

# Swimming behavior of Chinese sturgeon in natural habitat as compared to that in a deep reservoir: preliminary evidence for anthropogenic impacts

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**Abstract** Unusually deep water due to dam construction has the potential to negatively effect endangered sturgeons, which lack a physiological mechanism to inflate their swimbladder and may be unable to remain buoyant under high pressure at depth. In a previous study, some juvenile sturgeons released in a deep (>100 m) reservoir lost buoyancy and stayed nearly motionless on the bottom. However, it is not clear whether this behavior represents a negative effect of the dam, because natural sturgeon swimming behavior is unknown. In this study, we attached multi-sensor data loggers to nine wild adult Chinese sturgeons *Acipenser*

*sinensis* in an unimpounded reach of the Yangtze River, China. The depth utilization, tail beating activity, swim speed, and body inclination of these fish were monitored for 1–3 days. Fish swam up and down successively in the water column (mean depth, 9.9 m) with a cycle of 100–1,000 s during 64 % of the time on average, and stayed at depth, presumably on the riverbed, during rest periods. Tail beats were continuous (mean frequency, 0.77 Hz) throughout the records, indicating that their buoyancy was maintained. These results contrast with the previous study, suggesting that the behavior observed in the reservoir is unusual and that deep water poses a risk of losing buoyancy for sturgeons. Furthermore, all fish intensively swam (maximum speed, 3.0 ms<sup>-1</sup>) to the river surface at a mean frequency of 0.35 times per hour—a behavior that could explain why ship strikes are a serious cause of mortality in sturgeons.

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## Introduction

Sturgeons and paddlefishes (Order Acipenseriformes, representing 27 extant species) are among the most endangered fishes, with most species categorized as critically endangered, endangered, or vulnerable (Pikitch et al. 2005; IUCN 2010). One of the primary reasons for population declines is likely to be the construction of dams (Williot et al. 2002). Many species of Acipenseriformes are anadromous (i.e., ascending rivers

from the sea to spawn), and although some dams are equipped with fishways to aid migration (Rochard et al. 1990), access to their spawning grounds is blocked by dams in many rivers (Williot et al. 2002). Moreover, dams inevitably change the physical environment of the river (e.g., water temperature, river-bed substrates, bed-form morphology, and flow regime), which can cause the degradation of sturgeons' habitats and spawning sites (Baxter 1977; Rochard et al. 1990). Numerous studies have investigated the effects of such environmental characteristics on the ecology of sturgeons, such as habitat use, occurrence of spawning, and egg hatchability (Parsley et al. 1993; Auer 1996a, b; Paragamian et al. 2001; Jordan et al. 2006; Yang et al. 2006; Wei et al. 2009; Zhang et al. 2009; Chen and Wu 2011; Du et al. 2011). Consequently, the importance of those environmental factors on sturgeon conservation is now well recognized.

Little attention has been paid to the effects of increased water depth due to dam construction. Unusually deep water may pose a risk for sturgeons regarding buoyancy regulation, because this primitive fish lacks a physiological mechanism to secrete gases into the swimbladder (Berenbrink et al. 2005) and instead relies on air gulped at the water's surface to inflate the swimbladder. Air volume in the swimbladder decreases rapidly with depth due to increased pressure, resulting in strong negative buoyancy at depths and increasing difficulty for sturgeon to counteract this negative buoyancy at increasing depths. Note that this argument applies only to freshwater habitats (density,  $1,000 \text{ kg m}^{-3}$ ), because denser salt water (density,  $\sim 1,026 \text{ kg m}^{-3}$ ) will assist sturgeons (body density excluding air in the swimbladder,  $1,060 \text{ kg m}^{-3}$ ; Watanabe et al. 2008) in assisting with buoyancy regulation in the sea. Watanabe et al. (2008) reported that some cultured juvenile Chinese sturgeons *Acipenser sinensis* (body weight,  $\sim 15 \text{ kg}$ ) released into the freshwater Three Gorges Reservoir lost buoyancy, as exhibited by intensive tail-beating behavior only while ascending. These individuals remained nearly motionless for most of the time on the deep bottom ( $>100 \text{ m}$ ). However, it is not clear whether this behavior represents a negative effect of the dam, because the swimming behavior of wild Chinese sturgeons under natural conditions is unknown.

In addition, Watanabe et al. (2008) showed that some sturgeons released into the Three Gorges Reservoir occasionally swam to the water's surface, presumably to gulp air for swimbladder inflation. This result may have

important implications for conservation of sturgeons, as it may explain why ship strikes are a serious cause of injury and mortality (Gutreuter et al. 2003; Brown and Murphy 2010), especially in rivers that are not particularly shallow. Gutreuter et al. (2003) estimated that an average of 0.53 shovelnose sturgeons *Scaphirhynchus platyrhynchus* were killed per km of towboat travel in the Mississippi and Illinois River, USA. Brown and Murphy (2010) reported 14 dead Atlantic sturgeons *A. oxyrhynchus* apparently due to ship strikes in Delaware River, USA, from 2005 to 2008. Similarly, we observed 16 deaths of Chinese sturgeons apparently due to ship strikes in the Yangtze River, China, from 2005 to 2009 (Q. Wei, unpubl. data). Previous studies on the behavior of sturgeons in natural habitats have only focused on large-scale horizontal movements (e.g., McCleave et al. 1977; Yang et al. 2006), and fine-scale behavioral data (e.g., swimming depth and speed) have never been obtained. It is therefore unknown whether wild sturgeons under natural conditions show similar surfacing behavior to that exhibited by sturgeons released into the Three Gorges Reservoir.

The objectives of this study were to (1) provide insight into the swimming behavior of wild adult Chinese sturgeons under natural conditions, (2) study the possible effects of increased water depth on sturgeon swimming behavior by comparing the natural swimming behavior described in the first objective and that previously described in a deep reservoir (Watanabe et al. 2008), and (3) examine surfacing behavior, which might pose risks of vessel collision. To accomplish this, we deployed multi-sensor data loggers on wild adult Chinese sturgeons (estimated mean body weight, 198 kg) in the Yangtze River, China, to simultaneously record their swimming depth, speed, tail-beating activity, and body inclination (pitch). Like in many other species of Acipenseriformes, the population of this species has declined dramatically, largely because of the construction of Gezhouba and Three Gorges Dams that have blocked the sturgeon migration routes and changed the physical environment of the Yangtze River (Wang et al. 2011). Improved conservation measures for this species are urgently needed, and results of this study could be useful to design them.

## Materials and methods

Fieldworks were conducted from October to November 2006 and in November 2007, below the Gezhouba

Dam of the Yangtze River, China (30.7°N, 111.3° E), where Chinese sturgeons started to spawn after their migration route had been blocked by the dam (Wei et al. 1997). Many wild adult sturgeons migrating upstream reached the dam during the study periods, which were 1–3 weeks prior to typical spawning time of the species (Wei et al. 1998). A setline with 400–500 barbless hooks, held at the both ends by two fisherman boats, was drifted downstream with water current until a fish was hooked on the body. The captured fish was transported to the sand shore within 1–4 min, depending on the fishing location. When the fish appeared healthy enough, it was measured, tagged, and released within 30 min in most cases and 45 min at maximum; when it did not, it was immediately released without handling. Handling procedures were done in the water, and all fish tagged swam away slowly from the shore when released. Our prior observations have indicated that Chinese sturgeons captured and tagged as above usually behave and spawn normally after release (Wei et al. 1998; Wei 2003; Yang et al. 2006). A total of nine Chinese sturgeons were tagged for this study (Table 1). Total and standard body length was measured, sex was determined with biopsy, and body weight was estimated from standard body length (Q. Wei, unpubl. data).

A 256 Mbit W190L-PD2GT data logger (21 mm in diameter, 117 mm in length, 60 g in air; Little Leonardo Corp. Tokyo, Japan) was used to record swim speed, depth, and temperature at 1 s intervals, and accelerations along 2 axes (for detecting tail-beating activity and pitch angle) at 1/32 s intervals. Our archival loggers need to be recovered to obtain the data, but the recapture of sturgeons is nearly impossible. We therefore used an automatic time-scheduled release system and a recovery technique using VHF radio signals (Watanabe et al. 2004). 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 hole with a diameter of 4 mm was pierced through a scute on the back of the fish by an electric drill, 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 (see Fig. 2 in Watanabe et al. 2008 for design of the package). The release mechanism included a timer that was activated after 24, 48, or 72 h following the setup. The total weight of the packages (data loggers and recovery system) was 115 g (0.04–0.1 % of the body weight of the fish), and its buoyancy offset was 11 g in water. To increase the likelihood of recovery, we also externally

**Table 1** Descriptive information and swimming behavior of nine Chinese sturgeons *Acipenser sinensis*

Fish ID	Sex	Total length (m)	Body weight (kg) <sup>a</sup>	Date of release	Data length (h) <sup>b</sup>	Swimming depth (m)		Proportion of time in up-and-down movement (%)	No. of surfacings per hour	Swimming speed (m s <sup>-1</sup> )		Dominant tailbeat frequency (Hz)
						Mean	Max.			Mean	Max.	
A	f	3.47	252	23 Oct. 2006	8.3	7.9	21.9	100	0.48	1.17	2.32	0.69
B	f	3.45	267	26 Oct. 2006	71.1	12.6	39.1	40	0.13	1.09 <sup>c</sup>	2.56 <sup>c</sup>	0.81
C	f	3.20	252	31 Oct. 2006	23.7	10.7	26.2	51	0.13	1.08	2.80	0.69
D	f	3.05	210	1 Nov. 2007	23.5	12.1	40.6	53	0.38	1.23	3.25	0.88
E	m	2.85	173	3 Nov. 2007	23.4	10.9	21.3	58	0.34	0.99	2.77	0.69
F	m	2.70	140	3 Nov. 2007	47.7	10.0	23.7	90	0.57	1.30	3.42	0.94
G	m	2.45	111	16 Nov. 2007	70.9	7.0	31.0	33	0.08	1.01	3.76	0.66
H	m	2.60	147	17 Nov. 2007	71.5	8.3	34.7	56	0.27	0.89	2.37	1.13
I	f	3.15	230	20 Nov. 2007	23.4	10.0	22.3	93	0.81	- <sup>d</sup>	- <sup>d</sup>	0.44
Mean		2.99	198		40.4	9.9	29.0	64	0.35	1.10	2.96	0.77

<sup>a</sup> Estimated from standard body length

<sup>b</sup> Including putative recovery periods, which are the first 4.0, 1.4, and 1.4 h for fish C, D, and I, respectively

<sup>c</sup> Recorded only for the first 1.9 h due to trouble in sensor

<sup>d</sup> Not recorded due to trouble in sensor

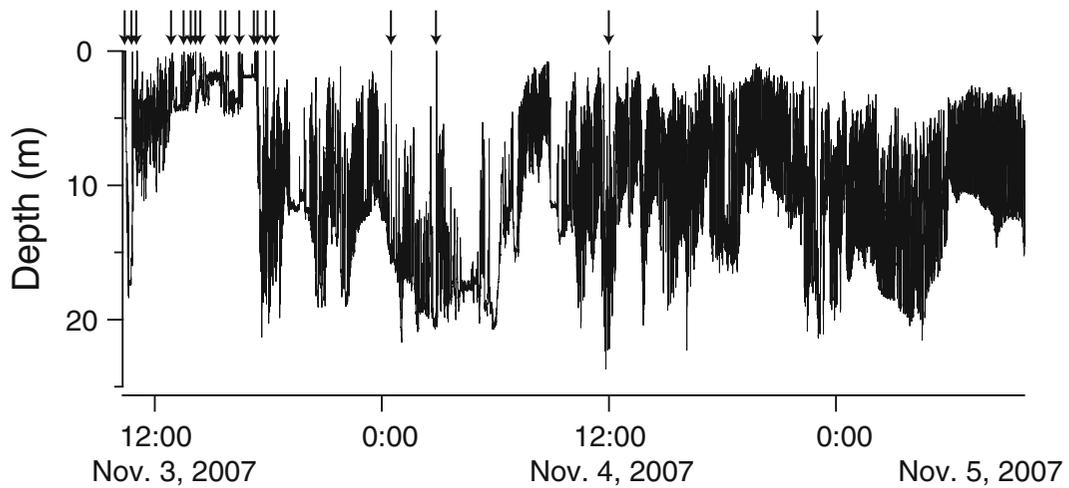
attached an acoustic transmitter (V16; 16 mm in diameter, 96 mm in length, 16 g in air, 14 g in water; Vemco, Nova Scotia, Canada) to a scute on the back of the fish, using a wire passed through a hole pierced by the drill. The transmitter allowed us to monitor the location of the fish occasionally using a hydrophone (VH110; Vemco) and receiver (VR100; Vemco) deployed on a boat until the package was released.

Relative swim speed was recorded as the number of revolutions per second ( $\text{rev s}^{-1}$ ) of a propeller mounted on the anterior end of the logger. These values were converted to actual swim speed ( $\text{m s}^{-1}$ ) using equations from a previous calibration experiment, where loggers were towed vertically in the water column at several known speeds (Watanabe et al. 2008). From longitudinal acceleration records, the pitch angle of the fish was calculated by filtering out high-frequency signals with IGOR Pro (WaveMetrics Inc., Lake Oswego, OR, USA). Positive pitch indicates head-up inclination and negative pitch indicates head-down inclination. To examine the periodicity of swimming depth, we applied continuous wavelet transformation to depth data using the Ethographer package (Sakamoto et al. 2009) with IGOR Pro. Strong periodicity was detected as high magnitude in the spectrogram. Changes in the frequency of surfacing events with time may represent the recovery of the fish from handling effects. Therefore, it was tested using the Generalized Linear Mixed Model (GLMM) with surfacing frequency as a response variable and individuals as a random effect. The models with and without the time elapsed since release of the fish was compared on the basis of Akaike's Information Criterion, and a Chi-square test was used to determine the effect of the term, with the statistical significance set at  $P < 0.05$ . The software R and the package lme4 (The R Project for Statistical Computing, <http://www.r-project.org/>) was used in the analysis. Means ( $\pm$  SD) were reported.

## Results

We collected a total of 364 h of data from the 9 fish (Table 1). The logger from fish "A" was accidentally detached 8.3 h after deployment before activation of the release mechanism, and was recovered from the river surface. Three fish (C, D, and I) stayed on the bottom without tail movements for the first 4.0, 1.4,

and 1.4 h, respectively, before starting to move actively. These fish were likely recovering from being handled, and therefore only data after these periods were analyzed. The propeller speed sensor was stopped, presumably by gravel from the riverbed, 1.9 h after the release in fish "B," during nearly the whole record in fish "I," and for 1.0, 1.8, and 15.4 h in the middle of records for fish "E," "F," and "H," respectively. All fish swam successively upward and downward (Figs. 1 and 2a, b). The depth spectrogram created by continuous wavelet transformation (Fig. S1 in Supplementary Material) indicated that such movements occurred  $64 \pm 24$  % ( $N=9$  individuals) of the time (Table 1), and the cycle of the movements lasted 100–1,000 s. During  $38 \pm 17$  % ( $N=9$  individuals) of the up-and-down movement periods, the depth profiles had flat bottoms (Fig. 2b), suggesting that fish were near the riverbed. There were no apparent sex differences in the swimming patterns (i.e., mean and maximum swimming depth, and the proportion of time spent in up-and-down movement) (Table 1), although our sample size ( $N=9$ ) is not enough to conclude it. Pitch of the fish was head-up when ascending ( $11 \pm 2^\circ$ ,  $N=9$  individuals, excluding very high pitch during surfacing behavior; see below) and head-down when descending ( $-9 \pm 3^\circ$ ,  $N=9$  individuals). During the rest of the time, swimming depth changed more slowly and less regularly (Fig. 2c), and the pitch of the fish was nearly horizontal ( $1 \pm 1^\circ$ ,  $N=8$  individuals). This type of movement was not observed in fish "A," which swam upward and downward successively throughout the record. Lateral acceleration records showed that all fish kept beating their tails throughout the records, with a mean frequency of  $0.77 \pm 0.2$  Hz (Table 1). All fish swam to the river surface at a mean frequency of  $0.35 \pm 0.24$  times per hour ( $N=9$  individuals) (Table 1, Fig. 1). Fish tended to show frequent surfacing behavior during early periods of the records ( $\sim 2$ –8 h, depending on individuals) (Fig. 1). Statistically, the frequency of surfacing events significantly decreased with time (GLMM,  $\chi^2=34$ ,  $P < 0.0001$ ). During each surfacing behavior, the fish swam upward with an increasing swim speed (up to  $3.0 \text{ m s}^{-1}$ ), tail-beat frequency (up to 10 Hz; see Table 1 for normal values), tail-beat strength (indicated by the magnitude of lateral accelerations), and pitch angle (up to  $80^\circ$ ) (Fig. 2d). Upon reaching the surface, the speed decreased abruptly, indicating that

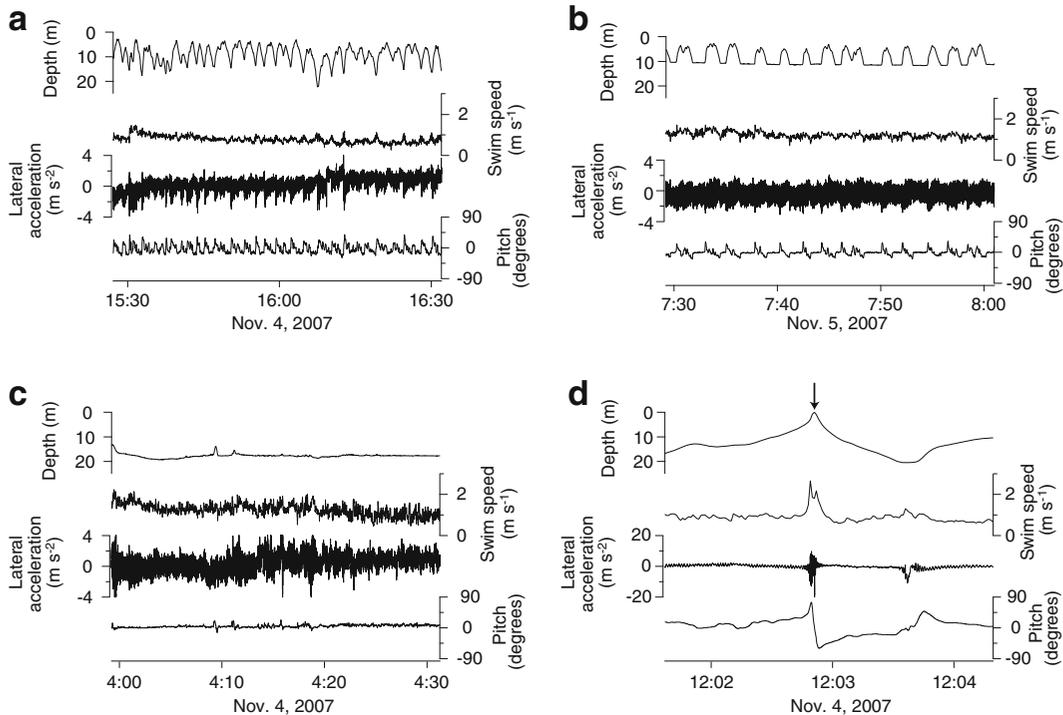


**Fig. 1** The whole record of swimming depth of the Chinese sturgeon “F”. Arrows on the top represent surfacing behavior

the logger propeller was in air at that time. The pitch also decreased abruptly to a negative value (down to  $-70^\circ$ ). During the following descent, speed, tail-beat frequency, and tail-beat strength progressively decreased, whereas pitch increased.

**Discussion**

Our short-term (up to 3 days) behavioral data should be interpreted with caution, because fish may not have been fully recovered from physical trauma and



**Fig. 2** The record of (a) up-and-down movements, (b) up-and-down movements presumably near the riverbed, (c) periods without up-and-down movements, presumably on the riverbed, and (d) a surfacing behavior (denoted by the *arrow*), showing

depth, swim speed, lateral accelerations (indicative of tail beats), and pitch angle. Note that the scale of lateral accelerations in (d) differs from (a)-(c)

physiological stress caused by capture and handling (Cooke and Suski 2005). Although we attempted to minimize such negative impacts (see **Materials and methods**), the initial motionless periods (1–4 h) observed in three of nine fish were similar to those reported in other fish (Campana et al. 2009), indicating that these fish were indeed stressed and recovering. Moreover, the fish in this study showed frequent surfacing behavior during the initial periods (2–8 h) of the records. Given that surfacing behavior might represent gulp of air into the swimbladders to regulate buoyancy (discussed below), our observation suggests that air was lost from the swimbladders while being handled. Nevertheless, all nine fish showed similar and consistent swimming patterns after the initial periods, and we assume that these swimming patterns are natural for the species.

The swimming patterns of wild adult sturgeons were characterized by successive up-and-down movements in the water column (64 % of the time) and occasional surfacing behaviors. The fish were apparently on the riverbed when they stayed at a depth with horizontal pitch angle (36 % of the time). The fish were presumably near the riverbed during up-and-down movements as well, when the depth profiles had flat bottoms (Fig. 2b). Our results show that wild sturgeons migrating upstream use a wide range of the river water column, from the surface down to the bottom. Despite these vertical movements, tail beats were continuous throughout the records in all fish, indicating that their buoyancy was maintained. This swimming behavior does not represent foraging, because wild adult Chinese sturgeons do not forage when migrating upstream (Wei et al. 1997).

In the previous study conducted for juvenile Chinese sturgeons in the deep Three Gorges Reservoir (Watanabe et al. 2008), some individuals showed up-and-down swimming patterns with continuous tail beats, similarly to the adults in this study, at the upper layer (~15 m depth) of the reservoir. However, others lost buoyancy, as indicated by intensive tail-beating behavior exhibited only while ascending, and became nearly motionless at the deep bottom of ~114 m. Such behavior was not observed in this study conducted for adults swimming in their natural habitat. These comparisons indicate that losing buoyancy and being motionless is unusual for the species, and can be attributed to unusually great depths experienced by the individuals. In other words, artificially increased

water depth might negatively affect sturgeon behavior. The individuals that kept swimming at the upper layer in the reservoir might have been under the risk of sinking as well, because losing buoyancy is a feedback process: when descending, the swimbladder compresses and the density of the fish increases, causing it to sink further (Alexander 1967). Once sturgeons lose their buoyancy, they cannot recover it without gulping air at the water surface, because they are not capable of secreting gases into the bladder (Berenbrink et al. 2005). Unfortunately, the behavioral data of the both present and previous studies were only up to 3 days, precluding us from confirming this possibility. Thus, longer-term studies are required to indicate whether individuals that lose buoyancy in deep water are eventually able to adapt to the new environment. Nevertheless, we suggest a previously unrecognized adverse effect of dams that complements previous studies that focus on blockage of migration routes and changes in flow regimes, riverbed substrates, bedform morphology, etc. (Parsley et al. 1993; Auer 1996a, b; Wei et al. 1997; Paragamian et al. 2001; Jordan et al. 2006; Wei et al. 2009; Zhang et al. 2009; Chen and Wu 2011; Du et al. 2011).

All fish in this study swam to the surface intensively at a mean frequency of 0.35 times per hour. The behavioral patterns during surfacing (Fig. 2d) were similar to those of the cultured sturgeons released in the Three Gorges Reservoir (see Fig. 3 in Watanabe et al. 2008), suggesting that the function of surfacing is the same. Surfacing behavior presumably represents gulping air to inflate the swimbladder (Watanabe et al. 2008), as observed in other physostomes (i.e., fishes with the pneumatic duct connecting the swimbladder to some part of the gut) in captivity (Evans and Damant 1928; Bishai 1961). Because gas in the swimbladder would be gradually lost by diffusion (Alexander 1972), it needs to be replenished occasionally in physostomes. However, surfacing may also be a form of communication (Sulak et al. 2002) or have other unknown functions. Whatever the reason, our observation of frequent surfacing behavior in wild sturgeons may have implications for the risk of a ship strike. The large (~200 kg) sturgeons in this study swam toward the surface at an increasing speed, tail-beat frequency, tail-beat strength, and pitch angle. Therefore, avoiding a ship positioned in the pathway of this surfacing behavior may be difficult for sturgeon. Notably, the Yangtze River is now increasingly frequented by

boats: the number of power-driven vessels in the basin increased 2.5 times from 2003 to 2008, to 1 251 000 vessels (Changjiang River Administration of Navigational Affairs, Ministry of Communication, China). Although avoiding ship strikes in the entire Yangtze River is unrealistic, we suggest that regulations should be made for ship navigation and a fish rescue network be set up along the river, particularly within nature reserves for Chinese sturgeons in Yichang.

In conclusion, although our data were collected on a relatively short time scale, our results provide preliminary evidence that the primitive mechanism of buoyancy regulation makes sturgeons especially vulnerable to anthropogenic impact. First, they cannot maintain buoyancy under high pressure, due to the lack of a physiological mechanism to secrete gases into their swimbladders. Thus, they are presumably under the risk of losing buoyancy in artificially deepened water. Second, they intensively swim to the water's surface presumably to gulp air into the swimbladders, thereby posing a risk of ship strikes. Multiple ship strikes have indeed been observed in Chinese sturgeons in the Yangtze River, Atlantic sturgeons in the Delaware River, and shovelnose sturgeons in the Mississippi and the Illinois River. Longer-term studies are required to understand the full extent of anthropogenic impacts on sturgeon survival.

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