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

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

In an experiment set up to assess the space use and activity cycles of the European catfish, 40 large individuals (subadults and adults whose body length ranged in 727 - 2150 mm) have been tracked by acoustic telemetry for three years in a 104-ha shallow eutrophic lake located in South-Eastern France. Within this period, the lake experienced a severe hypoxia, leading to the mortality of many fish from different species, including carp, eel and some small European catfish. However, fourteen months later, our telemetry tracking data revealed that all the 40 tagged catfish were still alive. Therefore, we aimed to analyse how large European catfish individuals could have resisted to hypoxia in natural conditions. More specifically, we examined how telemetry data could provide valuable information to highlight catfish individual tolerance and behaviour changes in response to hypoxia depending on catfish body size.

Material and methods

Study site

“Etang des Aulnes” is a shallow natural lake, mean depth 3.8 m, maximum depth 6 m, 104 ha area, located in South-Eastern France in a protected natural area. A primary canal and a secondary one collect irrigation waters that feed the lake. The lake then outflows in another canal (Figure 1). The lake water residence time is 300 days. The outflow is regulated to get high water levels in winter and low water levels in summer (maximal difference of 0.6 m).

The fish assemblage, determined by fyke nets, fishing traps and electro fishing in October 2017, 2018 and 2019 was composed of 16 species. The most dominant species were bream (*Abramis brama*, relative abundance 65%), European perch (*Perca fluviatilis*, 13%), pumpkinseed (*Lepomis gibbosus*, 8%), tench (*Tinca tinca*, 4%), pikeperch (*Sander lucioperca*, 4%), European catfish (*Silurus glanis*, 3%) and Northern pike (*Esox lucius*, 2%). In addition, two crayfishes were present: *Procambarus clarkii* and *Faxonius limosus*. Fishing is allowed but only during daytime from the eastern bank of the lake and no other activity is authorised.

Physical and chemical lake conditions

Hourly vertical profiles of water temperature (0.5, 3 and 5 m above the bottom) and dissolved oxygen concentration (DOC) (0.5, 1.5, 2.5 and 3.5 m above the bottom) were recorded at the deepest point in the lake (location 42 on Figure 1). HOBO data loggers U22 were used for temperature and U26 for DOC. The dissolved oxygen saturation rate (DOS) was calculated from DOC and temperature values. At 0.5 m above the bottom, there were no records from 09-02 03:00 to 09-04 12:00, because of a sensor failure. 0.5-1.5 m, 2.5-3 m and 3.5-5 m heights of measurements above the bottom are named bottom, middle and surface, respectively, in the following text. In addition, vertical profiles of temperature and DOC were recorded on 09-04 with a YSI Exo2 multiparameter sonde at different locations in the lake to get a spatial picture of what happened all over the lake at different depths (Figure 1).

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

Fish tagging

A total of 40 European catfish were caught by fyke nets, angling or electrofishing over two sampling campaigns: 10 in October 2017 and 30 in October 2018. Different techniques were used to sample the whole range of sizes among subadults and adults and individual behaviours (Harkonen et al., 2016). Once captured, catfish were stocked for a few hours in large aerated basins (2x1.25x0.5 m^3) filled with regularly changed lake water to check their condition. Fish were then individually anesthetised, which took 5-6 minutes, by immersion in a smooth and smaller tank 1.8x0.5x0.7 m^3 containing an aerated solution of benzocaine (80 mg/L). Once the fish had lost its balance (ventral side up), did not respond to stimuli anymore and had a very slow and steady operculum rate, it was weighed, measured and placed ventral side up in an identical tank containing an aerated solution of benzocaine (40 mg/L) to irrigate the gills during surgery. A 15 to 20 mm long incision was made with a scalpel in the middle of an imaginary line that would join the basis of the pectoral fin to the pelvic fin. An acoustic transmitter sterilised in surgical spirit and rinsed with physiological liquid was inserted into the peritoneal cavity. Vemco V13-1L acoustic transmitters (30.5 mm long, 9.2 g in the air, mean battery life 1825 days, 180 s - range 120-240s - mean burst interval for the 12 used in 2017 and 320 s - range 260-380s - in 2018) were used. The transmitter weight in the air did not exceed 2% of the fish body weight (Winter, 1996;

Snobl et al., 2015). The incision was closed using 2 to 3 simple surgical sutures (3-0 Polydioxanon resorbable monofilament) placed 5 mm apart. An antiseptic and antibiotic dressing was applied on the incision wound to help healing and limit the risk of infection. Two surgeons took turn every four fish to operate, one fish surgery taking 5-6 min. Fish were then put in large, aerated recovery basins (2x1.25x0.5 m^3), where they were continually observed until they recovered normal opercular activity, swimming ability, balance and behavioural response to stimuli, usually after 10 min. Fish spent 3 to 6 hours in this recovery basin before being released to their capture site. All individuals could be released in good shape.

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

Fish tracking

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

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).

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

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

The model could be written as follows:

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

where $\overline{\mathrm{METRICS}_{\mathrm{ind}}}$ is the expected daily mean individual speed, distance to the shore or home range, α is the overall intercept, SIZE is the size class (Table 1), s(ind) is a smoothing function modeling the individual effects (Wood, 2008), and "ε" is the error term following a normal distribution with zero mean. Means among days and among sizes by day were pairwise compared by using the *emmeans* R package (Lenth, 2016). The model fitting was assessed with regards to the homogeneity and normality of the residuals (Zuur et al., 2009) and to the percentage of explained variance (Hastie & Tibshirani, 1990). For mean individual distance to others, as we could not find a reliable model, we compared the distributions between days and between size classes among days by using Kruskal-Wallis tests and, if significantly different, we made pairwise comparisons by Fisher's least significant difference (R package *agricolae*, de Mendiburu, 2020).

All statistical analyses were made with R version 3.6.3 (R Core Team, 2020).

Results

DOC dynamics

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

DOC dynamics and fish activity

Several structural change points were found in the hourly mean speed and DOC time series (Figure 2). The corresponding dates for 2-month speed time series matched well those of surface DOC. Worthy of note, they did not match with dates of changes of deeper DOC (Online Resource 3). In the next, we focus on surface DOC.

The 08-27 23:00 to 09-06 06:00 period, that comprises the full anoxia, shows very large variations of hourly speed that appear different from the diel cycle that could be observed outside of this period (Figure 2b). Within this period, four subperiods were detected: at the beginning, fish activity appeared quite similar to the previous period; then, speed sharply increased for 32 hours before fish suddenly stopped and performed very few movements during one and a half day, after which they started to progressively move again. The surface DOC was different between all four speed subperiods (Kruskal-Wallis test, χ^2=94.010, 3 d.f., p<0.001): the surface DOC was 1.1 mg/L in average (DOS 13%) during the highest activity subperiod and 0.1 mg/L (DOS 1%) during the lowest. The daily analysis also showed that the speed increase (on 08-30) and decrease (on 08-31 and 09-01) were significant (Table 2a, Figure 3b). This enhanced activity corresponded to higher individual home ranges (Tables 2c, 2d, Figures 3e, 3f) and to larger areas visited by the pool of individuals (Figure 4b). Conversely, the home range 95% as well as the core area were considerably reduced when the activity was the lowest (Figures 3e, 3f) and most of individuals gathered in a tiny area (Figure 4c) where they aggregated (Figure 3d). On 09-02, when fish recovered their activity, the areas they travelled over were still reduced (Figure 3f) and nearby the area where they had aggregated (Figure 4d).

The highest activity subperiod started when surface DOC dropped down to 1.3 mg/L (DOS 16%) and ceased when the whole water column became anoxic. After the reduced activity subperiod, fish started to progressively move again when surface DOC raised up to 0.7 mg/L (DOS 8%) whereas the half lower of the water column was still anoxic (Online Resource 2).

Aggregation location and dynamics

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

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

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

Fish behaviour and size dependence

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

Discussion

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

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).

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

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

Figure captions

Fig1 Bathymetric map of « Etang des Aulnes » at the water level of 11.14 m above sea level and experimental setup. Acoustic receivers and their associated synchronising tags are represented by white dots. Reference tags are symbolised by white squares. Monthly (and also hourly for location 42) temperature and dissolved oxygen concentration profiles are located by crosses; location 42 is the deepest in the lake. One primary canal flows into the lake on the eastern bank at location 91 and a secondary one on the northern bank close to location 0. The lake outflows in a canal at its extreme south-west

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

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

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

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

Supplementary Information

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

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

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

Author contributions

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

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]

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		