博士論文（要約）

Distribution patterns of non-native channel catfish *Ictalurus punctatus* in Japan and its behavioral characteristics related to flow conditions

（日本における外来魚チャネルキャットフィッシュの分布様式
および流れに関連した行動特性）

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CHAPTER I　General introduction

（本章の内容は、学術雑誌論文として出版する計画があるため公表できない。5 年以内に出版予定。）

CHAPTER 2

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CHAPTER 3

Age, growth, diet and movement pattern of channel catfish in the Yahagi River

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CHAPTER 4

Swimming mode and buoyancy modification of channel catfish in relation to flow conditions

SUMMARY

Accelerometers were deployed on 6, 3 and 2 free-ranging channel catfish, *Ictalurus punctatus*, in Lake Kasumigaura, the Yahagi River and the Tone River, respectively, to quantify their swimming activity in both lentic and lotic environments.   Depth and acceleration data from 11 fish (9-100 h, 649 h in total) were analyzed to determine their buoyancy condition, whether they exhibit 'gliding', a swimming pattern that some previous studies assumed to conserve energy, and duration of resting period at the bottom.   Individual comparisons of swimming efforts between ascent and descent phases revealed that all fish in the lentic environment had negative buoyancy, while those in the lotic environment kept their buoyancy close to neutral.   Lentic individuals showed longer resting periods and exhibited more and longer glidings than lotic individuals, showing the utilization of negative buoyancy.   On the other hand, lotic individuals showed fewer glidings and shorter rest duration with bodies close to neutrally buoyant.   Difference in swimming mode between lentic and lotic individuals can be explained by their foraging patterns, as individuals in Lake Kasumigaura mainly forage on benthic prey items at the lake bottom while those in rivers feed on various prey items flowing at wide range of depths in the water column.   Those patterns, or depths relative to the lake/river bottom that were mainly occupied by the species, would determine the species' depth range as well as their buoyancy conditions, thus leading to varying behavioral patterns observed in different flow conditions.

INTRODUCTION

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 Almodovar, 2001; Copp et al., 2007; Katano et al., 2010), demonstrating their ability to adjust to a wide range of environments (Townsend and Winterbourn, 1992). 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. Animals in lentic habitats are able to utilize gravity to drive and assist their locomotion in a vertical direction, which is known as 'gliding' (Weihs, 1973). Beecham et al. (2013) conducted a laboratory experiment, using an angled swimming chamber, to calculate energy saving in channel catfish during non-horizontal swimming. Compared to horizontal swimming, these measurements predicted that the most efficient energy saving would have a value of up to 43%, in combination with gliding descents and stroking ascents with pitch angles of $-15°$ and $60°$, respectively. The results suggested the possibility that freshwater fish species save energy by gliding. In contrast, animals in lotic habitats do not benefit from gravity because they must compensate for the horizontal displacement caused by the flow of the surrounding medium by continuously moving their bodies. Given the different functional demands imposed by the extent of flow, the species in each habitat should exhibit contrasting swimming pattern to optimize their locomotion, and would be expected to adopt different buoyancy conditions: fish in lentic habitat would exhibit frequent gliding and have negatively buoyant body whereas those in lotic habitat would exhibit less gliding and have less negative buoyancy.

In the present study, accelerometers were deployed on free-ranging channel catfish in both lentic and lotic environments in order to determine how these animals behave under different flow conditions, their swimming performance during vertical movements, and their buoyancy condition

preferences. I then aimed to illustrate how aquatic animals behave differently in various environments, and how and in which situations they either utilize 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

In order to compare swimming performance in channel catfish between lentic and lotic conditions, the behaviors of fish were recorded in three locations in Japan: Lake Kasumigaura (Fig. 4-1), the Tone River (Fig. 4-1) and the Yahagi River (Fig. 4-2), during July 2012 and May 2015 (Table 4-1). The observed average current speed during the sampling periods, which was measured at the surface of the center of flow, was approximately 1 m s^{-1} for the Tone River (the Tonegawa-Karyu River Office; pers. comm.), and 0.7–1.2 m s^{-1} for the Yahagi River (the Toyohashi River Office; pers. comm.). Channel catfish were caught by trawling in Lake Kasumigaura, and trotlines and hoop nets were used in the Yahagi River and the Tone River, respectively. Data loggers were deployed on six, three, and two individuals in Lake Kasumigaura, the Yahagi River, and the Tone River, respectively (Table 4-1). The fish release and logger retrieval points are shown in Figs. 4-1 and 4-2.

Data loggers

To quantify the swimming behavior of channel catfish, 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) were used. 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

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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 individuals were equipped with the D3GT loggers (2012–2014), five individuals with the PD3GT loggers (2014), and one individual with the PD2GT logger (2015) (Table 4-1).

Data recovery

It is almost impossible to recapture channel catfish individuals, so an automatic time-scheduled release system (Watanabe et al., 2004) was used 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, Tokyo, Japan).   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 anaesthetized with 0.02% 2-phenoxyethanol solution, and measurements taken of body mass (g; *BM*), standard length (cm; *SL*), and/or total length.   The condition factor (*CF*; Mitani, 1986; Gaylord and Gatlin, 2000) of each individual was calculated using the following equation:

$$CF = 1000 \times \frac{BM}{SL^3}, (1).$$

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 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 anesthesia.   I observed the behavior 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

Igor Pro software (version 6.12; Wave Metrics, Inc., OR, USA) was used to analyze the behavioral 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).   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) were used to create a low- and a high-frequency signal.   The pitch angle of channel catfish was calculated based on the low-frequency component of acceleration.   The data logger was not always attached parallel to the animal's longitudinal axis, so the attachment angle was calibrated 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, the overall dynamic body acceleration (ODBA; Wilson et al., 2006) or the partial dynamic body acceleration (PDBA; Halsey et al., 2009) values was calculated as indicators of an individual's swimming effort (Gleiss et al., 2010), respectively.   Stroking movements were extracted from the

high-frequency acceleration data based on the set threshold value for each fish (0.10–0.32 m s^{-2}). Moreover, I 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 behavior.   The gliding period was defined as vertical movement without any stroking that lasted longer than 1 s.

To facilitate the analyses, I 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. The rest rate (%resting) was also calculated as the ratio of the total duration of the bottom phase to the total recording time for each individual.   Rest rates for lentic and lotic individuals were compared using a Mann–Whitney U test.

Swimming speed data were obtained 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°.

In order to obtain information about the buoyancy conditions of each fish, the swimming effort (ODBA/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 analyzed.   A generalized 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 condition factor—were set as candidate explanatory variables.   To avoid problems due 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. Individuals were set as a random effect.   I calculated an Akaike's Information Criterion (AIC) and selected the model with the lowest AIC value as the most parsimonious model.   The glmmML package in the R software (version 3.1.2; http://www.R-project.org/) was used for statistical analyses.   Values are presented as means ± SD, and $P < 0.05$ indicates statistically significant differences.

Measurement of body density

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 euthanized 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 euthanized fish sank in seawater, so salt were therefore added to the seawater until the fish became neutrally buoyant, and the water density (equivalent to the fish density) was then measured 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.

Measurement of maximum swim bladder volume

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 were also measured.   The swim bladder was first removed from the surrounding tissues.   The maximum volume of the swim bladder was obtained using the difference in weight before and after filling the swim bladder with freshwater after removing the whole tissue.   The body volume of each individual was estimated using the measured body mass and the body density obtained in this study.

RESULTS

General information

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

Figure 4-3 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 m, 1.1–2.1 m, and 3.6–4.7 m in Lake Kasumigaura, the Yahagi River, and the Tone River, respectively (Table 4-1).   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.

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Gliding behavior

Gliding phases were often observed during the descending movements of fish in the lentic environment (e.g. Fig. 4-4), but few instances were observed during ascents or when fish were in the lotic environment (Fig. 4-5; Table 4-2). 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 4-2). 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.

A GLMM revealed that glide occurrence was affected by depth, ascent/descent phase, condition factor, and habitat (or study site) (Table 4-3). Glide occurrence was higher in Lake Kasumigaura (lentic habitat) than in the Tone and Yahagi Rivers (lotic habitat), during descent than during ascent, and increased at deeper depths.

Swimming performance during vertical movements

As seen in the glide occurrence for each depth (Fig. 4-6), both ascents and descents of all the examined channel catfish were often accompanied by active tail beats (e.g. Fig. 4-7). The pitch angle, swim speed, and swimming effort during vertical movements in which stroking lasted longer than 5 s are summarized in Table 4-4. 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°, 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. 4-8). Swimming speed during vertical movements also varied between individuals, and the range for ascents and descents was 0.16–0.34 m s^{-1} and 0.16–0.42 m s^{-1}, respectively (Table 4-4). 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. 4-9). 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 4-4). In contrast, of the five individuals studied in the lotic environment, two individuals (fish Y06 and T02) showed significantly lower swimming effort during descents compared to ascents (Mann–Whitney U test: $P < 0.001$ for fish Y06 and T02; Table 4-4). Two other individuals (fish Y04 and T06) exhibited significantly higher swimming efforts during descents compared to 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 4-4). 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 4-4), 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. 4-10).

The tail beats of catfish were very weak or almost non-existent when the fish remained at a certain depth for several minutes (Fig. 4-7), which implied they were resting at the bottom of the river/lake. The median duration of bottom phases for lentic and lotic environments was 88–190 s and

80–96 s, respectively, whereas the maximum duration was 14.2–416 min and 6.4–40.3 min, respectively (Table 4-5). 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 4-5).

Body density

The net body density of channel catfish after swim bladder removal ranged from 1054 to 1088 kg m^{-3} (mean ± SD, 1078 ± 8 kg m^{-3}, N = 26; Table 4-6). Body density did not differ between lentic and lotic individuals (Mann–Whitney U test: U = 26.5, N = 26, P = 0.94; Fig. 4-11) or between sexes (Mann–Whitney U test: U = 26.5, N = 26, P = 0.94; Fig. 4-12). Neither was it significantly correlated with the standard length (Spearman's correlation test: P = 0.62, r_s = −0.10; Fig. 4-13) or body mass (Spearman's correlation test: P = 0.59, r_s = −0.11; Fig. 4-14) of the fish. However, there was a significant negative correlation between body density and the condition factor (Spearman's correlation test: P = 0.017, r_s = −0.46; Fig. 4-15).

Maximum swimbladder volume

The range of the maximum swim bladder volume was 62–100 cm^3, and the per cent by volume range of the swim bladder to the body was 5.8–9.3% (Table 4-7).

DISCUSSION

Behavioral differences between lentic and lotic environments

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 behavior. Individuals in Lake Kasumigaura experienced lentic conditions for the entire

recording period, whereas individuals in the Yahagi and Tone Rivers experienced lotic conditions.

Prior to this study, a telemetry tracking of a single channel catfish was conducted in the Yahagi River

(fish Y3 in Chapter 2).   This showed that the fish moved 8 km downstream within 6 h (see Chapter 2),

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.

Channel catfish in Lake Kasumigaura displayed a greater number of glides during descents compared

to ascents, whereas those in the Yahagi and Tone Rivers exhibited similar numbers of ascending and

descending glides (Fig. 4-5).   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 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.

Most individuals in the lentic environment employed increased and longer gliding during

the descent phase (Fig. 4-6, Table 4-2).   They also showed significantly lower swimming effort

during descent than ascent (Table 4-4), and exhibited longer resting periods (Table 4-5), 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* (Grey, 1835), had compressed gas in their swim bladders in deep water, the fish exhibited gliding during descents due 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 behavior 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 behavior observed in Lake Kasumigaura (Hanzawa, 2004).   Arayama (2010) described the feeding behavior 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 life style 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 4-2).   The shorter rest duration and lower rest rate of lotic individuals in comparison with lentic individuals suggested that remaining motionless in flowing water is far more difficult 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, and small stream fish and aquatic/terrestrial invertebrates were found from their

stomach contents (see Chapter 3), 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 (Liao, 2004), which utilizes the wake behind bluff bodies to produce thrust in a turbulent stream.   Fish in this swimming mode could hold a station, without any muscle activity, when the body position is placed appropriately in the Kármán vortex street, whether on the riverbed or not (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.

Buoyancy control

The body densities of channel catfish (1078 ± 8 kg m^{-3}; Table 4-6) could be balanced by a 7.8% gas volume 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.   Most individuals in lentic environments 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.   Individuals in lotic environments 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 its mouth and pneumatic duct. Channel catfish in a swimming tank frequently gulped air at the surface immediately after water was poured into the tank (Yoshida, personal observation), and this behavior possibly rapidly altered the bladder volume relative to the rising water level and increasing water pressure. A closely related species, the black bullhead, *Ictalurus melas*, can regain neutral buoyancy within two weeks after evacuation of all the gas in the swim bladder; 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.

Swimming performance of free-ranging fish compared to theoretical prediction

The swimming performance of free-living individuals during active swimming behavior did not correspond to some of the quantitative predictions previously made in experimental studies. Following the Weihs' theoretical prediction, Beecham et al. (2013) calculated the lowest-cost pitch angles of swimming channel catfish as up to 60° for ascents and approximately 15° 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°) than predicted, whereas the pitch angle during descents (−12.6 ± 8.2°) 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.

4-9).   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 a greater integration of existing

knowledge, to better interpret and understand the efficient swimming strategy of free-ranging animals

with animal-borne devices.

Ecological inference to the species' range expansion

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 one of the main traits that facilitate the invasiveness of this species, together 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 fresh water (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 optimize their buoyancy conditions relative to the surrounding environment might be utilized upon introduction into new waters, providing a suitable explanation for the adaptation of channel catfish to a wide range of environments.

Conclusion

Channel catfish in lentic environments maintained negative buoyancy and utilized 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 through controlling swim bladder volume by gulping or burping, enabling the fish to lower the costs associated with staying in and moving through flowing water.

Table 4-1. Descriptive information about the channel catfish used in the study.   Alphabets in fish IDs indicate the sites in which individuals were studied (K—Lake Kasumigaura; Y—the Yahagi River; T—the Tone River).   SL—standard length; BM—body mass; CF—condition factor.

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

Table 4-2. Summary statistics for gliding movements of channel catfish

Fish ID	N		Mean duration (s)	
	Ascent	Descent	Ascent	Descent
Lentic				
K01	3	188	2.6±0.8	4.9±2.2[*]
K02	0	60	-	3.4±0.7
K06	2	196	2.7±0.6	4.2±1.3[*]
K08	52	241	3.7±1.0	6.1±3.9[***]
K09	2	80	2.5±0.6	4.1±1.3[*]
K10	88	72	3.9±1.5	3.9±1.5[NS]
Mean			3.8±1.4	4.8±2.7
Lotic				
Y04	1	1	3.8	2.5
Y06	2	8	3.9±2.5	2.5±0.6[NS]
Y08	2	5	4.1±2.7	3.8±1.4[NS]
T02	28	71	3.3±0.8	4.5±2.1[***]
T06	70	57	3.7±1.1	3.6±1.3[NS]
Mean			3.6±1.1	4.0±1.8

Table 4-3. Generalized linear mixture models predicting the glide occurrence of channel catfish.

Variables	Best model				2nd Best model				3rd Best model			
	Coef.	SE	z	P	Coef.	SE	z	P	Coef.	SE	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**
CF	**0.29**	**0.12**	**2.43**	**0.015**	0.26	0.13	1.93	0.053	-	-	-	-
[†]Site—Tone	**-1.58**	**0.75**	**-2.12**	**0.034**								
[†]Site—Yahagi	**-3.35**	**0.75**	**-4.49**	**< 0.001**								
[†]Lotic habitat					**-2.52**	**0.71**	**-3.57**	**< 0.001**	**-1.98**	**0.73**	**-2.70**	**0.007**
AIC				1250				1251				1253

* Results with z-values >2.0 are shown in bold.

[†] Habitat type and study site indices were not included simultaneously in each model.

Table 4-4. Summary statistics for vertical movements with stroking (>5 s) and gliding of channel catfish. Asc—ascent; Dsc—descent. ER—effort ratio.

ID	N		Pitch angle (degrees)		Swim speed (m s^{-1})		ODBA/PDBA (m s^{-2})		ER
	Asc	Dsc	Asc	Dsc	Asc	Dsc	Asc	Dsc	
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
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
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
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
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
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
Mean			23.9±12.0	-12.2±7.0	0.26±0.08	0.22±0.05			
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
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
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^{NS}	0.87
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
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
Mean			18.5±10.6	-13.2±9.6	0.26±0.10	0.23±0.06			
Grand mean			**22.1±11.8**	**-12.6±8.2**	**0.24±0.12**	**0.21±0.11**			

*Significantly different between the ascent and descent phase: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. NS, not significant.

Table 4-5. Summary statistics for resting period of channel catfish (record duration >24 h)

Fish ID	Record duration (h)	Resting behavior				
		N	Total duration (h)	Median duration (sec)	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

Table 4-6. Measured body density of channel catfish

Fish No.	Sex	SL (cm)	BM (g)	CF	Body density (kg m^{-3})
Lentic 1	F	15.5	50	1.34	1075
Lentic 2	M	15.7	55	1.42	1074
Lentic 3	M	16.1	60	1.44	1083
Lentic 4	M	16.4	55	1.25	1070
Lentic 5	F	23.0	155	1.27	1086
Lentic 6	F	23.0	160	1.32	1086
Lentic 7	M	23.4	180	1.40	1085
Lentic 8	M	24.5	185	1.26	1085
Lentic 9	M	31.5	455	1.46	1076
Lentic 10	M	32.0	430	1.31	1086
Lentic 11	M	32.0	430	1.31	1088
Lentic 12	M	34.8	575	1.36	1076
Lentic 13	M	47.0	1620	1.56	1082
Lentic 14	F	47.5	1710	1.60	1076
Lentic 15	M	47.5	2105	1.96	1075
Lentic 16	F	48.6	1865	1.62	1071
Lentic Mean	-	-	-	-	1080±6
Lotic 1	M	19.4	95	1.45	1079
Lotic 2	M	20.2	102	1.50	1077
Lotic 3	F	20.3	101	1.48	1074
Lotic 4	F	22.5	115	1.48	1080
Lotic 5	F	23.6	131	1.47	1086
Lotic 6	M	23.6	154	1.54	1087
Lotic 7	M	27.0	280	1.55	1083
Lotic 8	F	35.2	873	1.43	1062
Lotic 9	F	40.0	1040	1.46	1054
Lotic 10	M	47.0	1325	1.44	1077
Lotic Mean		-	-	-	1076±10
Grand mean					**1078±8**

Table 4-7. Measured swim bladder volume of channel catfish

Fish No.	Sex	SL (cm)	BM (g)	CF	Bladder volume (cm³)	Bladder volume (%)
V1	F	47.6	1850	1.72	100	5.8
V2	M	39.5	1130	1.83	62	5.9
V3	M	42.4	995	1.31	86	9.3
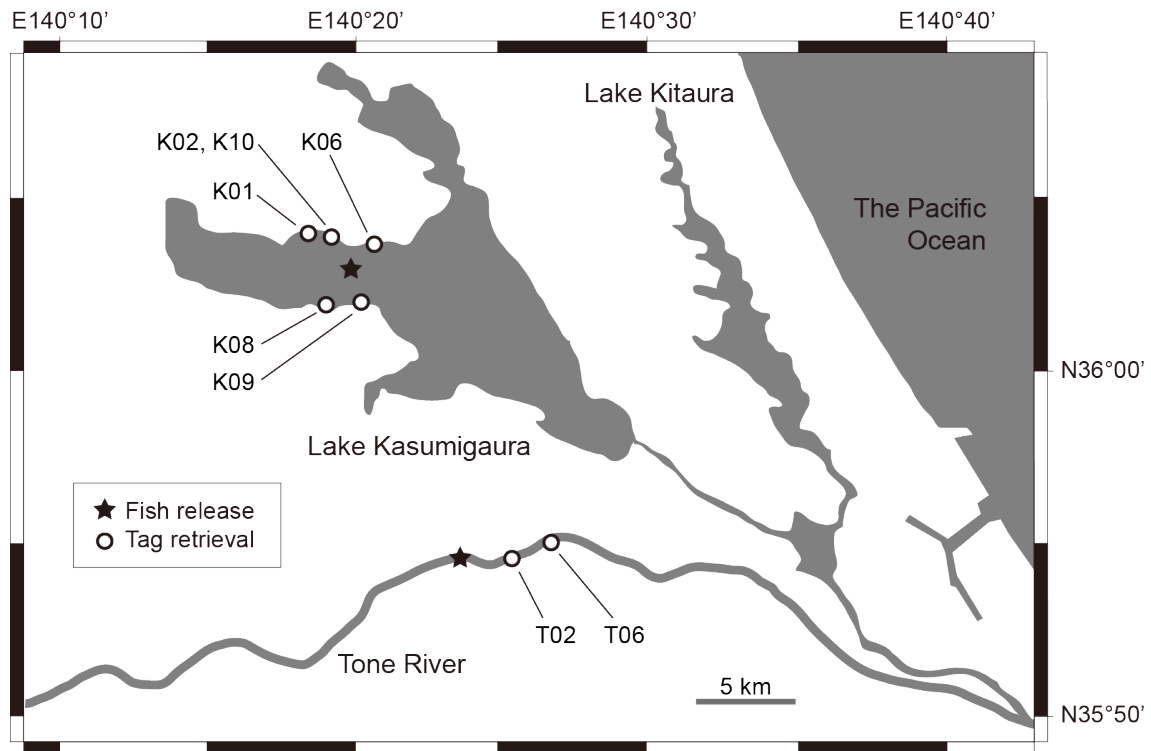
Figure 4-1. Locations of fish release and tag retrieval in the Tone River basin

Maps of the studied sites in Lake Kasumigaura and Tone River are shown. Black stars and open circles indicate the locations of fish release and tag retrieval, respectively.
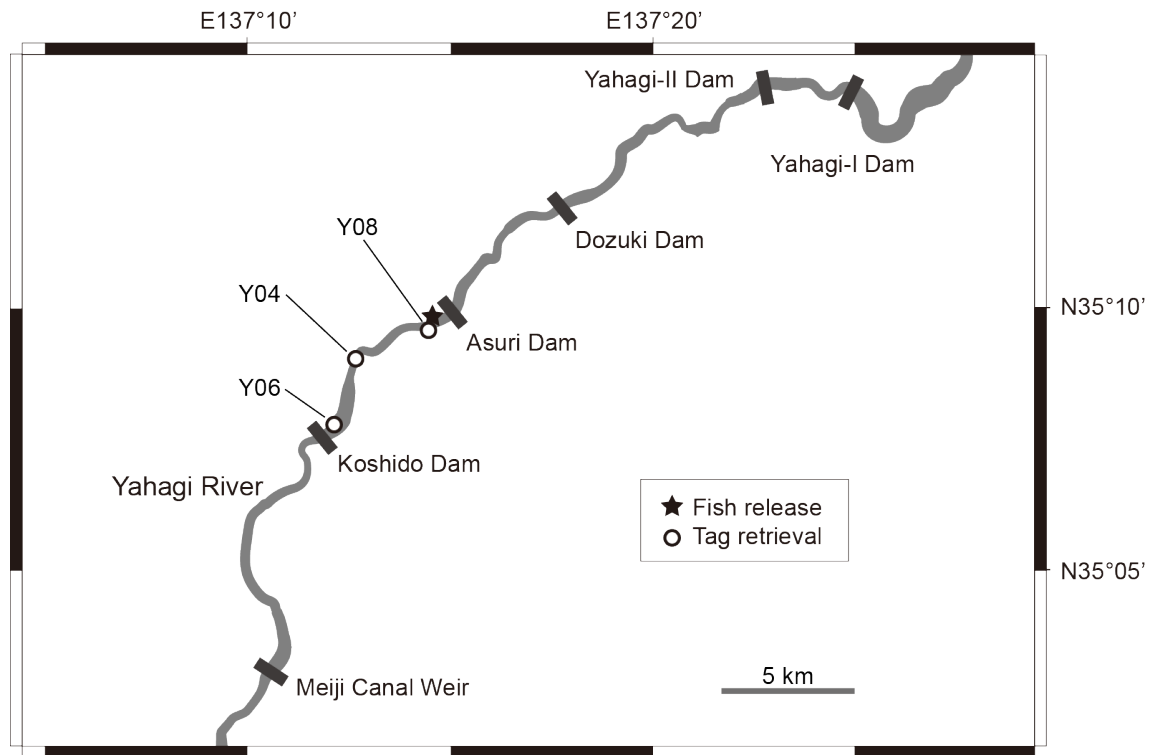
Figure 4-2 Locations of fish release and tag retrieval in the Yahagi River

Maps of the studied sites in the Yahagi River are shown.   Black stars and open circles indicate the

locations of fish release and tag retrieval, respectively.
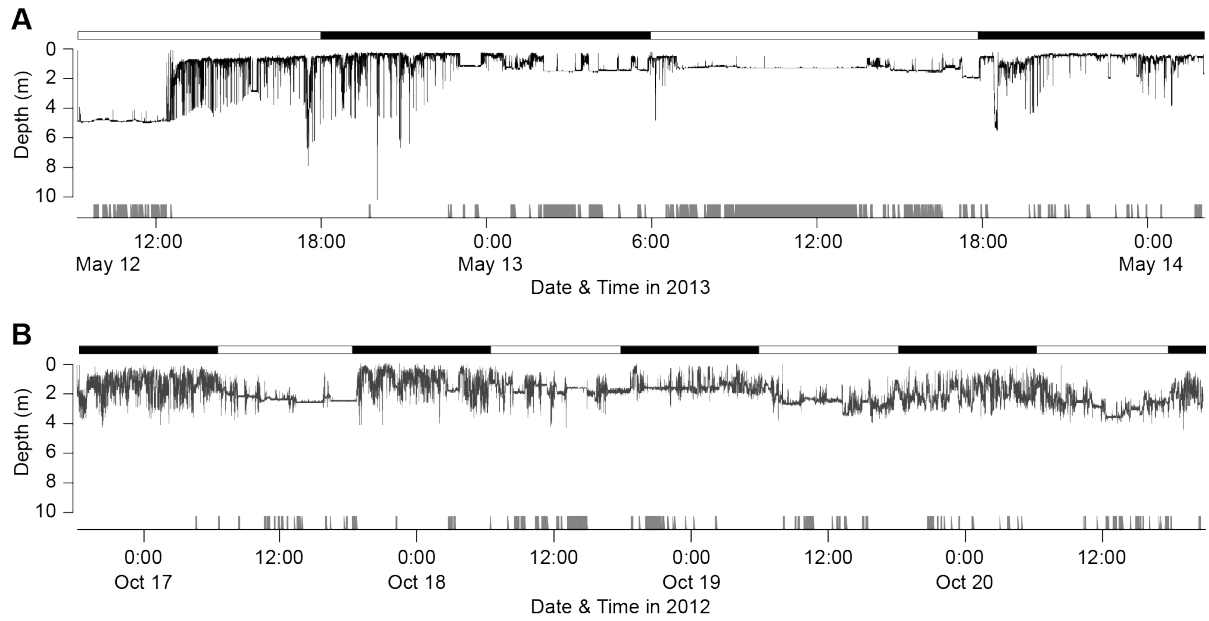
Figure 4-3 Swimming performances of channel catfish in lentic and lotic environments

Time-series depth data obtained from individuals in lentic (K01; A) and lotic (Y04; B) environments

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.
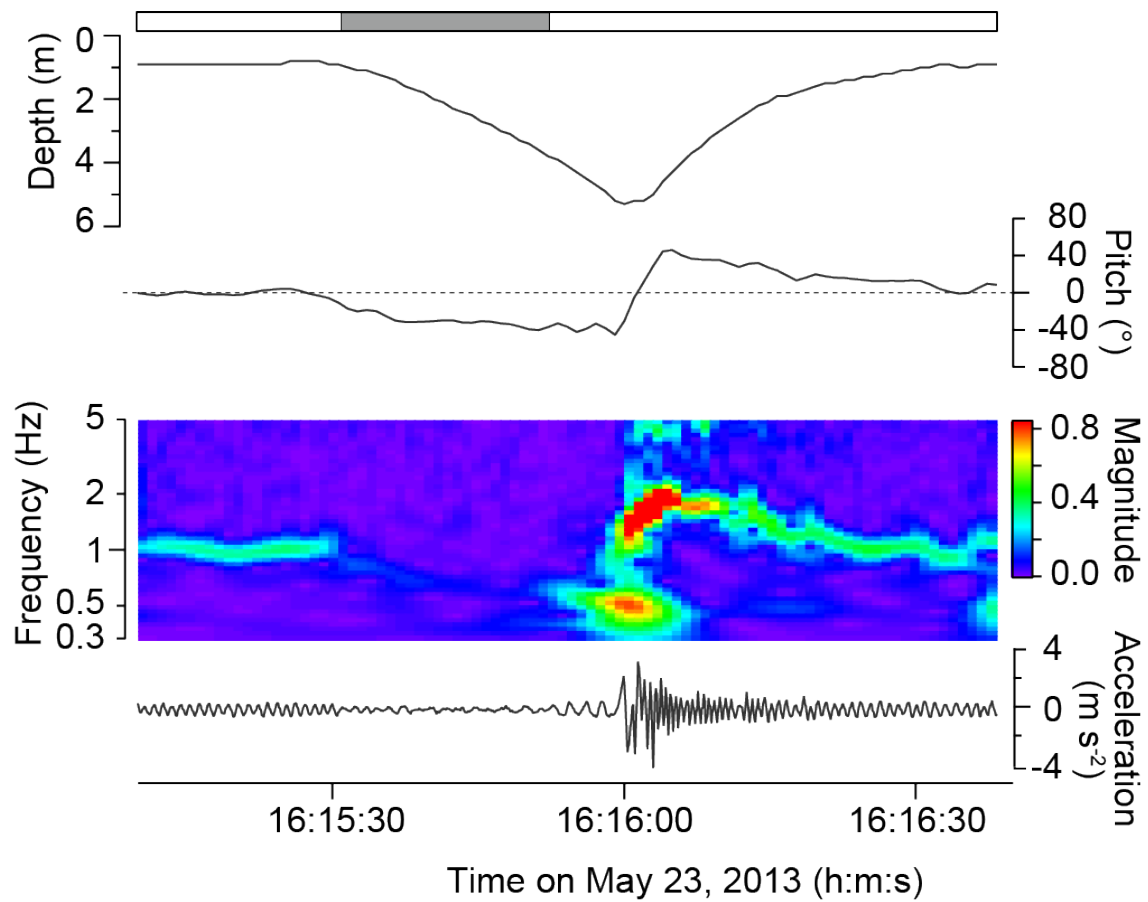
Figure 4-4. Swimming performances of channel catfish during vertical movements

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) and gliding periods (grey).

Warmer colors in the spectrogram represent stronger signals, whereas cooler colors represent weaker

signals.   There is a lack of a strong signal in the spectrogram during descent, which indicates the

individual was gliding.
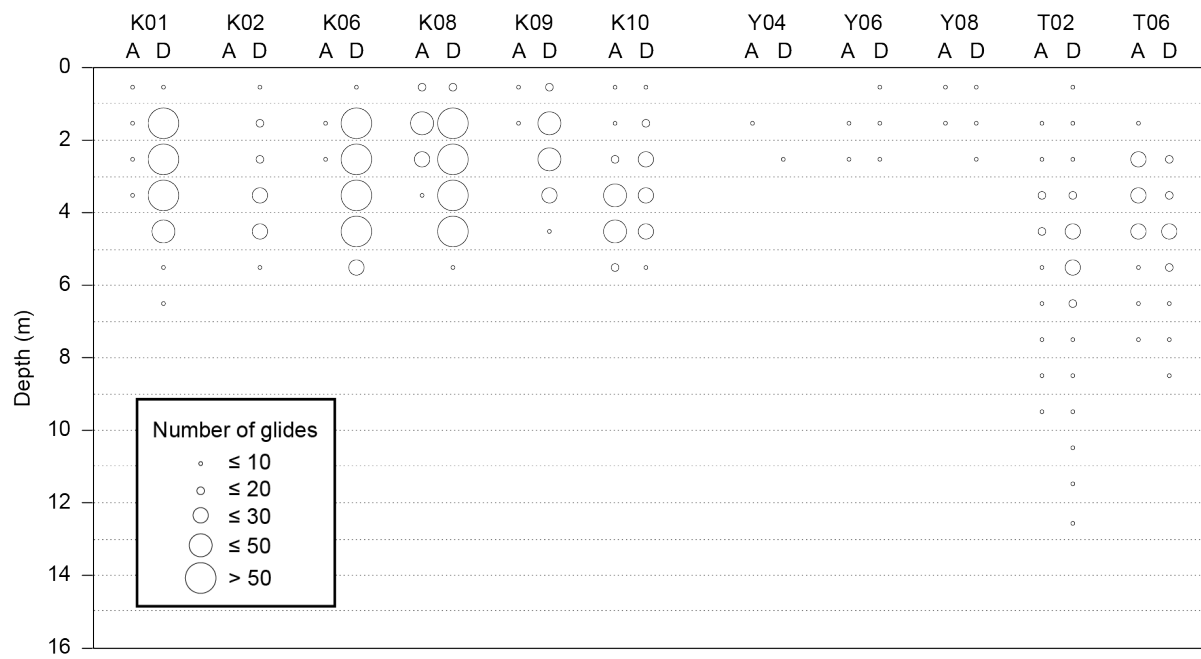
Figure 4-5. Depth distributions of channel catfish during gliding periods

The bubble charts show the depth distribution of each individual during gliding ascents (A) or

descents (D) .   The number of glides for each 1-m depth is shown as open circles of increasing size.
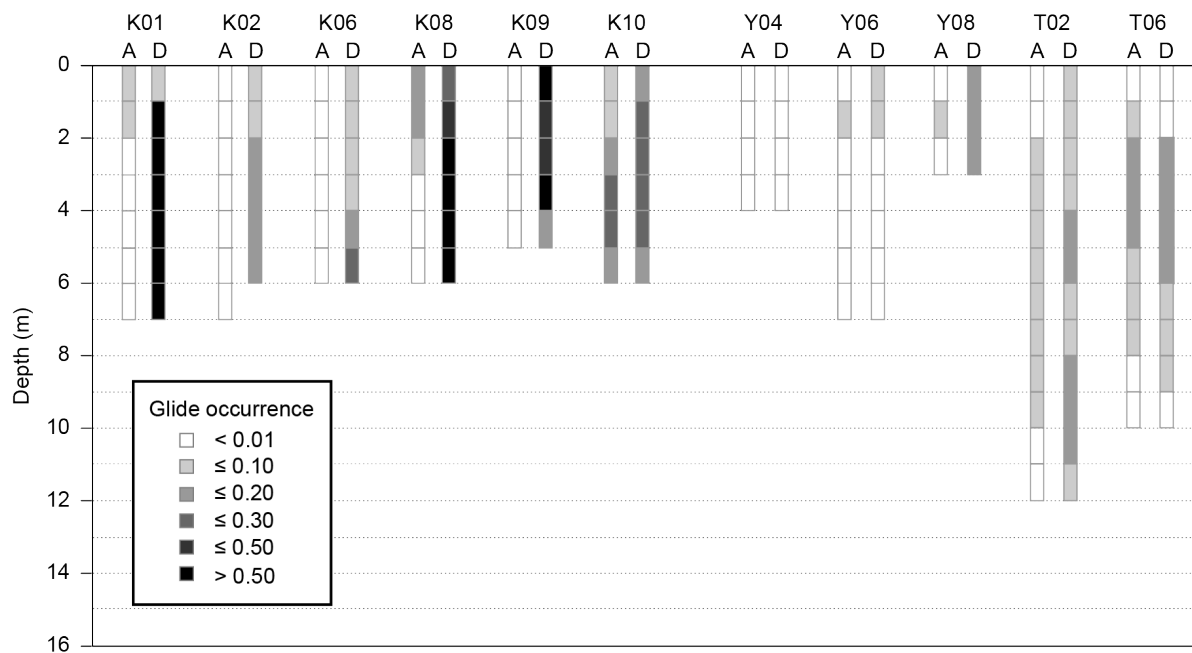
Figure 4-6. Depth distributions of channel catfish during gliding periods

The color 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.
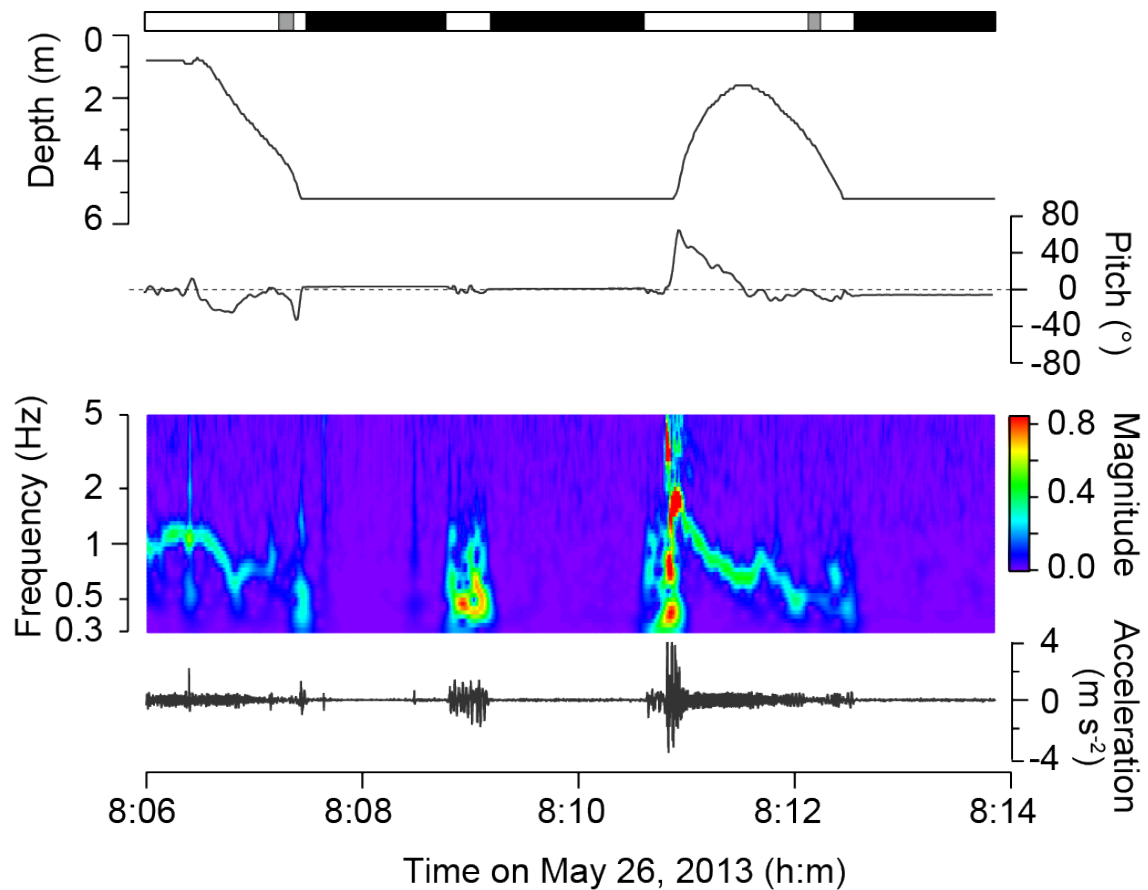
Figure 4-7. Stroking and resting behavior of channel catfish observed during recording period

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 colors in the spectrogram represent stronger signals, whereas cooler

colors represent weaker signals.　There is a lack of a strong signal in the spectrogram, which

indicates the individual was resting at the bottom.
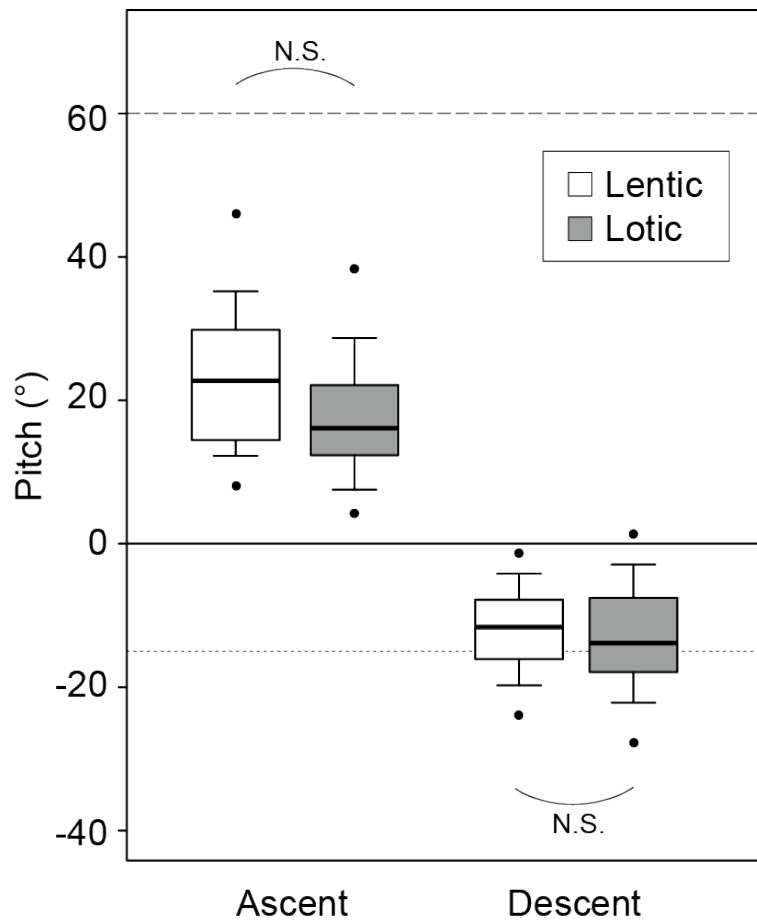
Figure 4-8. Comparison of pitch angles during vertical movements with stroking

Box plots show pitch angles during ascent and descent. White and grey boxes indicate lentic and lotic individuals, respectively. Boxes show 25th and 75th percentiles, and the center line shows the median. Whiskers show the SD and dots show 5% and 95% outliers. Dashed and dotted lines indicate the lowest-cost pitch angle: 60° for ascent and −15° for descent, respectively (see Beecham et al., 2013). There was no significant difference between lentic and lotic individuals in ascent or descent pitch angles (Mann–Whitney U test; $U = 21, N = 11, P = 0.33$ for ascent; and $U = 16, N = 11, P = 0.93$ for descent).
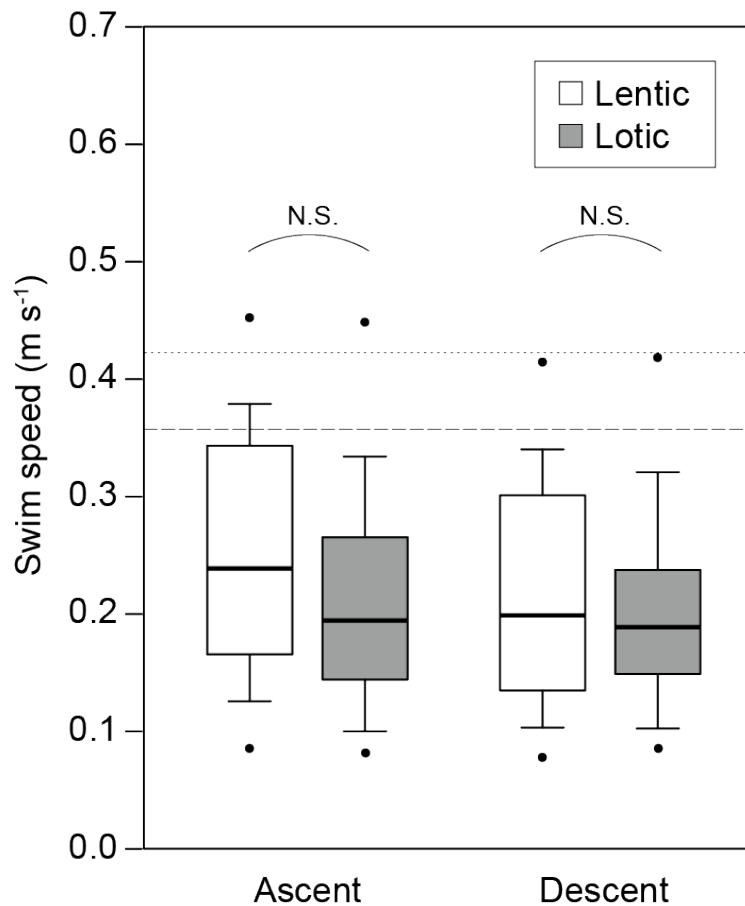
Figure 4-9. Comparison of swimming speeds during vertical movements with stroking

Box plots show swimming speeds during ascent and descent.   White and grey boxes indicate lentic and lotic individuals, respectively.   Boxes show 25th and 75th percentiles, and the center line shows the median.   Whiskers show the SD and dots show 5% and 95% outliers.   Dashed and dotted lines indicate the lowest-cost swim speeds: 0.36 m s^{-1} for ascent and 0.42 m s^{-1} for descent, respectively (see Beecham et al., 2013).   There was no significant difference between lentic and lotic individuals in ascent or 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).
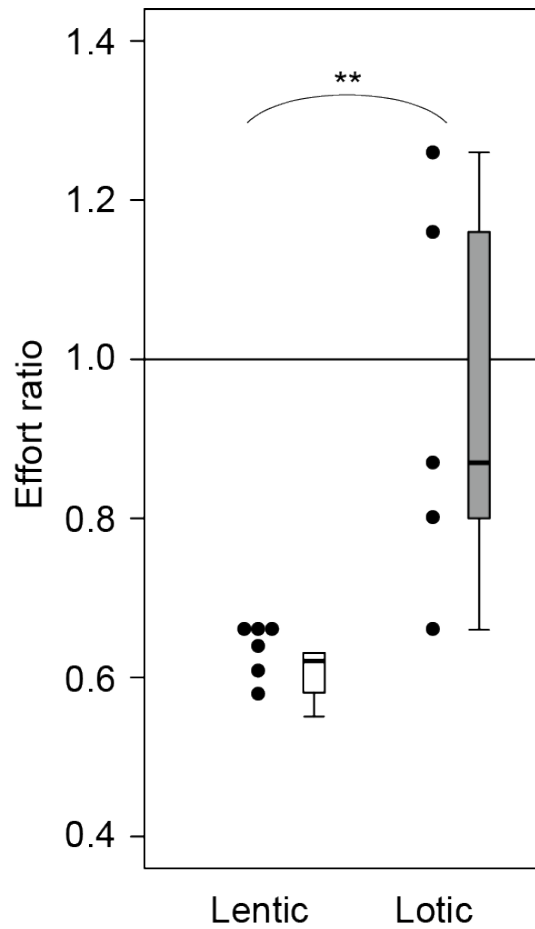
Figure 4-10. Comparison of effort ratios during vertical movements with stroking

Comparison of effort ratios between lentic and lotic environments is shown. 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 the value of 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 (Mann–Whitney U test: $U = 1.5$, $N = 11$, $P = 0.008$).
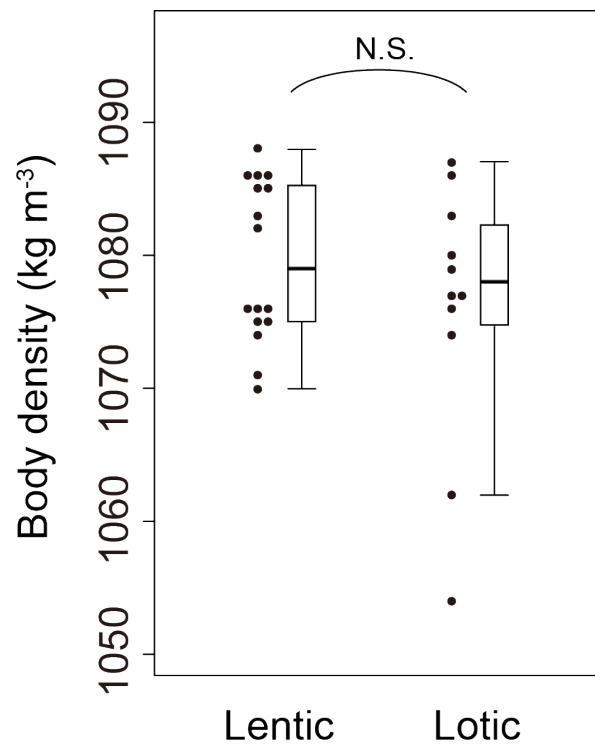
Figure 4-11. Relationship between body density and study site.

Measured body densities compared between study sites.   Each dot represents the measured body density of an individual.   The whiskers of the box plots indicate 1.5 of the interquartile range of the lower and upper quartiles.   Body density did not differ between lentic and lotic individuals (Mann-Whitney U test, $U = 26.5, N = 26, P = 0.94$).
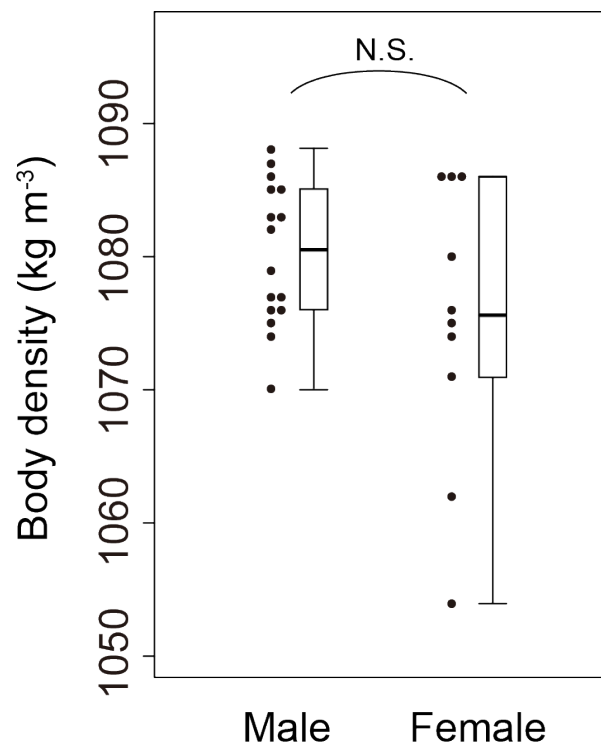
Figure 4-12. Relationship between body density and sex.

Measured body densities compared between sex. Each dot represents the measured body density of an individual. The whiskers of the box plots indicate 1.5 of the interquartile range of the lower and upper quartiles. Body density did not differ between sexes (Mann-Whitney U test, $U = 26.5$, $N = 26$, $P = 0.94$).
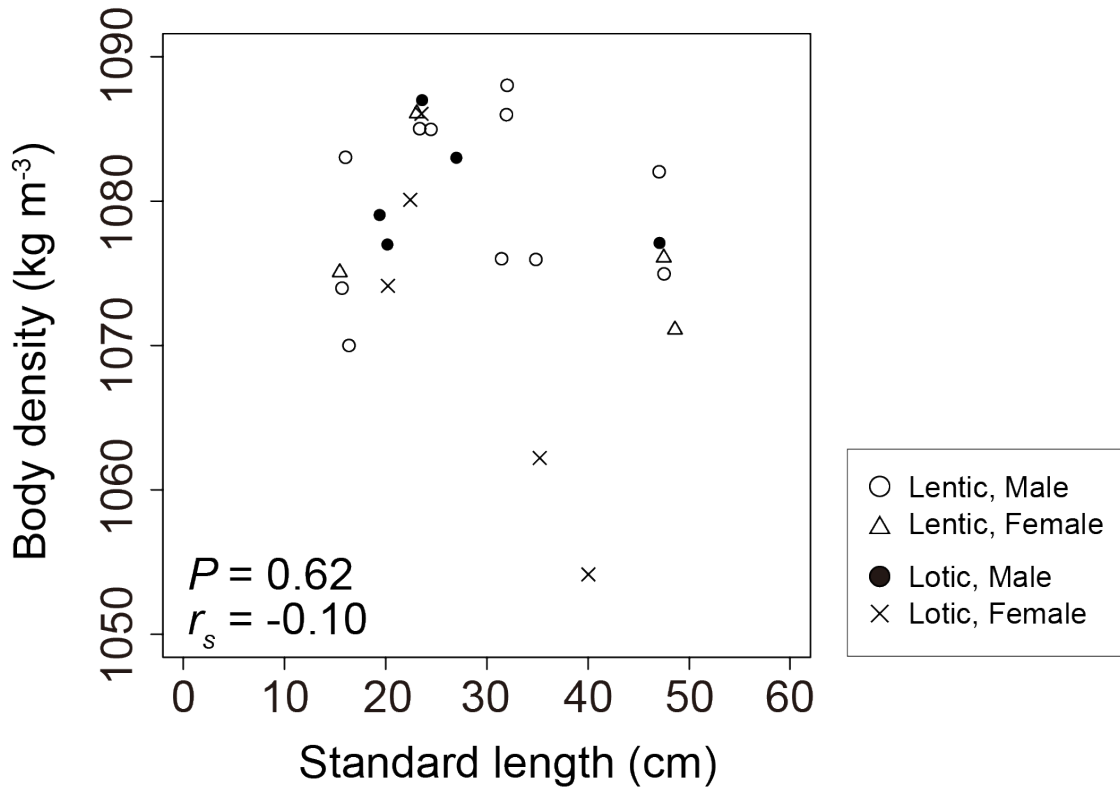
Figure 4-13. Relationship between body density and body size.

Measured body densities are plotted against standard length. Open circles and triangles indicate lentic males and females, respectively, and filled circles and cross marks indicate lotic males and females, respectively. Body density was not significantly correlated with the standard length of the fish (Spearman's correlation test, $P = 0.62$, $r_s = -0.10$).
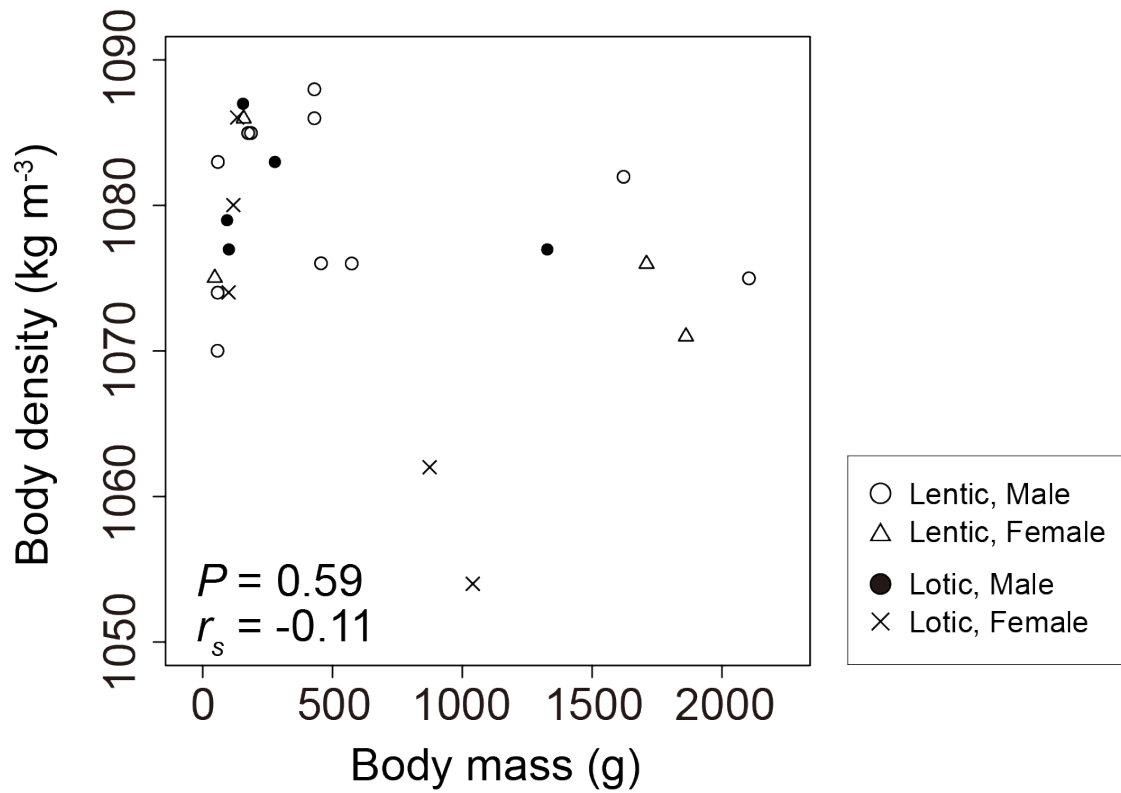
Figure 4-14. Relationship between body density and body mass.

Measured body densities are plotted against body mass.　Open circles and triangles indicate lentic

males and females, respectively, and filled circles and cross marks indicate lotic males and females,

respectively.　Body density was not significantly correlated with the body mass (Spearman's

correlation test, $P = 0.59$, $r_s = -0.11$) of the fish.

Figure 4-15. Relationship between body density and condition factor.

Measured body densities are plotted against condition factor. Open circles and triangles indicate lentic males and females, respectively, and filled circles and cross marks indicate lotic males and females, respectively. There was a significant negative correlation between body density and the condition factor (Spearman's correlation test, $P = 0.017$, $r_s = -0.46$).

CHAPTER 5

Oxygen consumption of channel catfish in relation to buoyancy conditions

（本章の内容は、学術雑誌論文として出版する計画があるため公表できない。5 年以内に出版予定。）

CHAPTER 6　General discussion

（本章の内容は、学術雑誌論文として出版する計画があるため公表できない。5 年以内に出版予定。）

List of symbols and abbreviations

AIC   Akaike's Information Criterion

BM   body mass [kg; g]

CF   condition factor

GLMM   generalized linear mixed model

ODBA   overall dynamic body acceleration

PDBA   partial dynamic body acceleration

SL   standard length [cm]

TL   total length [cm]

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SUMMARY

（本章の内容は、学術雑誌論文として出版する計画があるため公表できない。5 年以内に出版予定。）

APPENDICES

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