation location spanned over a much longer period: 3 days 6 hours 45 min (from 09-01 14:15 to
331 09-04 21:00). 26 individuals left it in 1 day 17 hours 45 min (from 09-02 02:15 to 09-03 20:00).

332

333 Fish behaviour and size dependence

334 The swimming activity, proxied by the mean daily speed, was significantly different among the days
335 during the hypoxic event, and, some days, size class behave differently (Table 2a). The distance to
336 shore was dependent on fish size and also different among days (Table 2b). In details on Figure 3b,
337 whatever their size, all fish significantly increased their activity on 08-30 when the bottom anoxia was
338 propagating to the surface. This corresponded to higher individual core areas for all fish whatever their
339 size and, to a lesser extent, home ranges 95% (Figures 3e, 3f). On both following days, when the
340 whole water column was anoxic and fish swimming activity the lowest, the larger individuals were
341 even less active than the smaller ones (Table 2a, Figure 3b) and occupied a more reduced area on 09-
342 01 (Tables 2c, 2d, Figures 3e, 3f); the smaller individuals were further to others than the larger ones
343 (Figure 3d). In general, the smaller fish were further to the shore (Table 2b, Figure 3c, p-values of
344 pairwise comparisons between Small and Large and Small and Medium <0.001) and had larger home
345 ranges 95% (Table 2c, Figure 3e, p-values of pairwise comparisons between Small and Large and
346 Small and Medium <0.05).

347

348 Discussion

349 Our dataset gave an excellent context to analyse the *in situ* response of a species to an environmental
350 stress. The high resolution and high frequency of the positions collected by telemetry and the number
351 of tagged individuals allowed to detect changes in behaviour at individual level and at timesteps
352 suitable to be confronted with DOC variations (Bauer & Schlott, 2006; Daněk et al., 2014).

353

354 **Catfish tolerance to low DOC**

355 All the 40 tagged catfish survived the severe hypoxic event that lasted more than two days and led to
356 the death of lots of other fish, including species known to manage very well with low oxygen
357 conditions such as carp and eel (Weber et al., 1976; Gesser, 1977). Subadult and adult European
358 catfish could go through very low oxygen conditions during the summer when water temperatures
359 ranged in 23-27 °C. Their behaviour was impacted only when, at the deepest point in the lake, the
360 lower half of the water column was anoxic and when DOC dropped down to 1.3 mg/L (corresponding
361 to a mean DOS of 16%) in the upper half. This DOC value was in the lower range of what Daněk et al.
362 (2014) found on juvenile catfish, 1.3-2.4 mg/L in winter conditions (water temperature around 5 °C).
363 It was in the range of Massabuau & Forgue (1995) laboratory results which concluded that very young
364 catfish (weighing 100-150 g) could maintain dioxygen homeostasis in 1-1.5 mg/L DOC range at 13°C
365 and even very probably in a 10-23 °C temperature range. However, increased temperature lessens
366 oxygen solubility and thus reduces oxygen supply for ichtyofauna; it also elevates basal oxygen
367 demand (Rogers et al., 2016). With comparable critical DOC but higher temperature, we can thus
368 reasonably hypothesise that oxygen supply was more critical in our study. The possible lower critical
369 oxygen threshold in our study could be explained by large differences in catfish body weights between
370 studies. Large fish could have an advantage thanks to their lower mass-specific metabolic rate
371 (Nilsson & Östlund-Nilsson, 2008). These tolerance values were in all cases much lower than the limit
372 of 3-3.5 mg/L reported by Mihalik (1995).

373

374 **Catfish behaviour in response to the hypoxia extent**

375 Horizontal catfish movements were not altered when anoxia was limited to the half lower part of the
376 lake. However, these extreme conditions are likely to considerably reduce the suitable habitats
377 regarding oxygen conditions in this shallow lake, by the way compressing fish habitat (Kraus et al.,
378 2015). The tags did not record the pressure and thus could not provide information on fish depth.
379 Nevertheless, we could suppose that catfish rose to the surface layer to find tolerable DOC, while they
380 are known to mainly occupy benthic habitats (Bruton, 1996; Cucherousset et al., 2018). This remains

381 questioning. One day before complete anoxia at the deepest point of the lake, catfish exhibited a
382 sudden higher level of activity and unusual large displacements over greater areas for about one day,
383 all fish sizes alike. Many fish species change their spontaneous swimming activity when exposed to
384 hypoxia, reducing or increasing their activity (Chapman & McKenzie, 2009). Usually, sedentary
385 species decrease their swimming speed to save energy (Domenici et al., 2013). Crucian carp
386 (*Carassius carassius*) that can endure anoxia for several hours and even days (at 9 °C) reduces its
387 activity by 50% (Nilsson et al., 1993). The increased activity observed in the tagged catfish was
388 unexpected for such a large species that tries to reduce its energy costs (Slavík et al., 2014) and usually
389 performs few movements (Carol et al., 2007; Capra et al., 2018). The stress caused by the resource
390 unavailability can significantly increase catfish movement activity (Slavík et al., 2016). Intense
391 agitation of fish in deep hypoxia could also be interpreted as an avoidance response that helps to find a
392 more suitable place (Domenici et al., 2000; Herbert & Steffensen, 2006; Chapman & McKenzie,
393 2009) as catfish not only became faster but also explored extended areas. Such an increase in activity
394 was also observed on juvenile catfish facing dissolved oxygen deficiency before they found a refuge
395 (Daněk et al., 2014) or on school of Atlantic herrings (*Clupeus harengus*) whose speed peaked during
396 severe hypoxia before decreasing until the school disrupted (Domenici et al., 2000). The reasons for
397 such an agitation need further investigations.

398

399 [Aggregation and refuge location](#)

400 Most of catfish finally converged and gathered where the main canal flows into the lake. They stayed
401 there or in close vicinity by considerably reducing their swimming activity for one and a half day.
402 With the inflow canal, this gathering place was likely the most oxygenated in the lake, able to fulfill
403 their oxygen requirements. In this summer period, irrigation led to quite a strong current in the main
404 canal that continuously brought cool and well oxygenated water flowing through the gathering place.
405 This place and places very close to the bank outside the receiver network were in general at the edge
406 of the telemetry coverage area so that individuals were less often located during the anoxia (Smith,
407 2013), which could sometimes be visible on the video (Online Resource 1). Overall unsuitable
408 environmental conditions temporarily forced catfish to share very limited space and resources. As a

409 consequence, competition between individuals likely increased. European catfish have been reported
410 to actively defend their access to resources (Cucherousset et al., 2018) and have been shown to expend
411 more energy when in contact with conspecifics in preferred areas of habitat (Slavík & Horký, 2009).
412 This could give advantage to the biggest individuals. High body mass was also shown to decrease
413 stress from limited availability of resources (Slavík et al., 2016) which could explain why the smallest
414 individuals were more active and further from the shore than the biggest during the anoxic event.
415 Catfish aggregation, that can be compared to a school, led to a high oxygen consumption. According
416 to the position in this school, in front of the inflow current or in the rear of the school, DOC can vary a
417 lot so that some individuals need to change position leading to a reshuffle (Domenici et al., 2002;
418 Herbert & Steffensen, 2006). The largest catfish, dominant, could occupy the most suitable positions,
419 while the smallest individuals would be left with the least favourable ones and would then move much
420 more often to change position toward better-oxygenated areas in the aggregation.
421 Remarkably, the synchronisation they showed to join the refuge place contrasted with the time needed
422 for all individuals to definitively leave the location. This would also need further investigations.

423

424 Hypoxic conditions are likely to become more frequent and severe with temperature rising and
425 increasing eutrophication of ecosystems due to human activities. Aside temperature, DOC is a key
426 environmental parameter driving space use by fish population. The ability of catfish to withstand very
427 low DOC, along with its high optimum temperature range, could lead to an extent of the suitable
428 geographical range for this species in the future. This is important to account for when engaged in
429 conservation or fisheries management.

430

431 **Figure captions**

432 **Fig1** Bathymetric map of « Etang des Aulnes » at the water level of 11.14 m above sea level and
433 experimental setup. Acoustic receivers and their associated synchronising tags are represented by
434 white dots. Reference tags are symbolised by white squares. Monthly (and also hourly for location 42)
435 temperature and dissolved oxygen concentration profiles are located by crosses; location 42 is the

436 deepest in the lake. One primary canal flows into the lake on the eastern bank at location 91 and a
437 secondary one on the northern bank close to location 0. The lake outflows in a canal at its extreme
438 south-west

439

440 **Fig2** Catfish mean speed and surface DOC during the summer period (from 1st August to 30
441 September 2019). Panel a: hourly surface DOC (in mg/L at 3.5 m above the bottom at the deepest
442 point of the lake, 5.5 m depth). Panel b: mean hourly speed over all individuals (in m/h). The dates of
443 structural changes over the 2-month time series and their 95% confidence interval are labelled on the
444 x-axis and represented by vertical dotted lines and interval at their basis. Hereafter, dates are given in
445 the format mm-dd hh. These dates and associated 95% confidence interval are 08-27 23 [08-16 10 ;
446 08-28 09], 09-06 06 [09-06 02 ; 09-08 06] and 09-18 17 [09-17 08 ; 09-21 04] for mean speed, and 08-
447 12 00 [08-11 05 ; 08-12 19], 08-28 03 [08-28 01 ; 08-28 04], 09-06 06 [09-06 00 ; 09-06 10], 09-18 16
448 [09-18 07 ; 09-19 04] for surface DOC. In addition, the dates of structural changes of mean speed time
449 series within the period 08-27 23 to 09-06 06, comprising the anoxia, are labelled above the panel and
450 represented by dashed vertical lines and associated 95% confidence interval at their basis

451

452 **Fig3** Catfish daily space use during the hypoxic period (from 28 August to 6 September 2019). Panel
453 a: mean daily DOC (at 1.5, 2.5 and 3.5 m above the bottom in dotted, dashed and solid line
454 respectively) at the deepest point in the lake, 5.5 m deep. In panels b, c and d, the boxplots represent
455 the minimum, the first quartile, the median, the third quartile and the maximum of the distribution. In
456 panels b, c and d, the dotted, dashed and solid lines represent the daily means over small, medium and
457 large catfish respectively. Panel b: distribution of mean daily individual speeds (m/h). Panel c:
458 distribution of mean individual daily distances to all others. Panel d: distribution of mean individual
459 daily distances to shore (m). Panel e: distribution of individual home ranges 95% (hectares). Panel f:
460 distribution of individual home ranges 50% (hectares). Letters above the boxplots stand for post-hoc
461 comparisons between days: days which share a same letter have distributions which do not
462 significantly differ (at the 5% significance level). Letters below the boxplots stand for comparisons
463 between sizes within a day; no letter means the three sizes do not differ; sizes that share the same letter

464 do not significantly differ (within a day, letters from left to right correspond to small, medium and
465 large catfish, respectively). As the interaction between size and day was not significant for distance to
466 shore, the comparison between sizes within a day has not been performed

467

468 **Fig4** Catfish home ranges during the hypoxic period (from 28 August to 6 September 2019). The
469 home range 95% and the core area (home range 50%) are mapped in pale grey with a dotted contour
470 and in grey with a solid contour, respectively. They have been calculated with all pooled individuals
471 over different grouping days brought out from figures 3e and 3f. Panel a stands for days 08-28 and 08-
472 29, b for day 08-30 when the activity was the highest, c for days 08-31 and 09-01 when the activity
473 was the lowest, d for day 09-02 when fish recovered their activity and e for days 09-03 to 09-06. The
474 corresponding areas (in hectares) are given in each panel

475

476 **Fig5** Vertical profile of DOC at different locations in the pond on 09-04. The labels of the legend
477 correspond to the different locations labelled on the lake map and symbolised by a cross. Data go from
478 the surface to approximately 0.5 m above the bottom. Points 91 and 93 are located near the main
479 inflow and point 11 is the closest to the outflow

480

481 [Supplementary Information](#)

482 **Online Resource 1** Video of catfish movements over 25 August - 6 September 2019

483 **Online Resource 2** Environmental conditions during the summer period (from 1st August to 30
484 September 2019)

485 **Online Resource 3** Catfish mean speed and DOC during the summer period (from 1st August to 30
486 September 2019)

487

488 [Author contributions](#)

489 S.W. designed the study and analysed the data. S.W. and S.B. wrote the paper. F.S. designed the paper
490 with S.W. and S.B., carefully read it and made substantial improvements.

491

492 **Significance statement**

493 Hypoxic events have always naturally occurred in freshwater ecosystems but are worsening due to
494 anthropogenic activities. Fish response to hypoxia are difficult to observe and quantify in nature for
495 very large species. We observed that subadult and adult European catfish (40 individuals, 0.7 – 2.3m
496 length) could resist to such a stress without any alteration in their behaviour down to 1.3 mg/L of
497 dissolved oxygen concentration in summer conditions. Below this threshold, they enhanced their
498 speed and the surface area they visited which led them to aggregate in a more oxygenated refuge zone.
499 They all survived this severe event which strenghtens their capacity to cope with global change.

500

501 **Declarations**

502 **Conflicts of interests**

503 The authors declare they have no conflicts of interest.

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506 **Ethics**

507 The care and use of experimental animals complied with French animal welfare laws, guidelines and
508 policies as approved by the French Ministry of Research through the authorisation number
509 APAFIS#11294-2017091809143058 v2.

510

511 **Data availability**

512 The datasets analysed during the current study are available from the corresponding author on
513 reasonable request.

514 **References**

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693

694 Tables

695

696 **Table 1** Total length (in mm, mean, sd in italics and range) and weight (in g, mean, sd in
697 italics and range) of all 40 tracked catfish, 9 smallest, 24 medium and 7 largest ones.

	Total length (mm)	Weight (g)
All 40 individuals	1 033 (<i>328</i>) [727 ; 2 150]	9 658 (<i>13 389</i>) [2 301 ; 64 380]

9 smallest individuals	812 (41) [727 ; 847]	3 370 (688) [2 301 ; 4 180]
24 medium individuals	944 (63) [855 ; 1 060]	5 563 (1 065) [3 760 ; 7 680]
7 largest individuals	1 623 (423) [1 100 ; 2 150]	31 786 (22 494) [8 380 ; 64 380]

699 **Table 2** Numeric results from the Generalized Linear Mixed-Effects Model that tested the
700 fixed effects of fish size, day and their interactions on mean individual daily speed (panel a),
701 mean individual distance to shore (panel b), individual home ranges 95% (panel c) and
702 individual core areas (panel d). Fish identity was used as a random effect.

Daily speed a			
	d.f.	F	p-value
Size	2	1.301	0.274
Day	9	12.083	< 0.001
Size: Day	18	3.897	< 0.001
Individual	16.26	0.79	0.004
Explained variance (%)	56.6		
Distance to shore b			
	d.f.	F	p-value
Size	2	3.163	0.043
Day	9	29.599	< 0.001
Size: Day	18	1.199	0.260
Individual	24.1	1.88	< 0.001
Explained variance (%)	59.6		
Home range 95% c			
	d.f.	F	p-value
Size	2	4.689	0.010
Day	9	11.069	< 0.001
Size: Day	18	2.517	< 0.001
Individual	6.887	1.88	0.207
Explained variance (%)	53.7		
Core area d			
	d.f.	F	p-value
Size	2	2.824	0.061
Day	9	11.984	< 0.001
Size: Day	18	2.963	< 0.001

Individual	15.67	0.712	0.001
Explained variance (%)	49.9		

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