Journal of Zoology

Journal of Zoology. Print ISSN 0952-8369

# Swimming behavior in relation to buoyancy in an open swimbladder fish, the Chinese sturgeon

Y. Watanabe[1], Q. Wei[2], D. Yang[2], X. Chen[2], H. Du[2], J. Yang[1,3], K. Sato[1], Y. Naito[4] & N. Miyazaki[5]

1 International Coastal Research Center, Ocean Research Institute, The University of Tokyo, Otsuchi, Iwate, Japan
2 Key Laboratory of Freshwater Fish Germplasm Resources and Biotechnology, Ministry of Agriculture of China, Yangtze River Fisheries Research Institute, Chinese Academy of Fisheries Science, Jingzhou, Hubei, China
3 Freshwater Fisheries Research Center, Chinese Academy of Fishery Sciences, Wuxi, Jiangsu, China
4 National Institute of Polar Research, Itabashi, Tokyo, Japan
5 Ocean Research Institute, The University of Tokyo, Nakano, Tokyo, Japan

**Keywords**
buoyancy; swimbladder; physostome; swim speed; tailbeat; release system; data logger; sturgeon.

**Correspondence**
Qiwei Wei, Key Laboratory of Freshwater Fish Germplasm Resources and Biotechnology, Ministry of Agriculture of China, Yangtze River Fisheries Research Institute, Chinese Academy of Fisheries Science, Jingzhou, Hubei 434000, China.
Email: weiqw@yfi.ac.cn

Editor: Gunther Zupanc

Received 14 November 2007; revised 29 April 2008; accepted 27 March 2008

doi:10.1111/j.1469-7998.2008.00451.x

## Abstract

The swimbladder of fishes is readily compressed by hydrostatic pressure with depth, causing changes in buoyancy. While modern fishes can regulate buoyancy by secreting gases from the blood into the swimbladder, primitive fishes, such as sturgeons, lack this secretion mechanism and rely entirely on air gulped at the surface to inflate the swimbladder. Therefore, sturgeons may experience changes in buoyancy that will affect their behavior at different depths. To test this prediction, we attached data loggers to seven free-ranging Chinese sturgeons *Acipenser sinensis* in the Yangtze River, China, to monitor their depth utilization, tail-beating activity, swim speed and body inclination. Two distinct, individual-specific, behavioral patterns were observed. Four fish swam at shallow depths (7–31 m), at speeds of 0.5–0.6 m $s^{-1}$, with ascending and descending movements of 1.0–2.4 m in amplitude. They beat their tails continuously, indicating that their buoyancy was close to neutral with their inflated swimbladders. In addition, their occasional visits to the surface suggest that they gulped air to inflate their swimbladders. The other three fish spent most of their time (88–94%) on the river bottom at a depth of 106–122 m with minimum activity. They occasionally swam upwards at speeds of 0.6–0.8 m $s^{-1}$ with intense tailbeats before gliding back passively to the bottom, in a manner similar to fishes that lack a swimbladder. Their bladders were probably collapsed by hydrostatic pressure, resulting in negative buoyancy. We conclude that Chinese sturgeons behave according to their buoyancy, which varies with depth due to hydrostatic compression of the swimbladder.

## Introduction

Buoyancy is one of the primary external forces acting on most aquatic vertebrates, from fish to whales, and as such can affect the swimming energetics of these animals. The force is proportional to the difference between the total density of the body and that of the surrounding water. In this regard, the substantial amount of gases present in the lungs of air-breathing divers or in the swimbladder of fishes can profoundly affect the overall body density, because the gas density is extremely low compared with that of the animals' tissues (Alexander, 1990, 1993). Furthermore, the volume of gas changes with hydrostatic pressure, causing changes in buoyancy. In short, when the animal ascends, the gases will expand and the density of the animal will decrease; when it descends, the gases will be compressed and the density of the animal will increase.

How aquatic vertebrates deal with buoyancy is relatively well understood in air-breathing divers, due to the recent advances in the development of animal-borne data loggers that make it possible for researchers to monitor stroking activity of animals in water. It is known, for instance, that seals (Williams *et al*., 2000; Davis *et al*., 2001; Sato *et al*., 2003; Watanabe *et al*., 2006) and some diving seabirds (alcids and cormorants, Watanuki *et al*., 2003, 2005, 2006; Lovvorn *et al*., 2004) stroke heavily at the onset of their dives probably to counteract positive buoyancy, and, as ambient pressure compresses air in the lung and their buoyancy progressively decreases, incorporate more and more periods of gliding. Similarly, penguins stop stroking during the final stages of ascents and return to the surface passively with increasing positive buoyancy (Sato *et al*., 2002; Wilson & Liebsh, 2003; Kato *et al*., 2006). Besides seals and seabirds, there are now numerous reports of similar stroke

  

patterns in relation to buoyancy in whales (Nowacek *et al.*, 2001; Miller *et al.*, 2004; Goldbogen *et al.*, 2006) and sea turtles (Hays *et al.*, 2004; Hays, Marshall & Seminoff, 2007).

In contrast to air-breathing divers, such investigations on fishes are still limited. The studies of Tanaka, Takagi & Naito (2001) on chum salmon *Oncorhynchus keta* and Kawabe *et al.* (2004) on Japanese flounder *Paralichthys olivaceus* are the only reports. These authors showed that, while fish with a swimbladder (salmon) beat their tails continuously both during ascent and descent phases (Tanaka *et al.*, 2001), those that lack a swimbladder (flounder) stroke actively only when ascending and glide passively when descending (Kawabe *et al.*, 2004). However, little is known about the effect of ambient pressure on the behavior of fishes, although fishes often move vertically as well as horizontally (Godø & Michalsen, 2000; Kitagawa *et al.*, 2000; Tanaka, Takagi & Naito, 2000).

An important difference between swimbladders of fishes and lungs of air breathers is that the former can inflate while the animal is submerged. Generally, modern fishes are capable of secreting gases from the blood into swimbladders, using a mechanism that evolved some 130–140 million years ago (Berenbrink *et al.*, 2005). A tight bundle of arterial and venous capillaries running closely together in opposite directions known as the rete mirabile plays a central role in this mechanism (Harden Jones & Marshall, 1953; Alexander, 1966, 1993). The rete mirabile is found in physoclists (fishes in which the swimbladder has no connections to the outside) and a proportion of physostomes (fishes with the pneumatic duct connecting the swimbladder to some part of the gut) (Harden Jones & Marshall, 1953). Fishes with a rete mirabile can regulate the swimbladder volume (and thus their buoyancy) in response to changes in ambient pressure (Harden Jones & Marshall, 1953; Alexander, 1966, 1993), so that the effect of depth on the behavior of these fishes is expected to be limited. However, because gas secretion into the swimbladder is slow, these fishes will experience negative buoyancy during short-term excursions to greater depths (Alexander, 1966, 1993; Strand, Jorgensen & Huse, 2005). On the other hand, some physostomes, especially primitive ones (Berenbrink *et al.*, 2005), lack a rete mirabile (Harden Jones & Marshall, 1953). These fishes are expected to experience drastic changes in buoyancy under different pressures, as shown in laboratory conditions (Evans & Damant, 1928; Bishai, 1961; Brawn, 1962). Accordingly, they are expected to show variable tail-beating activities with depth, similar in that to seals and seabirds.

A typical example of a fish that lack a rete mirabile are sturgeons (genus *Acipenser*; Fig. 1; Berenbrink *et al.*, 2005), a primitive ray-finned fish in the order Acipenseriformes (Bemis, Findeis & Grande, 1997). In this study, we attached acceleration data loggers to Chinese sturgeons *Acipenser sinensis*, swimming in the Yangtze River, China, to simultaneously record depth, tail-beating activity, swim speed and body inclination (pitch) of the fish. The objective of our study was to determine possible variations in the swimming behavior of Chinese sturgeons at different depths.

## Materials and methods

### Study site and animals

A total of seven Chinese sturgeons cultured at the Yangtze River Fisheries Institute were instrumented with data loggers (Table 1) and released from a boat in the Yangtze River, China, in 2005 and 2006. The release points were 200 km (30.97°N, 109.35°E) and 140 km (31.01°N, 109.76°E) upstream of the Three Gorges Dam in 2005 and 2006, respectively. Water depth in the study area is deep, occasionally exceeding 170 m, because of the presence of the dam. This study was conducted with permission from the Ministry of Agriculture of China.

### Data loggers

We used a 128 Mbit M190L-D2GT accelerometer (15 mm in diameter, 53 mm in length, 16 g in air; Little Leonardo Co., Tokyo, Japan) in 2005 and a 256 Mbit W190L-PD2GT

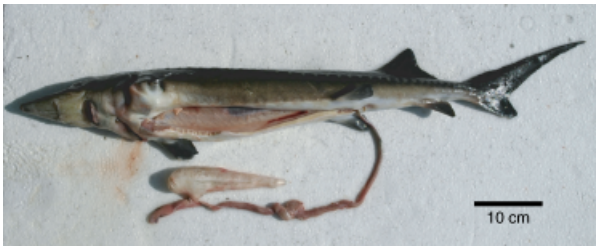


**Figure 1** Swimbladder of the physostome fish Amur sturgeon is connected to the esophagus by a pneumatic duct.

**Table 1** Descriptive information about the Chinese sturgeons used in the study

| Individual | Body mass (kg) | Body length (cm) | Type of data logger | Data length (h) | Month/year of the experiment |
|---|---|---|---|---|---|
| Fish05A | 7.7 | 95 | D2GT | 24 | 03/2005 |
| Fish05B | 5.9 | 78 | D2GT | 72 | 03/2005 |
| Fish05C | 10.1 | 110 | DSL | 6 | 03/2005 |
| Fish06A | 23.1 | 122 | PD2GT | 5 | 03/2006 |
| Fish06B | 18.0 | 113 | PD2GT | 24 | 03/2006 |
| Fish06C | 18.1 | 115 | PD2GT | 24 | 03/2006 |
| Fish06D | 20.0 | 114 | PD2GT | 48 | 03/2006 |

 

accelerometer (21 mm in diameter, 117 mm in length, 60 g in air) in 2006 (Table 1). In addition, one fish in 2005 was equipped with a 2 Gbit digital still-picture logger (DSL-380DTV; 22 mm in diameter, 138 mm in length, 73 g in air; Little Leonardo Co.). PD2GT-type loggers recorded swim speed, depth and temperature at 1 s intervals, and accelerations along two axes (for detecting tail-beating activity and pitch) at 1/32 s intervals. The D2GT-type loggers only recorded depth and temperature at 1 s intervals, and accelerations along two axes at 1/16 s intervals. The DSL-type logger recorded depth and temperature at 1 s intervals, and still color images (370 × 296 pixels) at 60 s intervals. The maximum range of the depth sensor was 190 m with a resolution of 0.046 m for the PD2GT and D2GT loggers, and was 380 m with a resolution of 0.093 m for the DSL logger.

## Data recovery

Our archival data loggers must be recovered to obtain the data. Because the recapture of sturgeons is almost impossible, we used a modified version of an automatic time-scheduled release system originally developed for Baikal seals (Watanabe *et al.*, 2004; Fig. 2). The data loggers were attached to a float of copolymer foam (Nichiyu Giken Kogyo Co., Saitama, Japan), on the top of which a VHF radio transmitter with a 24 cm semi-rigid wire antenna (Advanced Telemetry Systems Inc., Isanti, MN, USA) was embedded. A tiny hole was pierced on the back of the fish, above the pectoral fins, and a thin plastic cable connected to a time-scheduled release mechanism (Little Leonardo Co.) was passed through the hole and fastened around the logger package. The release mechanism included a timer that was activated after 5–72 h following the attachment (Table 1). Once the release mechanism had been activated, the plastic cable was severed by an electric charge, and the whole buoyant package was released from the fish. The package could be located via VHF radio signals using a receiver and a four-element Yagi antenna (Ham Center Sapporo, Hokkaido, Japan). A reward was offered for the return of the package to facilitate recovery in case we failed to locate it. The total weight of the packages (data loggers and recovery system) was 52, 115 and 104 g in air for D2GT, PD2GT and DSL system, respectively (0.5–1.0% of the body mass of the fish). Its buoyancy offset 10, 11 and 7 g in water for D2GT, PD2GT and DSL system, respectively.

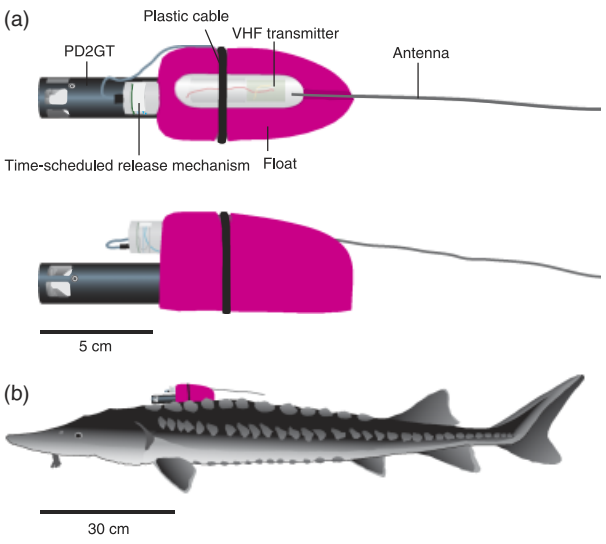


**Figure 2** (a) Top and side views of the time-release package containing the data logger and (b) method of attachment to the sturgeons.

In 2005, we did not try to locate the fish before the instrument was released. As a result, we failed to recover one of the three instruments by ourselves. Fortunately, it was found a day later by a fisherman and returned to us. In the next year, we deployed an acoustic transmitter (V16; 16 mm in diameter, 96 mm in length, 16 g in air, 14 g in water; Vemco, Nova Scotia, Canada) in tandem with the logger. The acoustic signals were detected by a hydrophone (VH110; Vemco) and a receiver (VR100; Vemco) deployed on the boat, allowing us to monitor occasionally the location of the fish until the package was released. The transmitter also provided us with depth data at 15–30 s intervals. With this system, we were able to retrieve all the loggers in 2006.

## Speed calibration

Relative swim speed was recorded by PD2GT loggers as the number of revolutions per second (rev $s^{-1}$) of a propeller mounted on the anterior end of the logger. To convert rotations to actual swim speed (m $s^{-1}$), a calibration experiment was conducted onboard the R/V '*Yayoi*' from the International Coastal Research Center of the University of Tokyo, while navigating in Otsuchi Bay, Japan in September 2006. A dead specimen of Amur sturgeons *Acipenser schrencki* (mass: 2.6 kg; body length: 62 cm), a species closely related to Chinese sturgeons, provided by the Sunrock aquafarm (Iwate, Japan) was successively equipped with two PD2GT loggers that had been previously used on free-ranging sturgeons. The dead fish was bound to a metal column, originally designed to accommodate water samplers, and attached to the wire of the *Yayoi*, so that the fish was in a head-up vertical posture in the water. We lowered the specimen into the water at a depth of *c.* 60 m, and pulled it vertically toward the surface with an electric winch at seven different speeds ranging from 0.14 to 2.25 m $s^{-1}$. The mean propeller revolution rates (rev $s^{-1}$) recorded by the logger were subsequently plotted against the speed of the electric winch (m $s^{-1}$). For both loggers, the relationships were linear ($R^2 = 1.00$ for both loggers) for speeds $\geq 0.20$ m $s^{-1}$. Speeds $< 0.20$ m $s^{-1}$ were considered indistinguishable from zero. Swim speed resolutions, which correspond to the speed equivalent to one revolution of the propeller, were 0.018 or 0.020 m $s^{-1}$, depending on the loggers. Accuracy of swim speed, that is, standard error of the regression (Zar, 1999) was 0.016 or 0.026 m $s^{-1}$, for the two loggers, respectively.

### Acceleration data analysis

From lateral acceleration records, we extracted information on tailbeats of the fish by filtering out the low-frequency signals with IGOR Pro (WaveMetrics Inc., Lake Oswego, OR, USA) (Sato *et al.*, 2003). Individual tailbeat was defined as the period taken by the tail to move from one extreme lateral position and back to the original position. Tailbeat frequency (Hz) was calculated as the number of tailbeats divided by the duration (s) of the period. For the fish that stayed on the riverbed with occasional upward active swimming followed by gliding periods (see 'Results' below), the irregularity of the signal during the active swimming periods prevented us from extracting tailbeat activity. From longitudinal acceleration records, we calculated the pitch of the fish by filtering out the high-frequency signals (Tanaka *et al.*, 2001). Ascents and descents were represented by positive and negative pitch values, respectively. To adjust the signal to the horizontal level, we corrected the pitch values recorded in the holding tank before releasing to 0°, because the instrumented sturgeons lay on the bottom of the tank.

### Measurement of body density

We measured the body density of Amur sturgeons in the facilities of the International Coastal Research Center. Four live fish (mass: $2.2 \pm 0.4$ kg; body length: $63.6 \pm 2.5$ cm) provided by the Sunrock aquafarm were kept in a tank for 1 day and then killed with overdose of 2-phenoxyethanol. Because the dead fish floated in seawater and sank in freshwater, we mixed seawater and freshwater until the fish became neutrally buoyant, before measuring the water density (equivalent to the fish density) with a gravimeter. We subsequently opened up the abdomen of the fish and removed the gas from the bladder with a syringe. After this operation, the fish sank in seawater. We added salt to seawater until the fish became once again neutrally buoyant, and measured the water density.

### Statistical analysis

We used Excel 2003 (Microsoft Corp., Redmond, WA, USA) and Stat View (SAS Institute, Cary, NC, USA) for statistical analysis. Value for statistical significance was set at $P < 0.05$. Means ($\pm$ SD) are reported.

## Results

We collected a total of 203 h of data from the seven fish. There were two distinct, individual-specific patterns in the swimming behavior of the fish. Four fish (Fish05A, Fish05C, Fish06A and Fish06C) swam at shallow depths (mean: Fish05A, 31.1 m; Fish05C, 10.0 m; Fish06A, 7.2 m; Fish06C, 10.2 m) throughout the recording periods (Fig. 3a). They moved successively upward and downward, beating their tails continuously (Fig. 3b and c), indicating that they swam in the water column. This was supported by the image data obtained for Fish05C; among 212 images taken, only four images (2%) showed the bottom (Fig. 4a) and the rest (98%) were empty (Fig. 4b). The mean amplitude of the vertical movements was $2.4 \pm 4.3$ m ($n = 1679$), $1.6 \pm 1.6$ m ($n = 523$), $1.0 \pm 1.3$ m ($n = 960$) and $1.5 \pm 1.3$ m ($n = 2565$), for Fish05A, Fish05C, Fish06A and Fish06C, respectively. The first 4.8 h of the 24 h record of Fish05A differed from the rest of the recording. Here, the slow speed, the near-constant depth and the little activity recorded in the acceleration signals suggest that the fish stayed on the riverbed, at a depth of 25–36 m. Occasional surfacing behaviors ($n = 20$ for the four fish) were observed while swimming off the riverbed (Fig. 3a and b). The fish actively swam toward the surface, increasing their speed up to 3 m s$^{-1}$ and their pitch up to 80° (Fig. 3d). Upon reaching the surface, the speed decreased abruptly, indicating that the propeller of the logger was in air at that time. The fish stayed at the surface for only a second or two. During the following descent, both the speed and the pitch progressively decreased, while the fish continued to beat its tail actively. In 18 of the 20 surfacings, the depths (averaged over one ascent–descent cycle) were greater after the surfacing than before (Fig. 3a and b).

In contrast, the other three fish (Fish05B, Fish06B and Fish06D) swam at greater depth (mean: Fish05B, 122.4 m; Fish06B, 112.7 m; Fish06D, 105.7 m) and spent most of the time (Fish05B, 94.4%; Fish06B, 87.9%; Fish06D, 93.9%) with little activity (Fig. 5). This, together with the correspondence between the depth data provided by the acoustic transmitter and the depth of the riverbed, indicates that these three fish stayed predominantly on the river floor. Occasional departures from the riverbed occurred at mean intervals of $12.5 \pm 25.9$ min ($n = 315$), $18.4 \pm 24.8$ min ($n = 67$) and $21.3 \pm 28.9$ min ($n = 124$) for Fish05B, Fish06B and Fish06D, respectively (Fig. 5a). During the excursions, they beat their tails only when ascending (Fig. 5b). The propeller of the loggers stopped during the descents (Fig. 5b), suggesting that the longitudinal axis of the fish was not parallel to the swimming direction during this phase. None of these individuals reached the surface during any of the excursions off the riverbed; the shallowest depths reached were 23.9, 0.9 and 11.1 m for Fish05B, Fish06B and Fish06D, respectively.

To facilitate analysis, we extracted ascents and descents during which changes in depth were $> 2$ m (Table 2). The pitch of the fish that swam at greater depths varied greatly (high standard deviation) both in ascent and descent phases, compared with that of the fish that swam at shallower depths. There were significant differences in pitch values between the six individuals, for both ascent (ANOVA, $P < 0.0001$) and descent phases (ANOVA, $P < 0.0001$). A Scheffe's *post hoc* test revealed that deep swimming fish displayed significantly higher pitch (i.e. more head-up attitude) during ascents than the other fish ($P < 0.0001$ for all the nine combinations). Furthermore, deep swimming fish frequently (Fish05B, 90.4%; Fish06B, 56.5%; Fish06D, 66.7%) descended with the mean pitch of $> 0°$ (i.e. head-up attitude). The speed of the two shallow swimmers equipped with PD2GT loggers (Fish06A and Fish06C) increased

 

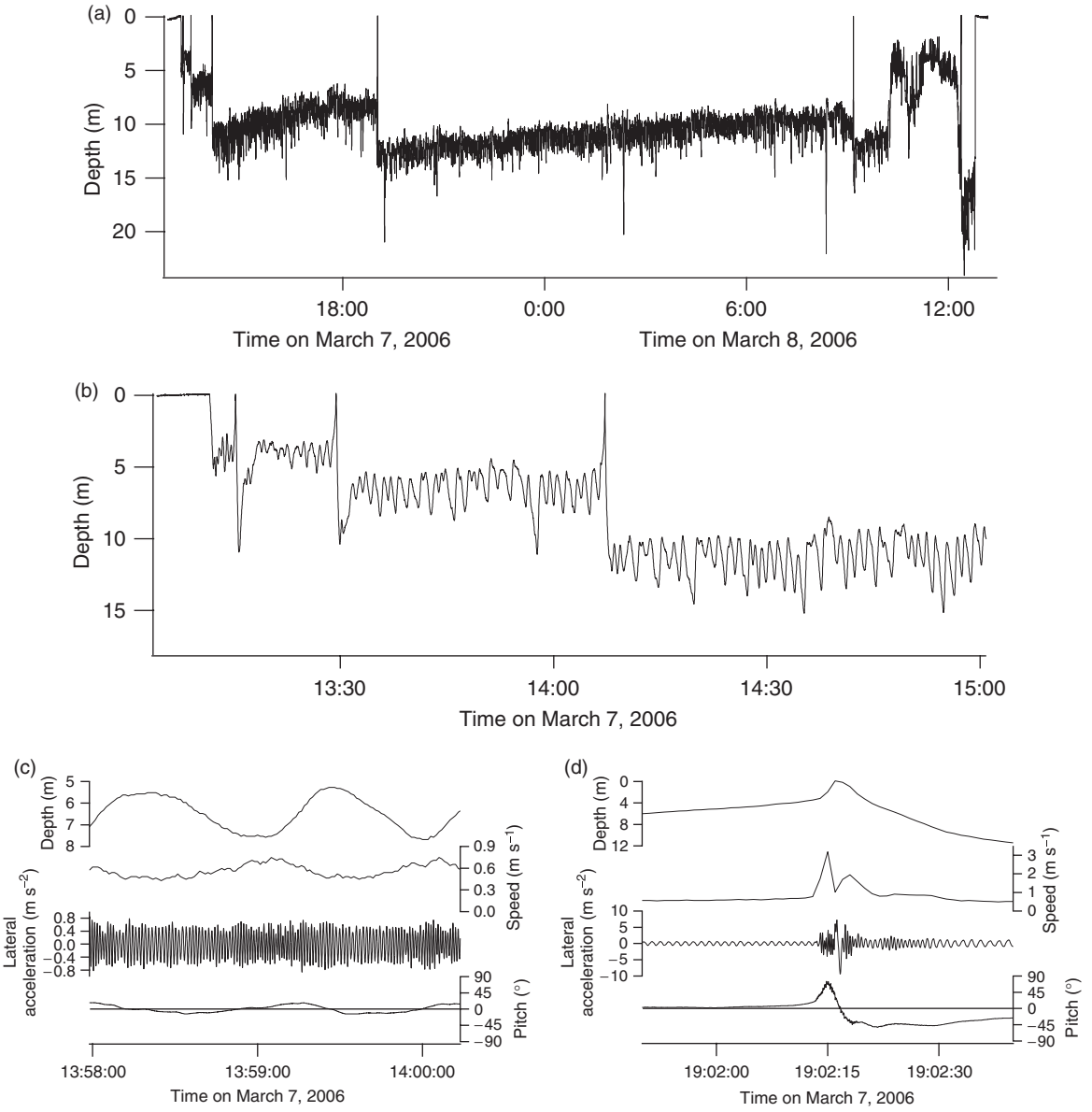


**Figure 3** Swimming behavior of sturgeon Fish06C that swam at shallow depths, showing (a) the complete depth record from fish release to package pop-up and recovery; and (b) an enlarged view of the first 2 hours. Depth, swim speed, lateral acceleration and pitch (i.e. angle between long axis of fish's body and water surface, with positive values indicating ascent and negative descent) during (c) ascending and descending movements, and during (d) a surfacing event.

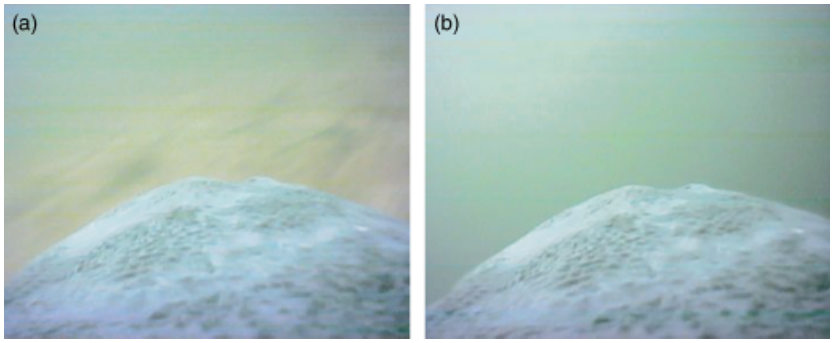


**Figure 4** Images taken by the fish-borne, digital still-pictures camera logger (looking forward over the fish's head), showing (a) the riverbed at 13.9 m and (b) an empty field taken at 11.2 m depth.

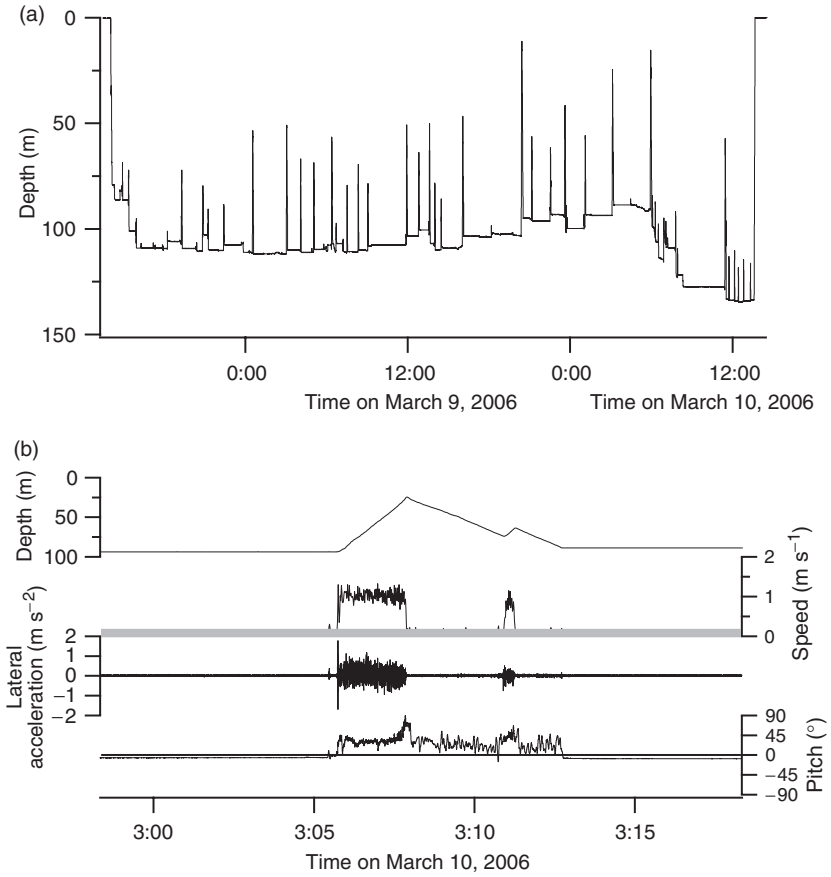


**Figure 5** Swimming behavior of sturgeon Fish06D that stayed predominantly at great depths, showing (a) the complete depth record from fish release to package pop-up and recovery; and (b) the depth, swim speed, lateral acceleration and pitch (i.e. angle between long axis of fish's body and water surface, with positive values indicating ascent and negative descent) during a 20-min period that included an excursion off the bottom. Note that speed is often below the stall speed (0.2 m $s^{-1}$) of the sensor (gray horizontal bar).

linearly with tailbeat frequency both during ascent (ANOVA, $P<0.0001$ for Fish06A and Fish06C) and descent phases (ANOVA, $P<0.0001$ for Fish06A and Fish06C; Fig. 6). In Fish06A, the slope of the regression line was significantly higher during ascents than descents ($t$-test, $P<0.05$; Zar, 1999), and the regression lines intersected at the tailbeat frequency of 1.38 Hz, which is actually higher than the maximum value recorded (1.19 Hz). There was little overlap in the 95% confidence intervals of the regressions, indicating lower swim speeds during ascents than descents at a given tailbeat frequency (Fig. 6a). In Fish06C, the slope of the regression line was significantly lower during ascents than descents ($t$-test, $P<0.005$), and the regression lines intersected at the tailbeat frequency of 1.02 Hz, a value in the middle of the recorded range. There was also considerable overlap in the 95% confidence intervals of the regressions, indicating that the speed achieved at a given tailbeat frequency did not differ between ascent and descent (Fig. 6b).

The body densities of Amur sturgeons before and after gas removal were $1007 \pm 2$ and $1060 \pm 3$ kg $m^{-3}$ ($n = 4$), respectively.

## Discussion

The seven Chinese sturgeons could be separated into two groups that exhibited distinct behavioral patterns. Four fish swam actively at shallow depths (7–31 m) in the water column, while the other three fish swam on the riverbed at greater depths (106–122 m) with occasional excursions from the river floor. Such individual-specific differences can be explained through biomechanical processes in relation to buoyancy, knowing that sturgeons are physostomes that lack a rete mirabile (Berenbrink *et al.*, 2005).

Fish that swam at shallow depths beat their tails continuously both during ascent and descent phases (Fig. 3c), suggesting that their buoyancy was close to neutral. Indeed, animals with highly negative or positive buoyancy often employ gliding when moving in the same direction as that of the buoyancy (Williams *et al.*, 2000; Sato *et al.*, 2002; Kawabe *et al.*, 2004), a strategy that was not used by the shallow swimming fish. At a given tailbeat frequency, Fish06A achieved lower speed when ascending than descending (Fig. 6a), indicating a slightly negative buoyancy.

 

**Table 2** Summary statistics for vertical movements >2 m

| Individual | *n* | Duration (s) | Depth change (m) | Vertical rate (m s$^{-1}$) | Swim speed (m s$^{-1}$) | Swim speed (body length s$^{-1}$) | Tailbeat frequency (Hz) | Pitch (degrees) |
|---|---|---|---|---|---|---|---|---|
| Shallow swimming fish | | | | | | | | |
| Fish05A | | | | | | | | |
| Ascent | 269 | 59.8 ± 26.2 | 6.6 ± 7.3 | 0.11 ± 0.07 | | | 1.08 ± 0.12 | 13.0 ± 6.3 |
| Descent | 359 | 74.5 ± 35.8 | 5.1 ± 5.7 | 0.07 ± 0.05 | | | 1.02 ± 0.11 | −4.9 ± 5.3 |
| Fish05C | | | | | | | | |
| Ascent | 71 | 37.3 ± 16.2 | 4.1 ± 2.3 | 0.12 ± 0.05 | | | | |
| Descent | 83 | 42.6 ± 15.6 | 3.6 ± 1.8 | 0.09 ± 0.04 | | | | |
| Fish06A | | | | | | | | |
| Ascent | 42 | 34.5 ± 14.3 | 3.7 ± 2.3 | 0.11 ± 0.06 | 0.49 ± 0.14 | 0.40 ± 0.12 | 0.77 ± 0.17 | 11.4 ± 5.5 |
| Descent | 41 | 35.2 ± 18.2 | 3.8 ± 3.1 | 0.11 ± 0.07 | 0.47 ± 0.10 | 0.38 ± 0.08 | 0.61 ± 0.14 | −16.3 ± 4.5 |
| Fish06C | | | | | | | | |
| Ascent | 381 | 44.3 ± 16.4 | 3.2 ± 1.5 | 0.08 ± 0.04 | 0.60 ± 0.08 | 0.52 ± 0.07 | 0.91 ± 0.11 | 6.4 ± 4.3 |
| Descent | 394 | 48.8 ± 21.5 | 3.1 ± 1.8 | 0.06 ± 0.04 | 0.55 ± 0.09 | 0.48 ± 0.08 | 0.85 ± 0.11 | −7.8 ± 3.0 |
| Deeply swimming fish | | | | | | | | |
| Fish05B | | | | | | | | |
| Ascent | 205 | 21.7 ± 9.7 | 6.1 ± 5.7 | 0.26 ± 0.12 | | | | 46.7 ± 8.2 |
| Descent | 218 | 32.8 ± 29.3 | 5.8 ± 6.1 | 0.17 ± 0.05 | | | | 28.7 ± 15.3 |
| Fish06B | | | | | | | | |
| Ascent | 130 | 23.1 ± 17.0 | 10.8 ± 11.4 | 0.40 ± 0.15 | 0.64 ± 0.21 | 0.57 ± 0.19 | | 34.0 ± 19.5 |
| Descent | 170 | 38.4 ± 47.0 | 8.3 ± 10.0 | 0.23 ± 0.05 | | | | −5.0 ± 45.1 |
| Fish06D | | | | | | | | |
| Ascent | 86 | 41.7 ± 38.2 | 18.6 ± 20.2 | 0.40 ± 0.11 | 0.83 ± 0.27 | 0.73 ± 0.24 | | 26.4 ± 17.0 |
| Descent | 84 | 71.7 ± 60.6 | 19.1 ± 16.9 | 0.26 ± 0.06 | | | | 4.7 ± 33.6 |

Individuals are separated into two groups based on their behavior (see text for details). Values are mean ± SD.

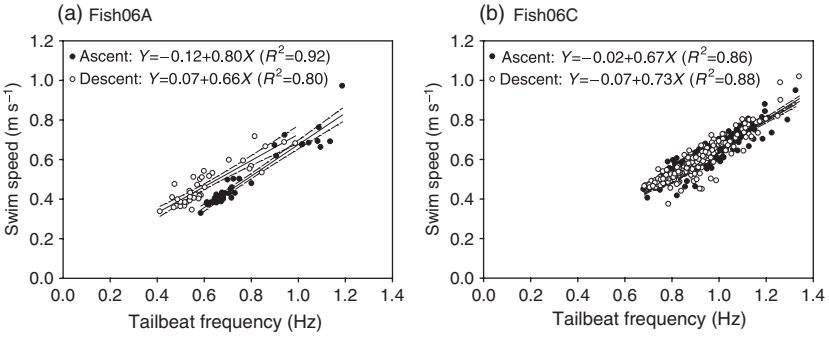


**Figure 6** Tailbeat frequency (Hz) increased linearly with swim speed (m s$^{-1}$) during ascending (filled circles) and descending phases (white circles) for (a) Fish06A and (b) Fish06C. Solid and broken lines represent the best-fit regression lines and the 95% confidence intervals of the regression, respectively. Ascents and descents are defined as vertical movements >2 m.

Fish06C, which swam equally fast at a given tailbeat frequency during ascent and descent phases (Fig. 6b), was probably neutrally buoyant. In addition, the intact, dead specimens of Amur sturgeons were also slightly negatively buoyant. Their mean body density of 1007 kg m$^{-3}$ was close to that of freshwater (1000 kg m$^{-3}$). Overall, this suggests that the swimbladders of the shallow swimming Chinese sturgeons were inflated, assisting them in their swimming behavior. Chum salmons display a similar tailbeat pattern (Tanaka *et al.*, 2001).

These sturgeons visited the surface occasionally (Fig. 3a, b and d), possibly to gulp air to inflate their swimbladders. It is unlikely that surfacing behavior is associated with foraging, because Chinese sturgeons are benthic feeders (Xiong, 1988). One could also argue that the air gulped could be used for respiratory purposes. Indeed, in some fish species, oxygen in the air gulped can be absorbed through the swimbladder, the oral cavity or some parts of the gut (Johansen, 1970). However, it is unlikely to be the case for sturgeons, because their swimbladders do not function for air breathing (Perry *et al.*, 2001). In addition, no previous studies, to our knowledge, reported respiratory functions in the oral cavity or gut of sturgeons. Note that the sturgeons dived to greater depths after each surfacing (Fig. 3a and b).

Some physostomes experimentally subjected to an increase in hydrostatic pressure (and hence a decrease of swimbladder volume) rise to the surface and gulp air to remain buoyant (Evans & Damant, 1928; Bishai, 1961; Brawn, 1962). Based on these observations, Alexander (1966) predicted that for free-ranging physostomes 'every adjustment to an increased depth would require a visit to the surface.' Our observations of sturgeons in the wild match this prediction, and suggest an active regulation of buoyancy in the physostomes.

Fish that swam at greater depths ($>100$ m) showed a substantial tail-beating activity only during ascent phases, while they employed gliding during descent phases (Fig. 5b). This indicates that these fish were negatively buoyant. A similar tailbeat-and-glide behavior, accompanied with zigzags in the depth profile, was previously reported in a flatfish, the Japanese flounder (Kawabe *et al.*, 2004), which lacks a swimbladder. It is therefore probable that the sturgeons' bladders were collapsed by the hydrostatic pressure at depths $>100$ m. Our laboratory experiment on Amur sturgeons with empty bladders supports this notion; the mean body density of 1060 kg m$^{-3}$ of the sturgeons is comparable to that of another flatfish with no swimbladder, the plaice *Pleuronectes platessa*, which was reported to be 1079 kg m$^{-3}$ (Arnold & Weihs, 1978). In other words, sturgeons with empty bladder in freshwater (density: 1000 kg m$^{-3}$) and flatfish in seawater (*c.* 1026 kg m$^{-3}$) are expected to display roughly the same magnitude of negative buoyancy. In the light of this, the similarities in the behavior of sturgeons swimming at depths $>100$ m and flatfish appear less surprising.

Negatively buoyant fishes often adopt a head-up posture while swimming (Evans & Damant, 1928; He & Wardle, 1986; Webb, 1993; Huse & Ona, 1996). By tilting its body, the thrust generated by the fish' swimming movements can have a vertical component, at the expense of the horizontal component, so that the fish avoids sinking (Alexander, 2003). This phenomenon was observed in the sturgeons that stayed close to the riverbed, which displayed more head-up attitude during ascents than that of shallow swimming fish. Furthermore, the deep swimming sturgeons showed head-up attitude even during the descents, suggesting that descending fish used their bodies as hydrofoils to generate lift, in a manner similar to landing airplanes. Sturgeons are known to generate lift from their ventral body surfaces and sometimes from their pectoral fins (Wilga & Lauder, 1999).

The shallowest depths reached by the sturgeons that stayed predominantly near the riverbed (Fish05B, 23.9 m; Fish06B, 0.9 m; Fish06D, 11.1 m) were within the range of the depths at which the other four buoyant fish swam. They, nonetheless, did not regain their buoyancy at those shallow depths and sank back to the riverbed as soon as they stopped beating their tails. Most likely, these deep swimming fish did not have any air left in the swimbladder. The hydrostatic pressure at depths $>100$ m is probably high enough to force the sphincter of the pneumatic duct to open and let the air escape (Harden Jones & Marshall, 1953), or to enhance the diffusion of the air into the blood.

In conclusion, because Chinese sturgeons cannot secret gases into their swimbladders, their swimming behavior is drastically affected by the volume of gas trapped in the swimbladder, which varies with depth. At shallow depths (7–31 m), fish retained a neutral or slightly negative buoyancy with their inflated swimbladders, and swam actively throughout the water column, much like salmons do. In addition, their occasional visits to the surface suggest that they gulped air to inflate their swimbladders. At greater depths (106–122 m), the swimbladders of the sturgeons collapsed, resulting in the fish becoming negatively buoyant. These fish stayed predominantly on the riverbed, interrupted by occasional upward active swimming followed by gliding back to the bottom, in a manner similar to that of flatfish.

## Acknowledgments

We thank T. Kudo and the members of the Yangtze River Fisheries Institute for their assistance with the fieldwork, the captain and crew of the R/V '*Yayoi*' from the International Coastal Research Center for their help with the calibration experiments, N. Katsumata for his help with density measurements, S. Hyodo for productive discussion, T. Kitagawa for helpful comments on the papers and the staff of Center for International Cooperation at the Ocean Research Institute for their logistic support. This work was funded by the Japan Society for the Promotion of Science (19255001, 19380111), the National Nature Science Foundation of China (30490231), the JSPS Research Fellowships for Young Scientists (to Y.W.) and the program 'Bio-logging Science of The University of Tokyo (UTBLS).'

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