

RESEARCH ARTICLE

Physostomous channel catfish, *Ictalurus punctatus*, modify swimming mode and buoyancy based on flow conditions

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ABSTRACT

The employment of gliding in aquatic animals as a means of conserving energy has been theoretically predicted and discussed for decades. Several studies have shown that some species glide, whereas others do not. Freshwater fish species that widely inhabit both lentic and lotic environments are thought to be able to adapt to fluctuating flow conditions in terms of locomotion. In adapting to the different functional demands of lentic and lotic environments on fish energetics, physostomous (open swim bladder) fish may optimise their locomotion and activity by controlling their net buoyancy; however, few buoyancy studies have been conducted on physostomous fish in the wild. We deployed accelerometers on free-ranging channel catfish, *Ictalurus punctatus*, in both lentic and lotic environments to quantify their swimming activity, and to determine their buoyancy condition preferences and whether gliding conserves energy. Individual comparisons of swimming efforts between ascent and descent phases revealed that all fish in the lentic environment had negative buoyancy. However, all individuals showed many descents without gliding phases, which was contrary to the behaviour predicted to minimise the cost of transport. The fact that significantly fewer gliding phases were observed in the lotic environment, together with the existence of neutrally buoyant fish, indicated that channel catfish seem to optimise their locomotion through buoyancy control based on flow conditions. The buoyancy optimisation of channel catfish relative to the flow conditions that they inhabit not only reflects differences in swimming behaviour but also provides new insights into the adaptation of physostome fish species to various freshwater environments.

KEY WORDS: Swimming behaviour, Gliding, Buoyancy, Physostome, Data logger, Accelerometry

INTRODUCTION

Some swimming animals exhibit undulating vertical movements, employing intermittent strokes and gliding, which utilise negative net buoyancy (Kramer and McLaughlin, 2001; Gleiss et al., 2011a). Weihs (1973) first proposed a theory describing energy savings in negatively buoyant fish. This theory raised questions of whether negative buoyancy would reduce the costs associated with animals moving through the water column, in turn resulting in reduced cost of transport. During the descent phase, negative buoyancy would reduce the cost of transport through powerless gliding. However, the

energy saved during these gliding phases would be countered by the subsequent ascent phase, because lifting the body against gravity requires extra energy (Miller et al., 2012). In pelagic fish (e.g. tuna and several shark species), undulating vertical movements might be related to energy savings, driven by the use of negative buoyancy when gliding during descents (Magnuson, 1973; Holland et al., 1990; Gleiss et al., 2011a,b). However, several studies concluded that some pelagic sharks with negative buoyancy primarily exhibited vertical movements when searching for prey, but that this was not associated with energy savings (Carey et al., 1990; Nakamura et al., 2011). Sato et al. (2013) reported that breath-hold divers, such as pinnipeds, optimise their horizontal movement under nearly neutral (neither negative nor positive) buoyancy conditions. Estimating buoyancy conditions, together with fine-scale behavioural data, could therefore provide valuable information about the behavioural strategies of aquatic animals.

Weihs' theory has been mainly examined in pelagic fish (Iosilevskii et al., 2012; Takagi et al., 2013). Vertical movement, however, is also observed in several freshwater physostome fish such as salmonids, silurids, sturgeons and anguillid eels (Clark and Levy, 1988; Mitamura et al., 2008; Watanabe et al., 2013, 2016). Compared with oceanic regions, freshwater systems are characterised by much shallower depths, more diverse aquatic ecosystems and highly variable environmental conditions (Helfman et al., 2009). However, Weihs' theory has not been researched in the context of lotic (flowing water) ecosystems. It has been assumed that freshwater fish in still water maintain neutral buoyancy, whereas those in swift streams use negative buoyancy to maintain their position on the bottom, with both strategies resulting in reduced energy expenditure (Saunders, 1965). Beecham et al. (2013) conducted a laboratory experiment, using an angled swimming chamber, to calculate energy saving in channel catfish, *Ictalurus punctatus* (Rafinesque 1818), during non-horizontal swimming. Compared with horizontal swimming, these measurements predicted that the most efficient energy savings would have a value of up to 43%, in combination with gliding descents and stroking ascents with pitch angles of -15 and 60 deg, respectively. The results suggested the possibility that freshwater fish species save energy by gliding. Based on Weihs' theory, which was examined in lentic (still water) habitats, it is possible that freshwater fish utilise different buoyancy conditions according to their surroundings in relation to locomotion energetics. Thus, the determination of an animal's buoyancy condition in lotic habitats would be expected to provide highly valuable information about the general principles of animal locomotion, as well as specific features concerning behavioural aspects of the studied species.

In freshwater systems, it is thought that animals must respond to the different functional demands of lentic and lotic environments, because the surrounding medium acts differently relative to their bodies. While animals in lentic habitats are able to utilise gravity to drive and assist their locomotion in a vertical direction, as

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illustrated by Weihs' theory, those in lotic habitats do not benefit from gravity. This is because they must compensate for the horizontal displacement caused by the flow of the surrounding medium by continuously moving their bodies. Thus, freshwater fish species that widely inhabit both lentic and lotic environments are thought to be able to adapt to fluctuating flow conditions in terms of employing efficient swimming strategies. Channel catfish are the most cultured freshwater fish species in North America (Hubert, 1999), and non-indigenous channel catfish are an invasive species in the waters of many countries (Elvira and Almodóvar, 2001; Copp et al., 2007; Katano et al., 2010), demonstrating their ability to adjust to a wide range of environments (Townsend and Winterbourn, 1992). Given the different functional demands imposed by the extent of flow, the species in each habitat should exhibit contrasting swimming patterns to optimise their locomotion, and would be expected to adopt different buoyancy conditions. In the present study, we deployed accelerometers on free-ranging channel catfish in both lentic and lotic environments in order to determine: (1) how these animals behave under different flow conditions, (2) their swimming performance during vertical movements and (3) their buoyancy condition preferences. We then aimed to illustrate how aquatic animals behave differently in various environments, and how and in which situations they either utilise or manage the external forces imposed by their surroundings, such as gravity and the flows of the surrounding medium itself.

MATERIALS AND METHODS

Study sites and animals

To compare swimming performance in channel catfish between lentic and lotic conditions, the behaviours of fish were recorded in three locations in Japan – Lake Kasumigaura (168.18 km², the second largest lake in Japan), the Yahagi River and the Tone River – during July 2012 and May 2015 (Table 1, Fig. 1). The observed average current speed during the sampling periods, which was measured at the surface of the centre of flow, was approximately 1 m s⁻¹ for the Tone River (Tonogawa-Karyu River Office, personal communication) and 0.7–1.2 m s⁻¹ for the Yahagi River (Toyohashi River Office, personal communication). Channel catfish were caught by trawling in Lake Kasumigaura, and long lines and hoop nets were used in the Yahagi River and the Tone River, respectively. We deployed data loggers on six, three and two individuals in Lake Kasumigaura, the Yahagi River and the Tone River, respectively (Table 1). The fish release and logger retrieval points are shown in Fig. 1.

Data loggers

To quantify the swimming behaviour of channel catfish, we used three types of accelerometer (ORI400-D3GT: 15 mm in diameter, 53 mm in length, 16 g in air; W190L-PD3GT or W190L-PD2GT: 21 mm in diameter, 117 mm in length, 60 g in air; Little Leonardo, Tokyo, Japan). D3GT-type loggers were used to record depth and temperature at 1 Hz and tri-axial acceleration at 10 or 20 Hz. PD3GT-type and PD2GT-type loggers were used to record swimming speed at 8 Hz, depth and temperature at 1 Hz, and acceleration along two (lateral and longitudinal) or three (lateral, longitudinal and dorsoventral) axes at 16 Hz. The maximum range of the depth sensors was 400 m with a resolution of 0.1 m for the D3GT loggers, and 190 m with a resolution of 0.046 m for the PD3GT and PD2GT loggers. Swimming speed through the water column was derived from the rotation of an external propeller with a resolution of 0.02 m s⁻¹, precision of ±0.01 m s⁻¹, accuracy of ±0.02 m s⁻¹, and a stall speed of 0.2 m s⁻¹. Of the 11 channel catfish examined, five were equipped with the D3GT loggers (2012–2014), five with the PD3GT loggers (2014) and one with the PD2GT logger (2015) (Table 1).

Data recovery

It is almost impossible to recapture channel catfish individuals, so we used an automatic time-scheduled release system (Watanabe et al., 2004) to retrieve the loggers. The data loggers were attached to small floats equipped with a VHF transmitter (MM130B; 16 mm diameter, 60 mm length, 20 g; Advanced Telemetry Systems, Inc., MN, USA) and a time-release mechanism (16 mm diameter, 25 mm length, 16 g; Little Leonardo). The floats were shaped to reduce drag, and provided just enough buoyancy to return the instrument package to the surface upon release. The complete package had 0.03–0.10 N of positive buoyancy (i.e. equivalent to 0.2–0.4% of the overall buoyancy of each fish) in freshwater.

Before deployment of the packages, each individual was lightly anaesthetised with 0.02% 2-phenoxyethanol solution, and measurements were taken of body mass (*M*), standard length (*L*) and/or total length. The condition factor (CF; Mitani, 1986; Gaylord and Gatlin, 2000) of each individual was calculated using the following equation:

$$CF = 1000 \times \frac{M}{L^3}. \quad (1)$$

The data logger packages were attached using a 1.5 mm-width plastic cable tie passed through a comparably sized hole pierced on the back of the fish (posterior to the dorsal fin); all procedures

Table 1. Descriptive information about the channel catfish used in the study

Fish ID	Study site	Habitat	Standard length (cm)	Body mass (g)	CF	Logger type	Release date	Record duration (h)	Depth (m) mean±s.d. (max.)	Water temperature (°C) mean±s.d.
K01	Kasumigaura	Lentic	49.0	2010	17.1	D3GT	12 May 2013	44.3	1.4±1.2 (10.2)	19.5±0.8
K02	Kasumigaura	Lentic	42.0	1240	16.7	D3GT	24 May 2013	99.5	1.3±0.9 (7.2)	22.3±0.9
K06	Kasumigaura	Lentic	58.0	3040	15.6	PD3GT	27 Jul 2014	66.2	2.2±1.2 (5.9)	29.5±0.4
K08	Kasumigaura	Lentic	59.1	3020	14.6	PD3GT	23 Aug 2014	47.2	3.3±1.2 (5.6)	29.2±0.5
K09	Kasumigaura	Lentic	55.8	2460	14.1	PD3GT	6 Sep 2014	8.8	1.0±0.9 (5.1)	26.0±0.2
K10	Kasumigaura	Lentic	55.8	2450	14.1	PD3GT	6 Sep 2014	87.8	4.3±1.6 (6.1)	24.8±0.4
Y04	Yahagi	Lotic	54.9 ^a	2380	14.4	D3GT	16 Oct 2012	98.5	2.1±0.7 (4.6)	18.1±0.5
Y06	Yahagi	Lotic	46.0	1520	15.6	D3GT	21 Aug 2013	64.1	1.1±0.9 (8.1)	26.7±0.8
Y08	Yahagi	Lotic	56.0	4160	23.7	PD3GT	5 Jun 2014	11.8	1.2±0.6 (6.9)	18.6±0.2
T02	Tone	Lotic	54.4	2425	15.1	D3GT	10 Sep 2014	46.4	4.7±1.9 (14.9)	22.4±0.2
T06	Tone	Lotic	50.0	2360	18.9	PD2GT	1 Jun 2015	74.0	3.6±1.5 (11.5)	24.1±0.3

^aEstimated value is shown because only total length was measured.

CF, condition factor.

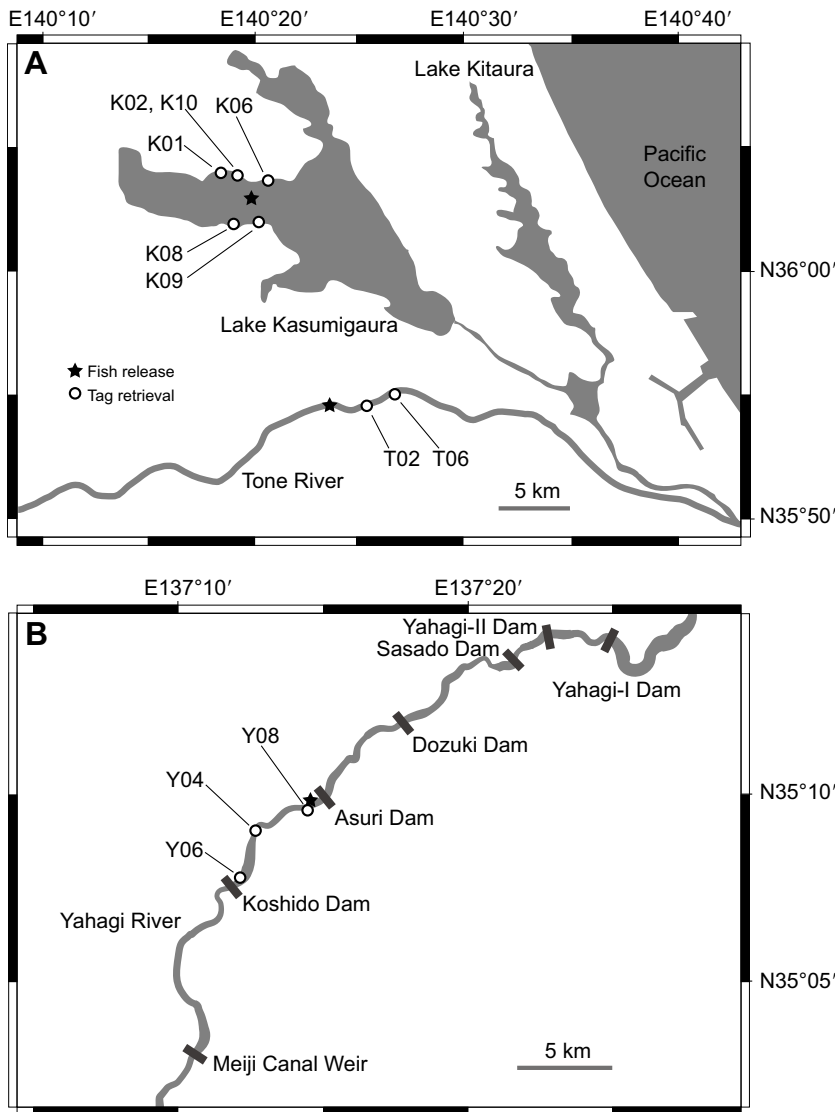


Fig. 1. Locations of fish release and tag retrieval. Maps of the studied sites in Lake Kasumigaura, Tone River (A), and Yahagi River (B) are shown. Black stars and open circles indicate the locations of fish release and tag retrieval, respectively.

typically took less than 5 min. After attaching the packages, each fish was retained in a tank for 20–30 min to recover from the anaesthesia. We observed the behaviour of channel catfish fitted with the loggers, and released them after they behaved in a manner similar to individuals with no attached package.

Data analyses

We used Igor Pro software (version 6.12; Wave Metrics, Inc., OR, USA) to analyse the behavioural data downloaded from the loggers. Recorded acceleration data included both low-frequency gravity components (caused by an individual's changing pitch angle) and high-frequency specific components (mainly caused by dynamic movements, such as tail beating). We used a filter at a threshold frequency, individual to each fish, defined by a power spectral density plot and a continuous wavelet transform filter contained in the Ethographer software (version 2.0.1; Sakamoto et al., 2009), to create a low- and a high-frequency signal. We calculated the pitch angle of channel catfish based on the low-frequency component of acceleration. The data logger was not always attached parallel to the animal's longitudinal axis, so we calibrated the attachment angle based on the relationship between the vertical speed and pitch angle measurements obtained by the accelerometer (Kawatsu et al., 2010).

Negative pitch values indicated that the individual had a head-downward posture. Using the sum of the absolute values of the high-frequency dynamic acceleration component along three or two axes, we calculated the overall dynamic body acceleration (ODBA; Wilson et al., 2006) or the partial dynamic body acceleration (PDBA; Halsey et al., 2009) values as indicators of an individual's swimming effort (Gleiss et al., 2010), respectively. We extracted stroking movements from the high-frequency acceleration data based on the set threshold value for each fish ($0.10\text{--}0.32\text{ m s}^{-2}$). Moreover, we assumed that the bottom phase (i.e. time spent on the bottom of the body of water) without any stroking was the resting period, indicating resting behaviour. The gliding period was defined as vertical movement without any stroking that lasted longer than 1 s.

To facilitate the analyses, we extracted bottom phases in which the durations were longer than 1 min, as well as ascents and descents during which depth changes were greater than 1 m. We also calculated the rest rate as the ratio of the total duration of the bottom phase to the total recording time for each individual.

We obtained swimming speed data only from individuals that were equipped with the PD3GT or PD2GT loggers, so the swim speed (for all individuals) during vertical movement was estimated from pitch angle and the rate of change in depth for each second,

using simple trigonometry (Miller et al., 2004). Swim speed was estimated during vertical movement in which pitch angle was greater than 30 deg.

To obtain information about the buoyancy conditions of each fish, the swimming effort (ODBA or PDBA) between ascent and descent was compared for each individual using a Mann–Whitney *U*-test. In addition, the effort ratio (descent swimming to ascent swimming effort) was calculated to compare the swimming effort of each individual during ascent and descent. Swimming depth should affect the buoyancy condition of fish in the form of water pressure, so the depth distribution of gliding ascents and descents were analysed. A generalised linear mixed model (GLMM) with a binomial distribution and a logit link function was used to evaluate the glide occurrence (proportion of gliding ascent/descent to all ascents/descents in number) during the ascent and descent phases. Glide occurrence for each depth was set as the response variable, and four factors – depth, index of habitat (or study site), index of ascent/descent and CF – were set as candidate explanatory variables. To avoid problems owing to co-linearity between habitat type and the source river of the fish, index of habitat and that of study site were not included simultaneously in models. Individual was set as a random effect. We calculated an Akaike's information criterion (AIC) and selected the model with the lowest AIC value as the most parsimonious model. We used the glmmML package in R software (version 3.1.2; <http://www.R-project.org/>) for statistical analyses. Values are presented as means±s.d., and $P<0.05$ indicates statistically significant differences.

Measurement of body density and swim bladder volume

Sixteen fish (mass range: 50–2150 g, standard length 15.5–48.6 cm) caught in Lake Kasumigaura and 10 fish (mass range: 95–1325 g, standard length 19.4–47.0 cm) caught in the Tone River were subsequently euthanised using 2-phenoxyethanol, and then transported to the Atmosphere and Ocean Research Institute at the University of Tokyo. The abdomen of each fish was opened, gas was removed from the swim bladder, and the body density of each fish was measured. The euthanised fish sank in seawater, so we therefore added salt to the seawater until the fish became neutrally buoyant, and we then measured the water density (equivalent to the fish density) using a gravimeter. The differences in body density between lentic and lotic individuals, as well as the differences between males and females, were determined using a Mann–Whitney *U*-test. The correlations between body density and standard length, body mass and CF were examined using a Spearman's correlation test.

We also measured the maximum swim bladder volumes of three fish (mass range: 995–1850 g, standard length 39.5–47.6 cm) caught in the Tone River. The swim bladder was first removed from the surrounding tissues. The volume of the swim bladder was obtained using the difference in mass before and after filling the swim bladder with freshwater. We estimated the body volume of each individual using the measured body mass and the body density obtained in this study.

Ethics statement

All experimental procedures were covered by an Atmosphere and Ocean Research Institute animal experiment project licence (P14-4) held by K.S., and were under the ethical approval of the Animal Ethics Committee of the University of Tokyo. We captured, transported and reared channel catfish in accordance with the Invasive Alien Species Act, under a licence (14000345) from the Ministry of the Environment.

RESULTS

We collected a total of 649 h of behavioural data from six, three and two individuals in Lake Kasumigaura, the Yahagi River and the Tone River, respectively (Table 1). There was no heavy rainfall in the studied area and no flooding in the rivers during the recording period. The maximum distance between the fish-release and tag-retrieval points was approximately 2 km in Lake Kasumigaura, and 4 km in both the Yahagi (fish Y04) and Tone Rivers (fish T06; Fig. 1). The water temperature that animals experienced ranged from 18.2 to 29.0°C, varying between different seasons and study sites (Table 1).

Fig. 2 shows typical vertical movement patterns exhibited by channel catfish in both lentic and lotic environments. In both lentic and lotic environments, they displayed frequent vertical movements with intermittent bottom phases. The mean depths at which the vertical movements were observed were 1.0–4.3, 1.1–2.1 and 3.6–4.7 m in Lake Kasumigaura, the Yahagi River and the Tone River, respectively (Table 1). Depth change during vertical movements was 1.8 ± 0.3 m for ascents and 1.8 ± 0.4 m for descents. Vertical movements were observed during the day and night in all 11 individuals.

Gliding phases were often observed during the descending movements of fish in the lentic environment (e.g. Fig. 2C), but few instances were observed during ascents or when fish were in the lotic environment (Fig. 3A, Table 2). Among the six individuals observed in lentic conditions, four individuals exhibited longer glides during descent than during ascent (Mann–Whitney *U*-test: $P<0.05$ for fish K01, K06 and K09; $P<0.001$ for fish K08; Table 2). Another individual (fish K10) showed no significant difference in glide duration between descent and ascent (Mann–Whitney *U*-test: $U=3271.5$, $N=160$, $P=0.72$), and the remaining individual (fish K02) only glided during descents. In contrast, among the five individuals observed in lotic conditions, only one individual (fish T02) showed longer glides during descent than ascent (Mann–Whitney *U*-test: $U=1438.5$, $N=99$, $P<0.001$), but there were no significant differences between descent and ascent for three individuals (Mann–Whitney *U*-test: $P>0.05$ for fish Y06, Y08 and T06). Moreover, the remaining individual (fish Y04) only displayed a single glide both during ascent and descent.

As seen in the glide occurrence for each depth (Fig. 3B), both ascents and descents of all the examined channel catfish were often accompanied by active tail beats (e.g. Fig. 2D). The pitch angle, swim speed and swimming effort during vertical movements in which stroking lasted longer than 5 s are summarised in Table 2. The absolute value of the pitch angle during vertical movements varied between individuals, and the ranges for ascents and descents were 16.6–35.2 and 8.0–24.1 deg, respectively. There was no significant difference between lentic and lotic individuals in ascent/descent pitch angle (Mann–Whitney *U*-test: $U=21$, $N=11$, $P=0.33$ for ascent; and $U=16$, $N=11$, $P=0.93$ for descent; Fig. 4A). Swimming speed during vertical movements also varied between individuals, and the range for ascents and descents was 0.16–0.34 and 0.16–0.42 m s⁻¹, respectively (Table 2). There was no significant difference between lentic and lotic individuals in ascent/descent speed (Mann–Whitney *U*-test: $U=21$, $N=11$, $P=0.31$ for ascent; and $U=17.5$, $N=11$, $P=0.71$ for descent; Fig. 4B). Based on a comparison of swimming effort for each individual, all six individuals studied in the lentic environment showed significantly less activity during descents than ascents (Mann–Whitney *U*-test; $P<0.001$ for fish K01, K02, K06, K08, K09 and K10; Table 2). In contrast, of the five individuals studied in the lotic environment, two individuals (fish Y06 and T02) showed

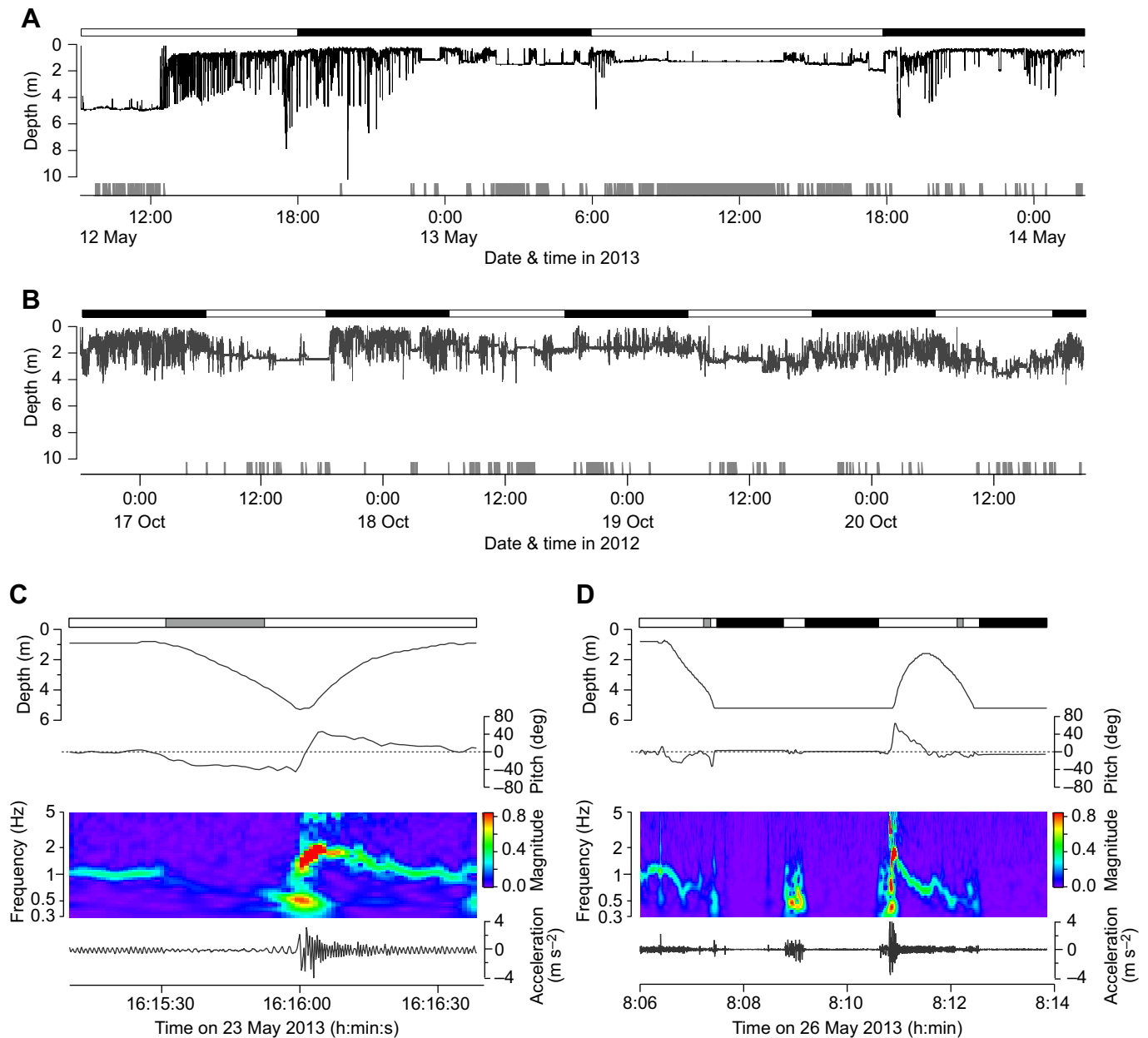


Fig. 2. Swimming performance of channel catfish during vertical movements and resting periods. (A,B) Time-series depth data obtained from an individual in lentic (upper panel; individual K01) and lotic environments (lower panel; individual Y04) are shown. Black and white bars above the time-series depth indicate night and day, respectively. Grey bars above the time axes show the resting periods of each individual. (C,D) Time series showing depth, pitch and swaying acceleration caused by tail beats, and a wavelet spectrogram of the swaying acceleration during the recording period for a single channel catfish (K02). The bars above the graph show swimming periods with tail beats (white), gliding periods (grey), and resting periods (black). Warmer colours in the spectrogram represent stronger signals, whereas cooler colours represent weaker signals. There is a lack of a strong signal in the spectrogram, which indicates the individual was gliding during descent (C,D) or resting at the bottom (D).

significantly lower swimming effort during descents compared with ascents (Mann–Whitney U -test: $P < 0.001$ for fish Y06 and T02; Table 2). Two other individuals (fish Y04 and T06) exhibited significantly higher swimming efforts during descents compared with ascents (Mann–Whitney U -test: $P < 0.01$ for fish Y04, and $P < 0.001$ for fish T06), and the remaining individual (fish Y08) showed no significant difference between swimming efforts during ascents and descents (Mann–Whitney U -test: $P = 0.96$; Table 2). The effort ratios of descent swimming effort to ascent swimming effort were 0.58–0.66 for lentic individuals and 0.66–1.26 for lotic individuals (Table 2), and the effort ratio was significantly lower in

lentic than in lotic individuals (Mann–Whitney U -test: $U = 1.5$, $N = 11$, $P = 0.008$; Fig. 4C).

A GLMM revealed that glide occurrence was affected by depth, ascent/descent phase, CF and habitat (or study site) (Table 3). Glide occurrence was higher in Lake Kasumigaura (lentic habitat) than in the Tone and Yahagi Rivers (lotic habitat), and during descent than during ascent. Glide occurrence increased at deeper depths, and individuals with greater CF (i.e. with denser bodies) glided more frequently.

The tail beats of catfish were very weak or almost non-existent when the fish remained at a certain depth for several minutes (Fig. 2D), which implied they were resting at the bottom of the

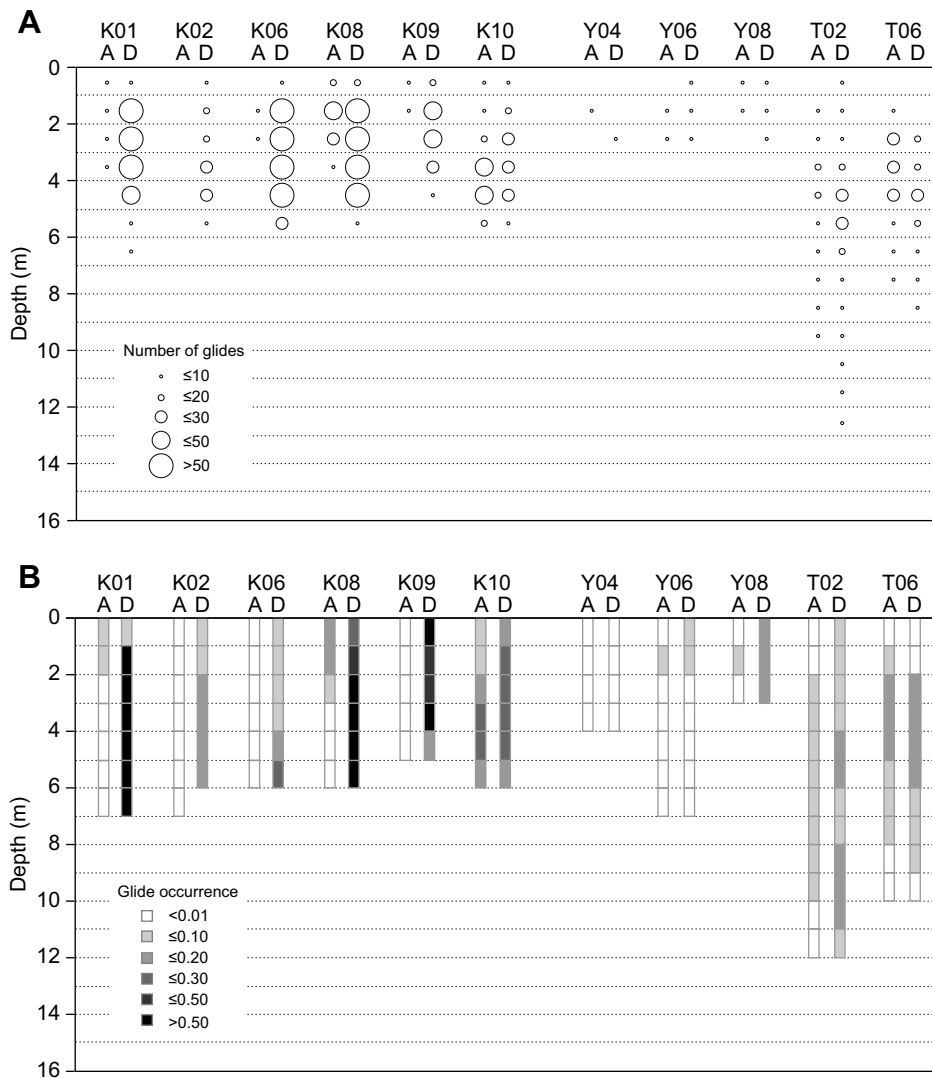


Fig. 3. Depth distribution of channel catfish during gliding periods. (A) Bubble charts show the depth distribution of each individual during gliding ascents and descents (A and D, respectively). The number of glides for each 1 m depth is shown as open circles of increasing size. (B) The colour of each box shows the glide occurrence (the proportion of the number of gliding ascents/descents to total number of ascents/descents) for each 1 m depth.

river/lake. The median duration of bottom phases for lentic and lotic environments was 88–190 and 80–96 s, respectively, whereas the maximum duration was 14.2–416 and 6.4–40.3 min, respectively (Table 4). The rest rate of the time spent in the bottom phase to the total recorded period was 0.07–0.74 and 0.07–0.35 for lentic and lotic individuals, respectively (Table 4).

The net body density of channel catfish after swim bladder removal ranged from 1054 to 1088 kg m⁻³ (mean±s.d., 1078±8 kg m⁻³, *N*=26; Table S1). Body density did not differ between lentic and lotic individuals (Mann–Whitney *U*-test: *U*=26.5, *N*=26, *P*=0.94) or between sexes (Mann–Whitney *U*-test: *U*=26.5, *N*=26, *P*=0.94). Nor was it significantly correlated with the standard length (Spearman's correlation: *r*_S=−0.10, *P*=0.62) or body mass (Spearman's correlation: *r*_S=−0.11, *P*=0.59; Fig. S1) of the fish. However, there was a significant negative correlation between body density and CF (Spearman's correlation: *r*_S=−0.46, *P*=0.017; Fig. S1). The range of the maximum swim bladder volume was 62–100 cm³, and the percent by volume range of the swim bladder to the body was 5.8–9.3% (Table S1).

DISCUSSION

The proportion of time channel catfish spent in different swimming modes varied greatly between the three study sites. This suggested that adaptation to a specific habitat comes in the form of active

regulation of behaviour. Individuals in Lake Kasumigaura experienced lentic conditions for the entire recording period, whereas individuals in the Yahagi and Tone Rivers experienced lotic conditions. Channel catfish in Lake Kasumigaura displayed a greater number of glides during descents compared with ascents, whereas those in the Yahagi and Tone Rivers exhibited similar numbers of ascending and descending glides (Fig. 3A). Prior to this study, we conducted telemetry tracking of a single channel catfish in the Yahagi River. This showed that the fish moved 8 km downstream within 6 h (M.A.Y., unpublished data), with an average net displacement rate along the stream of approximately 1.3 km h⁻¹. In contrast, the maximum distance travelled in the present study was 4 km, covered by the two longest-tracked fish within 74.0 and 98.5 h (T06 and Y04, respectively), which indicated that there was also little bias for upstream/downstream movement in both rivers. In order to avoid displacement, fish in a flow have to oscillate their fins or bodies to maintain their position, regardless of their buoyancy condition. Thus, the similar ratio of ascending to descending glides may be a common feature of locomotion in lotic habitats.

The frequency of glide occurrence seemed to differ between the two rivers, which could be a consequence of both geographical and morphological factors. The Tone River is deeper than the Yahagi River. Considering fish swimming at different depths, as a fish moves deeper, its buoyancy decreases according to the increased

Table 2. Summary statistics for vertical movements with stroking (>5 s) and gliding of channel catfish

Fish ID	Stroking behaviour						Gliding behaviour							
	N		Pitch angle (deg)		Swim speed (m s ⁻¹)		ODBA or PDBA (m s ⁻²)		Effort ratio		N		Mean duration (s)	
	Ascent	Descent	Ascent	Descent	Ascent	Descent	Ascent	Descent	Ascent	Descent	Ascent	Descent	Ascent	Descent
Lentic														
K01	188	143	21.8±6.4	-8.0±5.3	0.34±0.13	0.42±0.18	1.77±0.76	1.03±0.77***	0.58		3	188	2.6±0.8	4.9±2.2*
K02	283	226	23.6±7.3	-20.4±6.6	0.22±0.07	0.24±0.09	0.89±0.37	0.58±0.29***	0.66		0	60	—	3.4±0.7
K06	1064	1131	18.0±7.5	-11.2±5.3	0.33±0.14	0.33±0.09	1.21±0.37	0.74±0.42***	0.61		2	196	2.7±0.6	4.2±1.3*
K08	469	191	34.3±10.6	-9.5±7.5	0.31±0.11	0.16±0.12	1.35±0.69	0.87±0.90***	0.64		52	241	3.7±1.0	6.1±3.9***
K09	193	87	35.2±9.7	-17.4±7.5	0.22±0.09	0.27±0.07	1.14±0.64	0.75±1.39***	0.66		2	80	2.5±0.6	4.1±1.3*
K10	249	181	18.9±16.7	-9.1±4.9	0.16±0.10	0.17±0.10	1.24±1.25	0.82±0.64***	0.66		88	72	3.9±1.5	3.9±1.5 ^{n.s.}
Mean			23.9±12.0	-12.2±7.0	0.26±0.08	0.22±0.05							3.8±1.4	4.8±2.7
Lotic														
Y04	136	159	24.2±10.9	-16.4±7.9	0.21±0.08	0.20±0.07	0.64±0.24	0.74±0.39**	1.16		1	1	3.8	2.5
Y06	240	265	21.0±10.9	-8.2±8.4	0.29±0.13	0.30±0.16	3.31±1.63	2.63±2.09***	0.80		2	8	3.9±2.5	2.5±0.6 ^{n.s.}
Y08	26	23	22.9±13.6	-24.1±11.7	0.18±0.13	0.19±0.08	0.79±0.57	0.68±0.31 ^{n.s.}	0.87		2	5	4.1±2.7	3.8±1.4 ^{n.s.}
T02	468	420	16.6±7.8	-17.9±7.6	0.24±0.09	0.28±0.10	1.65±0.61	1.10±0.33***	0.66		28	71	3.3±0.8	4.5±2.1***
T06	322	252	16.8±12.2	-7.4±8.7	0.17±0.11	0.16±0.11	0.67±0.43	0.84±0.58***	1.26		70	57	3.7±1.1	3.6±1.3 ^{n.s.}
Mean			18.5±10.6	-13.2±9.6	0.26±0.10	0.23±0.06							3.6±1.1	4.0±1.8
Grand mean			22.1±11.8	-12.6±8.2	0.24±0.12	0.21±0.11								

Asterisks indicate a significant difference between the ascent and descent phase: * $P<0.05$; ** $P<0.01$; *** $P<0.001$; n.s., not significant. ODBA, overall dynamic body acceleration; PDBA, partial dynamic body acceleration.

water pressure, and more descent glides would therefore occur. The water current is similar in both rivers, but current velocity becomes slower in deeper water, facilitating gliding in channel catfish. Glide occurrence might also increase for fish with a low CF (i.e. a denser body), indicating that behavioural patterns may reflect individual morphological features, in addition to habitat differences.

Most individuals in the lentic environment employed increased and longer gliding during the descent phase (Fig. 3B, Table 2). They also showed significantly lower swimming effort during descent than ascent (Table 3), and exhibited longer resting periods (Table 4), suggesting that their buoyancy was negative. Physostomous fish can maintain their body density at near neutral buoyancy by retaining a certain amount of gas in their swim bladder. When the gas is exhaled, the body density becomes negatively buoyant, enabling the fish to glide during descent and rest on the bottom (Jones and Marshall, 1953). For example, Watanabe et al. (2008) reported that when Chinese sturgeons, *Acipenser sinensis*, did not have gas in their swim bladders in deep water; the fish exhibited gliding during descents owing to their negative buoyancy. The results of our study suggested that channel catfish usually have negative buoyancy in lentic environments, based on the combination of frequent gliding during the descent phase and long resting periods at the bottom; this behaviour was seen more often in the lentic environment. In general, channel catfish forage on benthic invertebrates and fish (Scott and Crossman, 1973; Wellborn, 1988; Hubert, 1999), with similar foraging behaviour observed in Lake Kasumigaura (Hanzawa, 2004). Arayama (2010) described the feeding behaviour of channel catfish as searching for prey with their barbels sweeping across the water bottom and attacking prey items from above. Gliding descents without fin movement would thus enable them to be undetected by prey and therefore to increased foraging success. The observed gliding and bottom resting phases during the recorded period may reflect the benthic lifestyle of channel catfish, and imply some advantages of being negatively buoyant in lentic environments.

Conversely, most individuals in the lotic environment employed fewer descending glides than observed in lentic individuals (Table 2). The shorter rest duration and lower rest rate of lotic individuals in comparison with lentic individuals suggested that remaining motionless is far more difficult in flowing water than in still water. In addition, the effort ratio of lotic individuals showed similar tail beat amplitudes during ascent and descent, implying a buoyancy close to neutral. It is commonly thought that fish maintain a more negatively buoyant body in flowing environments, to facilitate resting on the riverbed for 'flow refuging' (Saunders, 1965; Gee et al., 1974; Webb, 1998). In the Yahagi River, channel catfish were frequently captured near the water surface using baited floating long lines (Yamamoto et al., 2014), and small stream fish and aquatic/terrestrial invertebrates were found in their stomach contents (D.Y., unpublished data), implying that they frequently swim into the current to catch swimming or drifting prey items in the water column. Furthermore, in a river, dramatic changes in water level and flow rate caused by heavy rain or discharge from upstream dams can occur within short to long periods (e.g. minutes to hours) (Moyle and Light, 1996). This would force fish to contend with a higher water velocity, even if they evacuated from the main stream into a moderate flow area behind large rocks, or immediately above the riverbed. In this context, some recent studies demonstrate a flow resistance mechanism called the Kármán gait (e.g. Liao, 2004), which utilises the wake behind bluff bodies to produce thrust in a turbulent stream. Fish in this swimming mode could hold station, without any muscle activity, when the body position is placed appropriately in the Kármán vortex street, regardless of whether

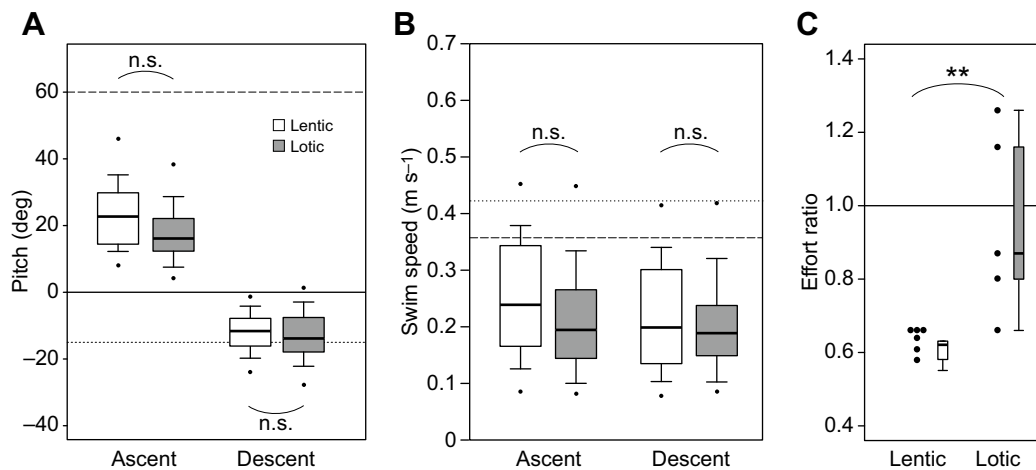


Fig. 4. Comparison of pitch angles, swimming speeds and effort ratios during vertical movements with stroking. (A,B) Box plots show pitch angles (A) and swimming speeds (B) during ascent and descent. White and grey boxes indicate lentic and lotic individuals, respectively. Boxes show 25th and 75th percentiles, and the centre line shows the median. Whiskers show the s.d. and dots show 5% and 95% outliers. Dashed and dotted lines indicate the lowest-cost pitch angle and swim speeds: 60 deg and 0.36 m s^{-1} for ascent and -15 deg and 0.42 m s^{-1} for descent (see Beecham et al., 2013). There was no significant difference between lentic and lotic individuals in ascent or descent pitch angles (A) (Mann–Whitney U -test; $U=21$, $N=11$, $P=0.33$ for ascent; and $U=16$, $N=11$, $P=0.93$ for descent) or speed (B) ($U=21$, $N=11$, $P=0.31$ for ascent; and $U=17.5$, $N=11$, $P=0.71$ for descent). (C) Comparison of effort ratios between lentic and lotic environments. Each dot represents the effort ratio of a single individual. The whiskers of the box plot indicate 1.5 of the interquartile range of the lower and upper quartiles. The horizontal line at 1.0 shows the point at which the swimming effort during descent is equal to that during ascent. The effort ratio was significantly lower in lentic individuals than in lotic individuals ($U=1.5$, $N=11$, $P=0.008$).

they are on the riverbed (Liao, 2007). From this perspective, maintaining neutral buoyancy to avoid the extra force loaded by gravity may be an efficient way to reduce the energy costs needed not only for their movement and activity but also for simply maintaining position in a flowing stream.

Channel catfish appear to control swim bladder volume to maintain a proper buoyancy condition according to their surrounding environment. The body densities of channel catfish ($1078 \pm 8 \text{ kg m}^{-3}$; Table S1) could be balanced by a gas volume of 7.8% in the swim bladder, allowing a channel catfish to achieve neutral buoyancy if it had a full swim bladder at a depth of 0–2 m. The results indicated that most individuals in lentic environments performed descent glides at 0–2 m depth, and that their body was negatively buoyant during the recorded period. Therefore, these results suggested that channel catfish maintain their negative buoyancy by retaining a gas volume that is lower than necessary to fill the swim bladder. Channel catfish have an auditory structure, called a Weberian apparatus, connected to the anterior part of the swim bladder, which enables the detection of sound vibrations (Alexander, 1966; Smith and Smith, 1994). Gas in the swim bladder amplifies sound vibrations, so a certain amount of gas must be retained in the swim bladder throughout life. The results provided evidence that individuals in lotic environments, which performed

similar numbers of ascent/descent glides and were estimated to have near neutral or slightly negative buoyancy, might control buoyancy by filling the swim bladder with more gas than required for the auditory function, thus attaining the optimum buoyancy condition.

Alteration of swim bladder volume in channel catfish appeared to be achieved by either inhaling or exhaling air through the mouth and pneumatic duct. Channel catfish in a swimming tank frequently gulped air at the surface immediately after water was poured into the tank (M.A.Y., personal observation), and this behaviour possibly rapidly altered the bladder volume relative to the rising water level and increasing water pressure. After evacuation of all the gas in the swim bladder, the black bullhead, *Ictalurus melas*, a closely related species, can regain neutral buoyancy within 2 weeks; it does this by secreting gas into the swim bladder through an organism called the gas gland (Machniak and Gee, 1975). Although channel catfish also appear to have a gas gland, and can slowly alter swim bladder volume by internal gas secretion, gulping or burping seems to play a main role in more rapid alteration of bladder volume. Thus, the open swim bladder system may help channel catfish adjust their buoyancy rapidly in highly fluctuating lotic environments.

The swimming performance of free-living individuals during active swimming behaviour did not correspond to some of the

Table 3. Generalised linear mixed models predicting the glide occurrence of channel catfish

Explanatory variables	Best model				2nd best model				3rd best model			
	Coefficient	s.e.	z	P	Coefficient	s.e.	z	P	Coefficient	s.e.	z	P
Depth	0.15	0.02	8.69	<0.001	0.15	0.02	8.79	<0.001	0.15	0.02	8.75	<0.001
Descent phase	2.21	0.07	33.6	<0.001	2.21	0.07	33.6	<0.001	2.21	0.07	33.6	<0.001
Condition factor	0.29	0.12	2.43	0.015	0.26	0.13	1.93	0.053	–	–	–	–
Lotic habitat	–	–	–	–	–2.52	0.71	–3.57	<0.001	–1.98	0.73	–2.70	0.007
Study site – Tone River	–1.58	0.75	–2.12	0.034	–	–	–	–	–	–	–	–
Study site – Yahagi River	–3.35	0.75	–4.49	<0.001	–	–	–	–	–	–	–	–
AIC	–	–	–	1250	–	–	–	1251	–	–	–	1253

Results with $|z| > 2.0$ are shown in bold. Habitat type and study site indices were not included simultaneously in each model.

Table 4. Summary statistics for resting period of channel catfish (record duration >24 h)

Fish ID	Record duration (h)	Resting behaviour				
		<i>N</i>	Total duration (h)	Median duration (s)	Maximum duration (min)	Rest rate
Lentic						
K01	44.3	210	14.8	102.5	65.2	0.33
K02	99.5	329	19.1	107	65.8	0.19
K06	66.2	118	4.3	88	14.2	0.07
K08	47.2	279	26.5	141	108.4	0.56
K10	87.8	321	64.9	190	416.0	0.74
Lotic						
Y04	98.5	218	6.5	80	14.7	0.07
Y06	64.1	220	6.1	83.5	6.4	0.10
T02	46.4	84	3.7	88.5	40.3	0.08
T06	74.0	571	26.4	96	39.0	0.35

quantitative predictions previously made in experimental studies. Following Weihs' theoretical prediction, Beecham et al. (2013) calculated the lowest-cost pitch angles of swimming channel catfish as up to 60 deg for ascents and approximately 15 deg for descents, and suggested that they could reduce the cost of transport by up to 43% using a combination of steep ascents and shallow descents. In the present study, all individuals performed significantly shallower ascents (23.9 ± 12.0 deg) than predicted, whereas the pitch angle during descents (-12.6 ± 8.2 deg) more closely followed the theoretical prediction. Beecham et al. (2013) also described the swimming speed at which channel catfish could achieve the lowest cost of transport as 0.36 m s^{-1} for ascent and 0.42 m s^{-1} for descent; these speeds were much faster than swimming speeds observed in the wild (Fig. 4B). These differences might be a consequence of drag caused by the externally attached tag, and fluctuations in the experienced water temperature. The added drag may cause the equipped individuals to slow down and have a higher active metabolic rate; varying water temperature should affect the standard metabolic rate of individuals. Altering swimming costs by increasing the metabolic rate could lead to differences in swimming performance, such as a shallower pitch angle during ascent and slower swimming speeds. However, the results of the intra- and inter-individual comparisons made in this study are based on measured data. This demonstrates the need for more quantitative research under experimental conditions, as well as a greater integration of existing knowledge, to better interpret and understand the efficient swimming strategy of free-ranging animals with animal-borne devices.

This study provides some ecological insights into the studied species, such as a possible explanation of the recent expanded distribution of channel catfish in Japan. Invasion success in freshwater ecosystems depends on a match between the physiological features of the invader and the characteristics of the invaded system (Moyle and Light, 1996). Channel catfish, which have invaded Japanese rivers, seem to be adapted to the local, highly seasonal, hydrologic regime in terms of flexible swimming modes and rapid buoyancy regulation. Therefore, these characteristics could represent the main traits that facilitate the invasiveness of this species, taken with morphological and ecological features such as anti-predatory spines on fins (Bosher et al., 2006), omnivorous diet (Hanzawa, 2004) and lack of natural predators. Furthermore, the fact that many physostome species mainly remain in freshwater (instead of seawater) (FishBase; www.fishbase.org, version 10/2015) might be indicative of a similar mechanism enabling them to control buoyancy and adapt to fluctuating environmental conditions. The ability to immediately control and optimise their buoyancy conditions relative to the surrounding environment might be utilised upon

introduction into new waters, providing a suitable explanation for the adaptation of channel catfish to a wide range of environments.

Our study is the first to demonstrate the differences in swimming modes based on the surrounding environment in a physostomous freshwater fish species. Channel catfish in lentic environments maintained negative buoyancy and utilised gliding while descending, whereas those in lotic environments exhibited a different swimming mode with less gliding, which possibly maintained either negative or nearly neutral buoyancy. The benthic lifestyle of channel catfish in still water confers a benefit, gained from swimming, feeding and resting near the bottom of the lake, with a negatively buoyant body. In contrast, continuous swimming in flowing water while negatively buoyant is much more costly than when neutrally buoyant, because extra energy is expended in generating uplift power against gravity. Channel catfish in lotic environments could maintain buoyancy at an efficient neutral condition by controlling swim bladder volume by gulping or burping, enabling the fish to lower the costs associated with staying in and moving through flowing water. This study illustrates active buoyancy regulation by physostomous fish and infers the possibility of utilisation of neutral buoyancy in flowing streams, providing new insight into the energetic strategy of aquatic animals. Our findings also aid in understanding the variability and diversity of physostomous freshwater fish species in lotic environments, which pose additional energy expenditures on the swimming animals that inhabit them.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

M.A.Y. and K.S. conceived and designed the experiments; M.A.Y. and D.Y. performed the experiments and compiled the raw data; M.A.Y. analysed the data; M.A.Y., D.Y. and K.S. wrote the paper.

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Supplementary information

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