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

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Abstract

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

Key Words

Aggregation, escape response, fish, hypoxia, lake

Introduction

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

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

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

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

Material and methods

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

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 ($2x1.25x0.5$ m^3) filled with

178   regularly changed lake water to check their condition. Fish were then individually anesthetised, which

179   took 5-6 minutes, by immersion in a smooth and smaller tank $1.8x0.5x0.7$ m^3 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   ($2\times1.25\times0.5$ 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

Space use metrics

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

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

Statistical analyses

We applied an algorithm to detect possible breakpoints corresponding to structural changes in the 2-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:

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

265

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(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

Results

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

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, χ^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

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

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

Catfish tolerance to low DOC

All the 40 tagged catfish survived the severe hypoxic event that lasted more than two days and led to

the death of lots of other fish, including species known to manage very well with low oxygen

conditions such as carp and eel (Weber et al., 1976; Gesser, 1977). Subadult and adult European

catfish could go through very low oxygen conditions during the summer when water temperatures

ranged in 23-27 °C. Their behaviour was impacted only when, at the deepest point in the lake, the

lower half of the water column was anoxic and when DOC dropped down to 1.3 mg/L (corresponding

to a mean DOS of 16%) in the upper half. This DOC value was in the lower range of what Daněk et al.

(2014) found on juvenile catfish, 1.3-2.4 mg/L in winter conditions (water temperature around 5 °C).

It was in the range of Massabuau & Forgue (1995) laboratory results which concluded that very young

catfish (weighing 100-150 g) could maintain dioxygen homeostasis in 1-1.5 mg/L DOC range at 13°C

and even very probably in a 10-23 °C temperature range. However, increased temperature lessens

oxygen solubility and thus reduces oxygen supply for ichtyofauna; it also elevates basal oxygen

demand (Rogers et al., 2016). With comparable critical DOC but higher temperature, we can thus

reasonably hypothesise that oxygen supply was more critical in our study. The possible lower critical

oxygen threshold in our study could be explained by large differences in catfish body weights between

studies. Large fish could have an advantage thanks to their lower mass-specific metabolic rate

(Nilsson & Östlund-Nilsson, 2008). These tolerance values were in all cases much lower than the limit

of 3-3.5 mg/L reported by Mihalik (1995).

373

Catfish behaviour in response to the hypoxia extent

Horizontal catfish movements were not altered when anoxia was limited to the half lower part of the

lake. However, these extreme conditions are likely to considerably reduce the suitable habitats

regarding oxygen conditions in this shallow lake, by the way compressing fish habitat (Kraus et al.,

2015). The tags did not record the pressure and thus could not provide information on fish depth.

Nevertheless, we could suppose that catfish rose to the surface layer to find tolerable DOC, while they

are known to mainly occupy benthic habitats (Bruton, 1996; Cucherousset et al., 2018). This remains

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

Aggregation and refuge location

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

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

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

Significance statement

Hypoxic events have always naturally occurred in freshwater ecosystems but are worsening due to

anthropogenic activities. Fish response to hypoxia are difficult to observe and quantify in nature for

very large species. We observed that subadult and adult European catfish (40 individuals, 0.7 – 2.3m

length) could resist to such a stress without any alteration in their behaviour down to 1.3 mg/L of

dissolved oxygen concentration in summer conditions. Below this threshold, they enhanced their

speed and the surface area they visited which led them to aggregate in a more oxygenated refuge zone.

They all survived this severe event which strenghtens their capacity to cope with global change.

Declarations

Conflicts of interests

The authors declare they have no conflicts of interest.

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Ethics

The care and use of experimental animals complied with French animal welfare laws, guidelines and

policies as approved by the French Ministry of Research through the authorisation number

APAFIS#11294-2017091809143058 v2.

Data availability

The datasets analysed during the current study are available from the corresponding author on

reasonable request.

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Tables

Table 1 Total length (in mm, mean, sd in italics and range) and weight (in g, mean, sd in 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 *(328)* [727 ; 2 150]	9 658 *(13 389)* [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]

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Table 2 Numeric results from the Generalized Linear Mixed-Effects Model that tested the

fixed effects of fish size, day and their interactions on mean individual daily speed (panel a),

mean individual distance to shore (panel b), individual home ranges 95% (panel c) and

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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