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Migrations and movements of adult Chinese sturgeon *Acipenser sinensis* in the Yangtze River, China

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From 2006 to 2009, 27 ultrasonic-tagged wild adult Chinese sturgeon *Acipenser sinensis* [eight males, 19 females; total length (L_T) range = 245–368 cm] were captured on the spawning ground just downstream of Gezhouba Dam (GZD) in the Yangtze River. Twenty-six individuals were tracked for 7 to 707 days (mean number of relocations = 859; range = 3–4549). *Acipenser sinensis* movements were divided into four categories: (1) spawning migration, two tagged *A. sinensis* (one female and one male) returned to the Yangtze River and migrated from the Yangtze Estuary (river kilometer, rkm, 0) to the spawning ground (1678 rkm) between June and October. Their mean upstream ground speed was 1·41 km h^{-1} (range = 0·26–2·35 km h^{-1}). The speed of the male was faster than the female; (2) pre-spawning holding, four of five females tagged in November 2008 stayed within 1678·00–1674·15 rkm for *c*. 1 year before the spawning period; (3) spawning movements, all *A. sinensis* swam mostly from the tailrace of the GZD (1678 rkm) to the Miaozui (1674·15 rkm) reach and some moved downstream *c*. 18·21 rkm (range = 3·93–24·64 rkm), but then, returned upstream to the GZD. Most tagged *A. sinensis* were on the spawning ground on the day when the spawning occurred; (4) post-spawning migration males ($n = 6$) and females ($n = 2$) departed the spawning area on a different time schedule, females leaving before males. The mean seaward ground speed of six *A. sinensis* was 4·87 km h^{-1} (range = 0·68–7·60 km h^{-1}). There were no significant differences ($P > 0·05$) in ground speeds among reaches or between sexes within reaches between telemetry receivers. These broad spatiotemporal scale results will help establish an effective protection strategy for the species in the Yangtze River.

Key words: anadromous fish; post-spawning movements; spatio-temporal movements; spawning movements; ultrasonic telemetry.

INTRODUCTION

Chinese sturgeon *Acipenser sinensis* Gray 1835 is an anadromous fish and one of the most endangered fish species worldwide. Construction of Gezhouba Dam (GZD) at river kilometre (rkm) 1678 in 1981 blocked the upstream migration of *A. sinensis* to their historical spawning reaches. After GZD was completed, a new and also last

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spawning ground was discovered just downstream of GZD (Deng *et al*., 1985; Wei *et al*., 1997; Zhang, 2009).

In the late 20th century, the populations of *A. sinensis* declined dramatically because of overfishing and habitat degradation (Wei *et al*., 1997). The lack of access to historical Yangtze River spawning grounds upstream of GZD led to further adverse effects on the population. The impounding of the reservoir at Three Gorges Dam (TGD) in 2003 has greatly changed the natural river hydrological rhythm which affected the spawning of *A. sinensis* (Ban & Li, 2007). The spawning cohorts below the GZD spawning ground was estimated in the 1980s at 2176 individuals (Ke and Wei, 1992). The number, however, declined to *c*. 200 individuals by 2002 (Qiao *et al*., 2006). The species was classified as critically endangered (CR) on the IUCN Red List in 2010 (http://www.iucnredlist.org/apps/redlist/details/236/0).

Early studies and observations by fishermen provide a general conceptual model for the freshwater part of life-history in the Yangtze River. Before construction of the GZD, adult *A. sinensis* migrated to the upper Yangtze River and lower Jinsha River (2700–3500 rkm) where they spawned. Once entering fresh water from the sea, adult *A. sinensis* stopped feeding and their gonads gradually became mature. After spawning, the fertilized eggs incubated at the spawning ground. After hatching, early life stages migrated downstream and reached the Yangtze Estuary *c*. 6–8 months after spawning. Juveniles entered the sea, reared in unknown coastal waters, and foraged in the sea until they returned to the Yangtze River. When they are sexually matured, female are 14–26 years old and males are 8–18 years old (Yangtze Aquatic Resources Survey Group, 1988; Wei, *et al*. 1997).

Recent investigations of spawning focused on the present GZD spawning ground. Wei *et al*. (1998), Wei (2003) and Yang *et al*. (2006) investigated movements and distribution of adult *A. sinensis* on the spawning ground during the spawning season. These researchers found that adult *A. sinensis* spent most of the time near the dam, especially in the tail water of the Dajiang power plant. Hydroacoustic technology was also used to study the distribution and abundance of spawning *A. sinensis* on the spawning ground and results indicated that the size of the spawning cohorts on the sole spawning ground was *c*. 200 individuals in 2002 (Qiao *et al*., 2006). Watanabe *et al*. (2008) employed an acoustic transmitter to monitor depth utilization, tail-beating activity and swimming speed. Du *et al*. (2011), Zhang *et al*. (2007*a*,*b*, 2008, 2011) and Zhang (2009) described the spawning environment, including depth, topography, velocity and substratum type. All results revealed the environment influenced spawning, and even determined whether spawning was successful. Wei *et al*. (2009) conducted a long-term monitoring of spawning success by capturing early life stages. Moreover, Yi *et al*. (2010) calculated a habitat suitability index (I_{HS}) of *A. sinensis* during spawning, hatching, juvenile and adult growth based on recent published papers and found that the habitat suitability in 1999 was better than the habitat suitability in 2003 when the river was impounded by TGD.

McDowall (1987, 1988, 1992) classified the migrations of fishes into four widely accepted patterns: diadromous, anadromous (*A. sinensis* belongs to this pattern), amphidromous and potamodromous. Moreover, the spawning migrations were further classified into three patterns: one-step spawning migrations, short two-step spawning migrations and long two-step spawning migrations (Kynard, 1997). *Acipenser sinensis* is the typical acipenseriform of long two-step spawning migration and the length of their migration route (1678 rkm) is much further than other acipenseriforms (Bemis & Kynard, 1997). Based on the current understanding of migrations and movements for adult *A. sinensis* in the Yangtze River, this paper hypothesized there are four categories: spawning migration, adult *A. sinensis* enter the river from the sea and swim to the spawning ground; pre-spawning holding, adult *A. sinensis* hold within the spawning ground during the pre-spawning staging period; spawning movement, fish move associated with active spawning behaviour; post-spawning migration, post-spawning adult *A. sinensis* move downstream towards the sea.

Basic information on migration timing and residence period of adult in the Yangtze River is unknown and this lack of information prevents the appropriate spatiotemporal management of adult *A. sinensis* in the river. This paper addressed movements of adult *A. sinensis* during their freshwater period. Specific questions addressed were: (1) the timing of spawning migrations and the swim during upstream migration, (2) the timing of reaching the spawning ground and their movements before, during, and after spawning, and (3) the timing and movement speed of the post-spawning downstream migration. Adult *A. sinensis* were internally or externally tagged with ultrasonic transmitters and a combination of mobile tracking and a series of stationary telemetry receivers spaced along the river were used to monitor movements of tagged adult *A. sinensis*.

MATERIALS AND METHODS

STUDY AREA

The Yangtze River is the third largest river in the world based on the river length and total drainage area. The total river length is >6300 km and the drainage area is *c*. 1·80 million km^2. It flows from west to east and drains through the Yangtze Estuary into the East China Sea at Shanghai. According to the geographical environment and hydrological features, the river can be divided to three reaches: (1) the source to Yichang reach (6300–1700 rkm), (2) Yichang to Hukou reach (1700–770 rkm) and (3) Hukou to the Yangtze Estuary (770–0 rkm). These three reaches (upstream to downstream) are also known as the upper, middle and lower reaches. Study reaches include the middle reach and the Yangtze Estuary reach, which is *c*. 1678 rkm (longitude from Gezhouba Dam, 30° 44′ N; 111°15′ E to 0 rkm, 31° 46′ N; 121° 06′ E) (Chen *et al*., 2007; Fig. 1).

The spawning ground of *A. sinensis* is located in the reach from the GZD to Huyatan, *c*. 25 rkm, which is in the core reach of the *A. sinensis* Nature Reserve at Yichang. It is the sole spawning ground found since construction of the GZD which was also identified as two specific spawning sites: the upstream spawning site and the downstream spawning site (Fig. 2; Wei, 2003). Thirty-six spawning activities have occurred in 21 years (1983–2003), including two spawning periods in each of 15 years (Wei *et al*., 1997; Wei, 2003). Adult *A. sinensis* have returned to this spawning ground annually for many years, although the small area is probably <1% of the historical spawning ground. Pre-spawning and spawning movements of adult *A. sinensis* were monitored in this reach. The reach from the GZD to Miaozui (*c*. 3·85 km long) is the dominant spawning area (Wei *et al*., 1997; Fig. 1). This reach has the topography of a sharply adverse slope and a substratum dominated by cobble and gravel (Wei, 2003; Zhang *et al*., 2008; Zhang 2009).

The reach from Huyatan (1653 rkm) to the Yangtze Estuary is a migration route and also provides probable refuge and holding reaches for pre-spawning or post-spawning adult *A. sinensis* (Yangtze Aquatic Resources Survey Group, 1988). Spatiotemporal movements of tagged adult *A. sinensis* (pre-spawning and post-spawning migrants) were investigated in this reach.

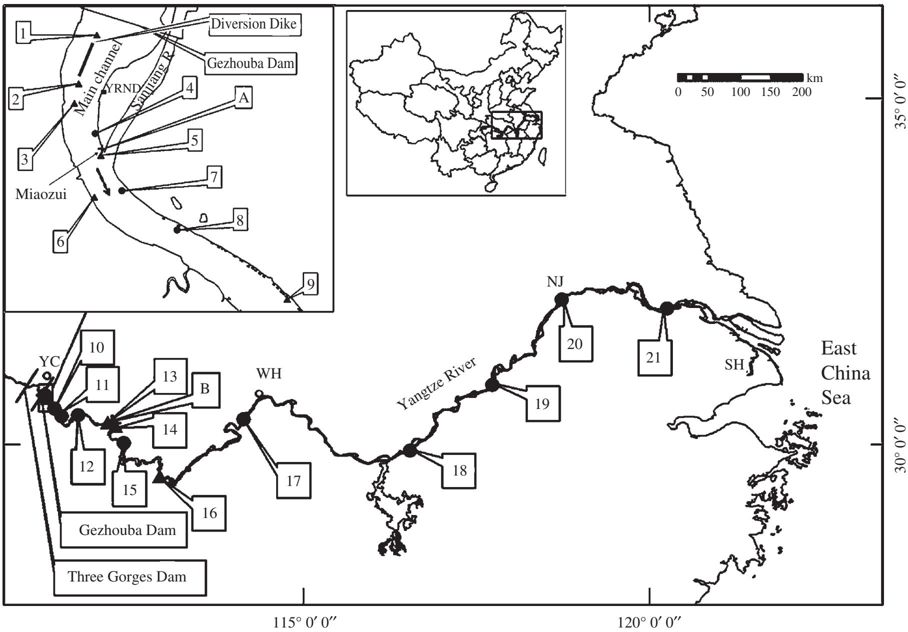

FIG. 1. Map of VR2 (W) receiver sites monitoring movement of adult *Acipenser sinensis* (numbers 1–21). ●, 12 long-term monitoring sites; ▲, nine short-term monitoring sites. A, tagged fish release sites October to November 2006–2008; B, release site of tagged fish recovered at the Beijing Aquarium on 22 April 2007. YC, Yichang; WH, Wuhan; NJ, Nanjing; SH, Shanghai; YRND, Yangtze River Navigation Dockyard.

TAGGED *ACIPENSER SINENSIS*

Adult *A. sinensis* were captured between the tailrace of Dajiang power plant and the Yangtze River Navigation Dockyard (YRND; the area where spawning occurred; Fig. 1) from 20 October to 10 November 2006, 25 October to 20 November 2007 and 20 October to 22 November 2008. Adult *A. sinensis* were captured using the historical fishing method of a series of snag hooks spaced on a long setline spread between two fishing boats.

Captured adult *A. sinensis* were immediately tethered by caudal peduncle using a special cotton bandage and ropes and were pulled into shallow water along a sand beach at Miaozui (1674·15 rkm). Captured adult *A. sinensis* only sustained superficial wounds and appeared not to be harmed during capture and transport. In addition, two other *A. sinensis* (JZ0701 and JZ0702, see Table I) were released at the Jingzhou reach (1521 rkm). They were captured just below the GZD during the spawning seasons in 2005 and 2006, respectively, and transported to and recuperated at the Beijing Aquarium before releasing in the river.

TAGGING

Healthy and active individuals were selected for ultrasonic-tagging. Captured individuals were measured for total length (L_T), and identified for sex and stage of gonad development using an ultrasonography technique, and traditional *in vitro* inspection. Using the development staging for the acipenseriform gonad developed by Conte *et al*. (1988) and Chen (2004), a fish classified as stage IV was close to mature and will spawn that spawning season; however, a stage III fish will spawn in the following spawning season. Each adult was tagged for identification with a passive integrated transponder (PIT) tag, and also, with a single-barb plastic dart tag (size, 10 cm long with appropriate contact information if recaptured by a fisherman).

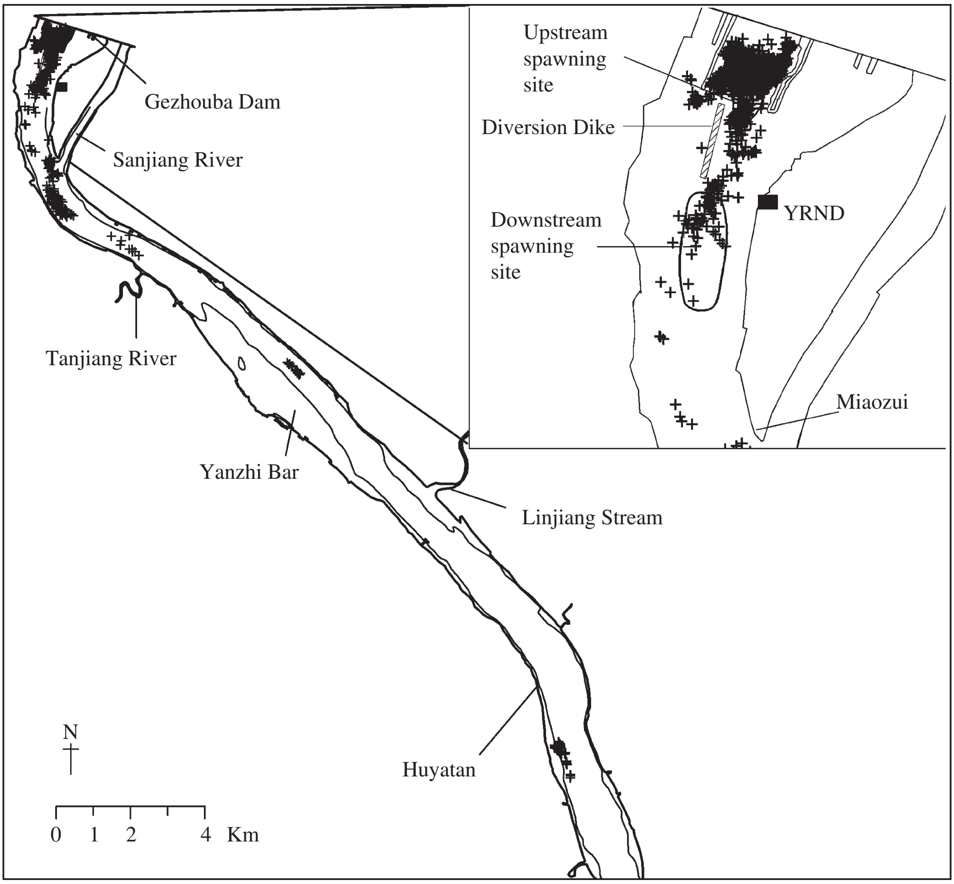

FIG. 2. Locations of adult *Acipenser sinensis* in the Gezhouba Dam spawning ground during the spawning seasons of 2006–2009. (+, tracking locations of adults; YRND, Yangtze River Navigation Dockyard).

An ultrasonic transmitter was implanted into the dorsal musculature or into the abdominal cavity of adult *A. sinensis* depending on the size of the individual (larger fish were tagged in the dorsal musculature, smaller fish were internally tagged). For dorsal musculature implantation, the dorsal muscle adjacent to the fifth back scute was cut with a 3–4 cm long incision using a scalpel and the tag (coated by disinfectant and anti-inflammatory which was composed with penicillin, Yunnan baiyao powder and vaseline) was inserted into the incision and closed using biodegradable medical sutures. For tags inserted into the abdominal cavity, the ventral mid-line adjacent to the sixth ventral scute was cut with 3–4 cm long incision, and the way of implanting tag and suturing the incision was the same as the dorsal muscle implantation. The head of *A. sinensis* was kept immersed in water throughout the whole process. Fish were not anaesthetized as they were too large. Implantation of tags took <30 min for the entire procedure. All tagged adult *A. sinensis* were immediately allowed to swim free into the river.

Six types of V16 (P) ultrasonic transmitters (Vemco Ltd; www.vemco.com) and one type of CHP–87 ultrasonic transmitter (Sonotronics Ltd; www.sonotronics.com) were used and four sizes, diameter × length of (16 × 95, 16 × 98, 16 × 71, 18 × 110 mm) and mass of 36, 36, 25 and 38 g in air, respectively. Transmitter tags V16 (P) and CHP–87 tags transmitted on 69 and 40 kHz acoustic frequency. Each transmitter tag was pulse coded, which provided a unique identification code for each adult. CHP–87 tags were only able to be detected by the

TABLE I. Biological characteristics, tagging-release date and site, number of days fish were located, and fate for tagged adult *Acipenser sinensis* in 2006–2009

Code	Sex	L_T	Gonad stage	Tag–release Date	Tag–release Site	Number days fish located	Fate of fish
MZ0601	F	347	IV	23/10/2006	Miaozui	22	alive
MZ0602	F	325	IV	25/10/2006	Miaozui	20	alive
MZ0603	F	345	IV	25/10/2006	Miaozui	20	alive
MZ0604	F	335	IV	27/10/2006	Miaozui	11	alive
MZ0605	F	298	IV	30/10/2006	Miaozui	7	alive
MZ0606	F	320	IV	31/10/2006	Miaozui	20	alive
JZ0701	F	368	IV	22/4/2007	Jingzhou	547	killed
JZ0702	F	288	IV	22/4/2007	Jingzhou	12	alive
MZ0703	M	300	IV	28/10/2007	Miaozui	177	alive
MZ0704	F	290	IV	29/10/2007	Miaozui	422	alive
MZ0705	M	280	IV	29/10/2007	Miaozui	25	alive
MZ0706	M	320	IV	29/10/2007	Miaozui	101	alive
MZ0707	F	305	IV	1/11/2007	Miaozui	45	alive
MZ0708	M	270	IV	3/11/2007	Miaozui	23	alive
MZ0709	M	285	IV	3/11/2007	Miaozui	144	alive
MZ07010	M	270	IV	3/11/2007	Miaozui	23	alive
MZ07011	F	312	III	10/11/2007	Miaozui	0	alive
MZ07012	M	245	IV	15/11/2007	Miaozui	10	alive
MZ07013	M	260	IV	16/11/2007	Miaozui	707	killed
MZ07014	F	315	IV	19/11/2007	Miaozui	13	alive
MZ0801	F	355	III	17/11/2008	Miaozui	350	alive
MZ0802	F	355	IV	18/11/2008	Miaozui	42	alive
MZ0803	F	330	IV	19/11/2008	Miaozui	7	alive
MZ0804	F	340	III	20/11/2008	Miaozui	87	alive
MZ0805	F	316	III	22/11/2008	Miaozui	380	alive
MZ0806	F	340	III	24/11/2008	Miaozui	343	alive
MZ0807	F	312	III	25/11/2008	Miaozui	381	alive

F, female; M, male; L_T, total length.

VH100 hydrophone and were not recorded by VR100 receivers and VR2 (W) receivers. The longevity of transmitters used in the study ranged from 159 days to 3 years. No tag exceeded 0·47% of a fish's body mass.

MOBILE TRACKING AND PASSIVE MONITORING

Mobile tracking usually occurred immediately after release of tagged *A. sinensis* by a boat-mounted Vemco Model VR100 receiver and Model VH100 hydrophone. Thereafter, mobile tracking periods were conducted from 0800 to 1730 hours during the entire spawning season (mid-October and mid-November). During 17–20 November 2008, mobile tracking was done day and night. In addition, in April 2007, two boats with the mobile tracking system was used to track adult *A. sinensis* from the Jingzhou reach (1521 rkm), one tracking adult *A. sinensis* upstream to the GZD (tracking distance of 157 rkm) and the other boat tracking for adult *A. sinensis* downstream from GZD to the Jiangyin reach (94 rkm; tracking distance, 1427 rkm).

The hydrophone was mounted to a tracking boat by a stainless steel tube and extended 1 m under the water surface. The tracking boat was 6·25 m long and was powered by an

62·5 kW gasoline engine, the noise of which at idle did not interfere with tag detection by the hydrophone system. Before beginning tracking, the locations of all adult *A. sinensis* were identified within a short reach using the VR2 (W) receivers. Then the boat moved slowly to search for tagged adult *A. sinensis* using a Z route, which was navigated using GPS. Once a tagged individual was located, the following data were collected: time, place (nearest rkm), identification of tag, signal intensity, longitude and latitude and water depth (if the transmitter had a pressure sensor).

VR2 (W) receivers were placed at 12 river sites for long-term monitoring of adult movements when they passed each receiver. Furthermore, during the spawning period of adult *A. sinensis* and during April to November 2007, nine additional VR2 (W) receivers were placed temporarily within the spawning ground and the Jingjiang reach to know specific spawning sites or the refuge reaches (Fig. 1). The selected monitoring sites had the following features: slow flow and on the side of the main channel. These features could help to maximize the likelihood of detecting tagged *A. sinensis*.

Monitoring receivers were installed on wharf boats (National Channel Bureau or Marine Bureau). Receivers were placed 1·5 m under the water surface by three ropes, and two iron weights were mounted 0·5 m under the receivers to keep the ropes (and receiver) positioned vertically. The tag detection distance was tested in order to verify the monitors would detect and log the signal by a tagged fish in the river.

EGGS OF *ACIPENSER SINENSIS* COLLECTION

A D-shaped bottom-anchored drift net was employed to capture the eggs of *A. sinensis* in 2007–2009. Detailed methodology was described by Wei *et al*. (2009). The distributions of eggs were used to determine the specific spawning site and the period of embryos development was extrapolated to determine the spawning timing (Chen, 2004).

DATA COLLECTION AND TREATMENT

Data were usually downloaded from the VR2 (W) receivers every 2 weeks during the non-spawning season, but the frequency of data downloading from the receivers on the spawning ground was increased to once or twice a day during the spawning season in order to know the detailedly diurnal movement of adult *A. sinensis* and give a guidance for mobile tracking. To ensure the consistency of the time selected, the ground speed of fish between two monitoring sites was calculated using the time of fish first detection from a series of continuous records of each receiver. The total *A. sinensis* locations were introduced into ArcGIS 9·3 software (www.esri.com) to plot fish locations and relative modules were used to calculate the distance from the thalweg. A one-way ANOVA was used to analyse the differences among adult *A. sinensis* and between sexes for ground speed between receivers located at different reaches.

WATER TEMPERATURE AND DISCHARGE

Water temperature data were collected from the Yichang gauging station located 4·5 km below the GZD in 2008–2009. Water level and discharge data were only obtained from the Yichang gauging station in 2006–2008.

RESULTS

CAPTURE AND TAGGING

Fifty-seven adult *A. sinensis* were captured on 92 days during the four tagging periods from 20 October 2006 to 22 November 2008. Twenty-seven adult *A. sinensis* were ultrasonically-tagged, of which, 26 were located for 7 to 707 days (mean number of relocations = 859; range = 3–4549). One adult was never located after release (Table I).

Spawning site and time

By collecting eggs, the main spawning site was located at the downstream spawning site in 2007 and at the uptream spawning site in 2008 and 2009 (Fig. 2). In addition, depending on the age extrapolation of the embryos captured on the spawning site, the time when the spawning occurred was identified by year as follows: 2006–2330 hours, 12 November; 2007–2300 hours, 23 November; 2008–2100 hours, 26 November; 2009–2000 hours, 23 November.

DETECTION OF ADULT *ACIPENSER SINENSIS*

In October and November 2006, six adult *A. sinensis* with stage IV gonads (pre-spawning stage) were tagged and released at Miaozui just downstream of GZD during 23–31 October. Adult *A. sinensis* were detected for a mean of 16·67 days (range = 7–22 days), which was prior to the day of spawning. In April 2007, two adult *A. sinensis* that were recuperated in the Beijing Aquarium were tagged and released at Jingzhou (1521 rkm; Table I). One of these *A. sinensis* (JZ0701; Table I) was detected for 547 days, which included their upstream migration, downstream migration and time in the sea. The other Beijing Aquarium *A. sinensis* (JZ0702; Table I) was detected for 7 days including the downstream migration from the release site (Jingzhou, 1521 rkm) to the Yangtze Esturary. In October and November 2007, one adult with stage III gonads and 11 adult *A. sinensis* with stage IV mature gonads were tagged and released (Table I), of which the 11 adult *A. sinensis* with stage IV gonads were detected for a mean of 153·64 days (range = 13–707 days). The one adult with stage III gonads was not detected after release. Of the stage IV adult *A. sinensis*, one was tracked during upstream migration, 11 were tracked during the spawning period, and four adult *A. sinensis* were tracked during their downstream migrations. In October and November 2008, five *A. sinensis* with stage III gonads and two *A. sinensis* with stage IV gonads were tagged and released at Miaozui (Table I), and their movements detected for a mean of 227·14 days (range = 7–381 days). The movements of five of these *A. sinensis* were detected during the pre-spawning period, and the movements of three *A. sinensis* were detected during the post-spawning period.

Spawning migration

One large female (JZ0701, mass = 451 kg) released on 22 April 2007 at Jingzhou (Table I) probably returned to the sea and *c*. 1 year later entered the Yangtze River and was detected at Jiangyin (94 rkm) on 15 June 2008. It arrived at the spawning ground at the GZD on 14 November 2008 (Fig. 3). Unfortunately, it was killed by fishermen. The mean migration ground speed was 0·54 km h^{-1} (range = 0·26–1·77 km h^{-1}). Upstream ground speed in the lower reach (estuary to Pengze, 94–707 rkm) was slower than in the upper middle reach (Zhijiang to GZD, 1580–1678 rkm). Upstream ground speed in the lower middle reach (Pengze to Zhijiang, 707–1580 rkm) was the slowest, especially in the Wuhan–Zhijiang reach (1071–1580 rkm), suggesting that short-term refuge exist in this reach [Fig. 4(a)]. Because the reaches where the VR2 (W) receivers were deployed were gradually getting shallower with increasing distance from the estuary to the GZD, the water depth adult *A. sinensis* used was gradually shallower [mean depth = 28·32 m; range = 0·61–58·20 m; Fig. 5(a)]. The other male *A. sinensis* (MZ0713) tracked on 16 November 2007 also re-entered the Yangtze River and passed Tongling (513 rkm) on 9 October 2009 and

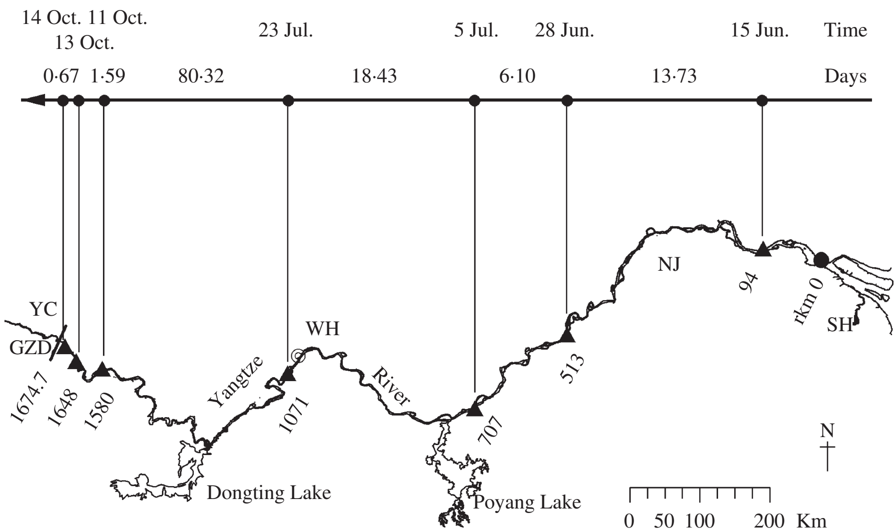

FIG. 3. Movement timing of *Acipenser sinensis* JZ0701 in the middle and lower reaches of the Yangtze River, showing its upstream migration (GZD, Gezhouba Dam; YC, Yichang; WH, Wuhan; NJ, Nanjing; SH, Shanghai; ▲, locations of VR2 (W) receivers; Time, the time when *A. sinensis* JZ0701 passed each VR2 (W) receiver; Day, the number of migration days it took for *A. sinensis* JZ0701 to swim between two receivers).

Wuhan (1071 rkm) on 19 October 2009, but was also killed by fishing at Yueyang (1253 rkm). The mean upstream ground migration speed was 2·20 km h^{-1} (range = 1·82–2·35 km h^{-1}), which was greater than for JZ0701 [Fig. 4(a)]. The fish used a mean depth of 20·67 m [range = 15·20–32·10 m; Fig. 5(a)].

Pre-spawning holding

The movements of five females with stage III gonads tagged in November 2008 were tracked. Four *A. sinensis* used the reach between the GZD tailrace and the downstream end of the spawning ground (3·26 rkm) for *c*. 11 months (November 2008 to September 2009). The mean depth used was 13·64 m (range = 3·60–34·60 m). One other *A. sinensis* (MZ0804, female) departed from this reach and moved downstream at Honghuatao (1648 rkm) on 15 February 2009. After then, the signal was lost and the *A. sinensis* was not detected again, presumably she was captured by fishermen.

Spawning movement

In 2006, six females with stage IV gonads were tagged and released. They stayed in deep water near the release site *c*. 1·87 h (range = 0·20–4·00 h). Subsequently after migrating downstream *c*. 1·5 rkm, one *A. sinensis* (MZ0603) migrated upstream to just below the GZD. Two *A. sinensis* (MZ0605 and MZ0606) also migrated upstream to just below the GZD. One *A. sinensis* (MZ0604) migrated downstream to the middle Yanzhiba Bar (1666 rkm), and the two remaining *A. sinensis* (MZ0601 and MZ0602) migrated downstream to the Huyatan reach (1653 rkm). The water depth used by these six *A. sinensis* in this period of movement was 12·45 m

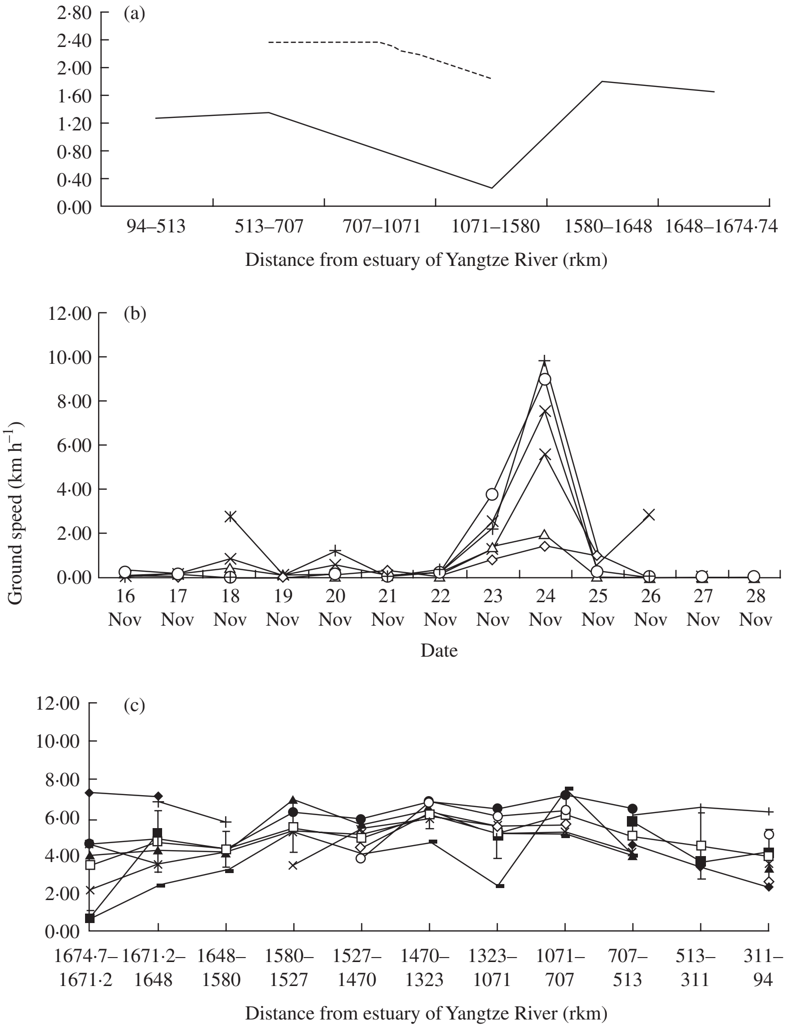

FIG. 4. Ground speeds of *Acipenser Sinensis:* (a) during the pre-spawning migration of JZ0701 (—) and MZ0713 (- - -), (b) of five males (-◇-, MZ0712; -△-, MZ0713, -×-, MZ0718; -✳-, MZ0703; -○-, MZ0706; -+-, MZ0709) moving over the spawning ground in 2007 before, during, and after the spawning day (2300 hours, 23 November) and (c) during downstream migration of 10 *A. sinensis* in different river reaches, which included: -□-, mean ground speed of 10 *A. sinensis*; *A. sinensis* MZ0807 (-◆-), MZ0805 (-■-), MZ0713 (-▲-), MZ0703 (-×-), MZ0706 (-✳-) and MZ0709 (-●-) were tracked during post-spawning out-migration; *A. sinensis* MZ0802 (-+-) and MZ0714 (-▬-) were tracked during pre-spawning out-migration; *A. sinensis* JZ0701 (-◇-) and JZ0702 (-○-) initiated downstream migration after being released during the non-spawning season.

(range = 1·60–30·60 m). Until transmitter life expired or the tag was shed from these females, these *A. sinensis* had a small movement range.

Between 2007 and 2009, two of 15 female *A. sinensis* with stage IV gonads departed from the GZD spawning ground prior to the spawning period and migrated downstream to the sea. The movements of 11 *A. sinensis* (six males and five females) were considered to be the best examples for movements of this stage. These

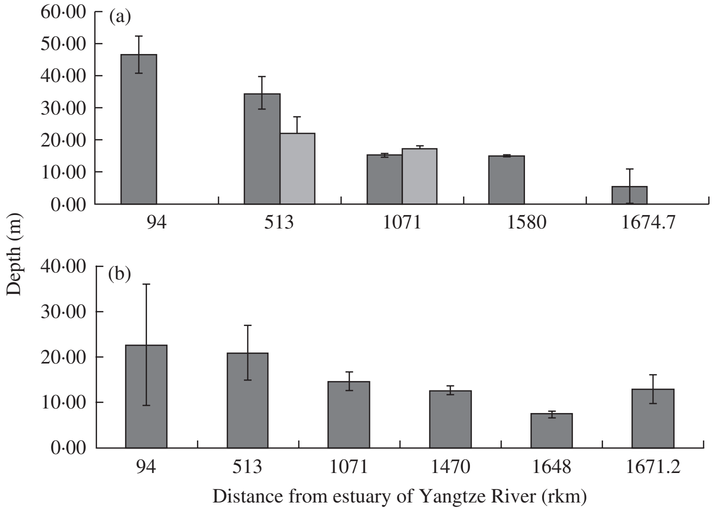

FIG. 5. Mean ± S.D. water depths used by *Acipenser sinensis* at receivers located at increasing distance from the river mouth monitoring stations: (a) JZ0701 (■) and MZ0713 (□) during upstream and (b) post-spawning *A. sinensis* during downstream migration.

A. sinensis mostly used the tailrace of GZD to the Diversion Dike before spawning (Fig. 2). Two females tracked continuously day and night while swimming upstream were always located in the main channel. Similarly, it was also found that *A. sinensis* moved in the main channel (the distance from the locations of *A. sinensis* to thalweg *v*. distance from the river boundary to thalweg was 1:4·7). Five *A. sinensis* in which the transmitters had a pressure sensor used a mean water depth of 9·71 m (range = 3·00–36·30 m).

Specific spawning sites determined the zones where *A. sinensis* would move on the spawning day. For example, depending on the extra VR2 (W) receivers at the upstream and downstream spawning sites in 2007, seven *A. sinensis* were found at the downstream spawning site for a mean of 5·76 h (range = 2·92–8·20 h) before spawning occurred in 2007. In addition, one *A. sinensis* was at the upstream spawning site in 2008. This *A. sinensis* shed its tag on the upstream spawning site, perhaps during spawning. Both of these two *A. sinensis* were on the upstream spawning site when the spawning occurred in 2009.

The movements of six male *A. sinensis* were documented in 2007. The mean ground speeds per day on the spawning day were greater than on the other days [Fig. 4(b)]. Furthermore, on a mean of 8·57 days (range = 1·20–21·70 days) before spawning, pre–spawning *A. sinensis* moved downstream from the spawning ground a mean of 18·21 rkm (range = 3·93–24·64 rkm), and then, returned to the spawning ground. Their mean up and downstream ground speeds were 3·94 km h^{-1} (range = 2·04–5·36 km h^{-1}) and 1·98 km h^{-1} (range = 0·86–2·77 km h^{-1}), respectively.

Post-spawning migration

Males and females left the spawning ground on a different time schedule. Based on the monitoring of intensive receivers, two females were found to leave within

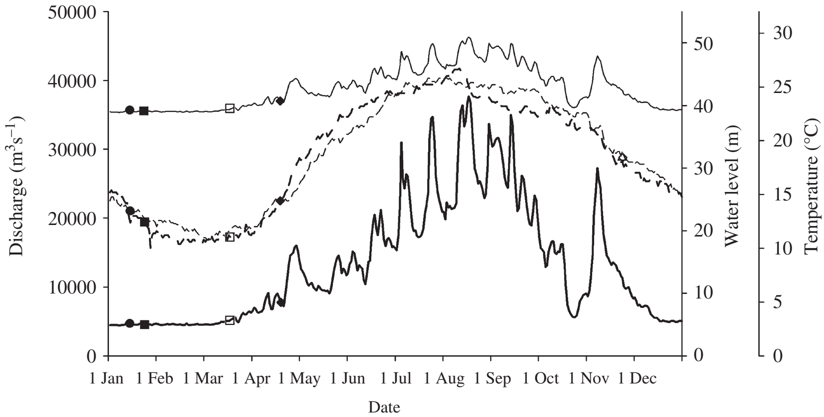

FIG. 6. Start of the post-spawning migration of six *Acipenser sinensis* in relation to discharge, water level and water temperature at the Gezhouba Dam in 2008 and 2009. (Discharge, water level and water temperature were measured at the Yichang gauging station (1673 rkm); ▬, discharge 2008; —, water level 2008; - - -, temperature 2008; _ _ _, temperature 2008; ●, MZ0713; □, MZ0709; △, MZ0807; ■, MZ0706; ◆, MZ0703; ◇, MZ0805).

a few hours after spawning, but four males remained for a longer period (mean duration = 76·30 days, range = 2·5–148·0 days). Additionally, seaward migration of four males (spawned in November 2007) occurred before the arrival of the first significant increase in river flow in 2008 (Fig. 6). In 2008 and 2009, the downstream migration of four *A. sinensis* (two males spawned in November 2007 and two females spawned in November 2008) occurred when water temperature was declining and two males (spawned in November 2007) at beginning of increase in water temperature (Fig. 6). In general, both males and females departed during low water levels and discharge, and low temperature.

The ground speed during seaward migration of adult *A. sinensis* was rapid and it only took a few days (mean = 15 days; range = 13–17 days) to complete the entire migration (Fig. 7). The mean ground seaward speed of six *A. sinensis* from the spawning ground to the Yangtze Estuary was 4·87 km h^{-1} [range = 0·68–7·60 km h^{-1}; Fig. 4(c)]. There were no significant differences of mean ground speeds within reaches (ANOVA, $P > 0.05$) or between sexes (ANOVA, $P > 0.05$). In addition, there were two *A. sinensis* that left the spawning ground before the spawning day (one *A. sinensis* captured in November 2007 left 1·67 h after release and another captured in November 2008 left 2 days after release). The mean downstream ground speeds of these two *A. sinensis* was 4·66 km h^{-1} (range = 0·72–7·40 km h^{-1}). This mean speed was not different from the speed of the post-spawning *A. sinensis*. The mean water depth used by the three *A. sinensis* during the migration period was 14·37 m (range = 5·46–43·10 m), which was shallower than during the upstream migration [Fig. 5(b)].

SPAWNING CYCLE

The spawning cycle of one female *A. sinensis* (JZ0701) and one male *A. sinensis* (MZ0713) are the most complete example from the study. Female JZ0701 was captured on 4 November 2005 with degraded gonads. It was transferred and recovered

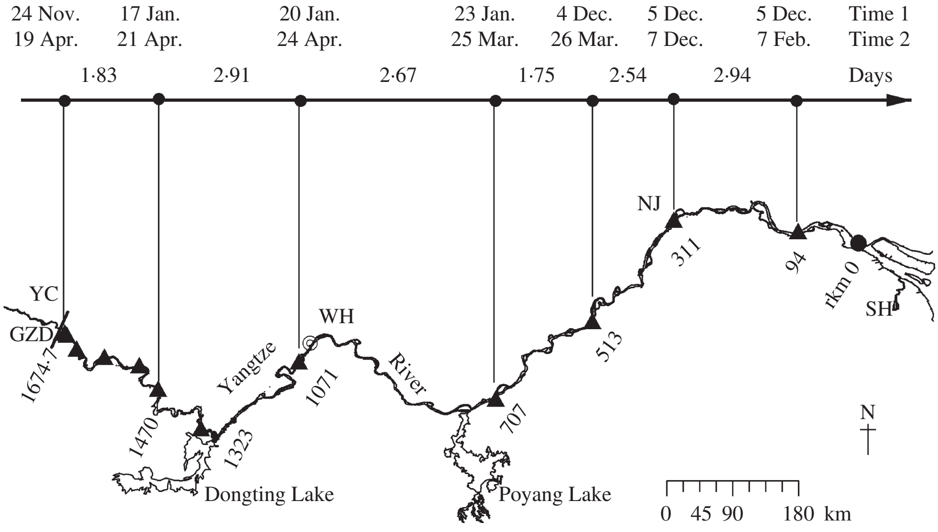

FIG. 7. Downstream movement of six tagged *Acipenser sinensis* during the post-spawning migration. (GZD, Gezhouba Dam; YC, Yichang; WH, Wuhan; NJ, Nanjing; SH, Shanghai; ▲, locations of VR2 (W) receivers; Time1 and Time2, the time when the first and last post-spawned *A. sinensis* passed the receiver; Day, the number of migration days of six *A. sinensis* between two receivers).

at the Beijing Aquarium. It was released in the Jingzhou reach (1521 rkm) on 22 April 2007 and arrived at the Yangtze Estuary on 3 May 2007 (11 days). It re-entered Yangtze River on 15 June 2008 and migrated upstream to the GZD spawning ground by 14 October 2008. Male MZ0713 spawned on 23 November 2007 and returned to the Yangtze Estuary by 31 January 2008. It re-entered Yangtze River in October 2009 after 20 months. Thereafter, both *A. sinensis* died by fishing. Using data from all tracked adult *A. sinensis*, it is speculated that the spawning cycle of this female is 4 years and for male, the cycle is 3 years.

DISCUSSION

Ultrasonic telemetry has been used to study migrations and movements of many acipenseriforms. The migrations of green sturgeon *Acipenser medirostris* Ayres 1854 in the Sacramento, Klamath and Trinity Rivers, CA, U.S.A. were described using ultrasonic telemetry (Benson *et al*., 2007; Heublein *et al*., 2009). Additionally, ultrasonic telemetry was also employed to study partial or entire migrations of gulf sturgeon *Acipenser oxyrinchus desotoi* Vladykov 1955, white sturgeon *A. transmontanus* Richardson 1836, shortnose sturgeon *A. brevirostrum* LeSueur 1818, Atlantic sturgeon *Acipenser oxyrinchus* Mitchill 1815, in fresh water (Kieffer & Kynard, 1993; Fox *et al*., 2000; Parsley *et al*., 2008; Fernandes *et al*., 2010). Ultrasonic telemetry was also an optimal approach to track movements of and determine the migrations and movements of adult *A. sinensis* in the Yangtze River relative to four categories. Also, the results provided the first direct evidence of the spawning cycle for *A. sinensis*.

There are great differences in upstream migration timing and water temperature and river discharge may be important proximate factors affecting the timing of these migrations. Two *A. sinensis* were found re-entering the Yangtze River in the summer (June) or in early autumn (October), both migrations occurring during periods of high discharge and warm temperatures. For other anadromous acipenseriforms, like *A. o. desotoi,* water temperature seems the trigger for migration. Adults enter the Choctawhatchee River, AL, U.S.A. from March to mid-May and enter the Suwannee River earlier in mid-February probably because the Suwannee River, FL, U.S.A. is warmer earlier in the year (Fox *et al*. 2000). The upstream pre-spawning migrations of *A. brevirostrum* varies depending on sex and energetic conditions of fish with day length triggering departure from wintering sites and a high river discharge triggering upstream migration for foraging or pre-spawning holding (Kynard 1997; Kieffer & Kynard, 2012). The timing of up-migration of southern *A. medirostris* in the Sacramento River was in March and April while the northern *A. medirostris* entered later in April and July (Benson *et al*., 2007; Heublein *et al*., 2009). In short, these suggest that temperature is probably a major environmental cue triggering migration of pre-spawning adult *A. sinensis* leaving the sea and entering their natal river.

Upstream migration is a time-consuming process for adult *A. sinensis*. One *A. sinensis* spent $>$121 days completing the upstream migration with a length $>$ 1678 rkm and the other acipenseriforms only executed three quarters of the total migration routes. During upstream migration, one tagged *A. sinensis* stayed between Wuhan and Zhijiang for a long time (80 days), indicating that the fish may use the reach as a refuge or holding reach. Historical catch information also indicates this reach was an aggregation zone (Yangtze Aquatic Resources Survey Group, 1988). This reach also had a high bycatch of the tagged *A. sinensis*. In this reach, the channel is sinusoidal with many low velocity and deep water areas that could provide energy conserving refuges.

After arriving at the Miaozui spawning grounds, adult *A. sinensis* with immature stage III gonads remained within a reach of 3·25 km below the GZD for a year. They moved within a reach of 3·25 km. Unlike the other acipenseriforms of unhindered rivers preferring deep water and low velocity, *A. sinensis* below the GZD usually chose areas with high flow as the pre-spawning refuge. These movements indicate fish seek to continue to use fast current that could be a route to move them further upstream past the dam (Yang *et al*., 2006). *Acipenser medirostris* below Glen Colusa Irrigation District (GCID) in the Sacramento River show similar characters (Heublein *et al*., 2009).

The spawning movement and spawning occurring were triggered by some imperative conditions. Yang *et al*. (2006) and Wang *et al*. (in press) found adult *A. sinensis* did not move to the area below the Erjiang hydro-power plant which exhibits the highest water velocities at all times along the spillway, and they also did not appear in area of the Sanjiang River which has slow currents all along. The Yangtze Aquatic Resources Survey Group (1988) and Wei (2003) concluded that the water level (range = 40·69–47·32 m, mean = 44·01 m), flow regime and water velocity (0·81–1·98 m s^{-1}) were critical for spawning success of *A. sinensis* and the water temperature (range = 16·1–20·6° C, mean = 18·6° C) determined the beginning of spawning. The correlation of water temperature on spawning timing was also found in other acipenseriforms (Parsley *et al*., 1992; Paragamian *et al*., 2002). In addition, *A. sinensis* choose a particular river bedform morphology to spawn (Zhang *et al*., 2008). An understanding of spawning ground requirements for females is critical to assess the effect of anthropogenic alternations on this threatened population.

After spawning was completed, males would stay in the spawning ground for days while the females left immediately. The similar pattern was also found in *A. brevirostrum* (Kieffer & Kynard, 2012). Males and females showed a different timing of downstream migration, which had not been reported in other acipenseriforms (Kynard, 1997; Benson *et al*., 2007; Heublein *et al*., 2009). Both males and females chose to depart during a low water level, low discharge and stable temperature. This pattern is different from *A. medirostris*, which departed during increased river flows (Benson *et al*., 2007). Migration speed and water depth of adult *A. sinensis* during the downstream migration were different than found for other acipenseriforms. Seaward migration ground speed (116·88 km day^{-1}) of *A. sinensis* was faster than the few other acipenseriforms that have been monitored. For example, Connecticut River, CT, U.S.A. *A. brevirostrum* left the spawning ground and moved downstream at a rate of 32 km day^{-1} (Kynard, 1997). Furthermore, although the water velocity among the reaches was different, the ground speed of *A. sinensis* was not different within reaches, suggesting that fish are swimming at a rather constant speed. The depth adult *A. sinensis* used during upstream migration (27·19 m) was much deeper than during the downstream migration (14·37 m). Both selections could be related to conservation of energy, *i.e.* using deeper and slower flows during upstream migration to conserve energy for the long holding period before spawning while selecting faster flow during downstream migration to reach food quicker.

In the Yangtze River, human activities in recent years had largely changed the status of adult *A. sinensis*. Acipenseriforms and paddlefishes (polyodontidae) exhibit unusual combinations of morphology, habits and life history characteristics, which make them highly vulnerable to effects of human activities, particularly fisheries (Boreman, 1997). For the only two tagged *A. sinensis* re-entering the Yangtze River, both were killed in the bycatch of fishermen during the spawning ground or migration passage. Except for these cases, death of *A. sinensis* was usually attributed to fishing or to a propeller strike by boats (according to the information from the fishermen and Chinese Fisheries Administration). Additionally, the construction of the GZD blocked the up-migration passage to the spawning ground and *A. sinensis* were forced to spawn below the GZD. Damming led to shrinking the migratory routes with the length of 822–1622 rkm and the sizes of spawning ground by *c*. 99% (Wei *et al*., 1997). The impounding of the reservoir at TGD in 2003 has greatly changed the natural river hydrological rhythm. These changes probably influence spawning movements and success of *A. sinensis* (Wang *et al*., in press).

Understanding migrations and movements of adult *A. sinensis* while in the Yangtze River is necessary to protect the species from fishing and to ensure the river reaches and habitats used by the species are conserved. Information about spawning migration and spawning habitat is essential to maintain and restore ultimately populations of endangered and threatened species of anadromous fishes (Fox *et al*., 2000). Depending on the conclusions of this paper and the knowledge of human activities in the Yangtze River, specific protection should be given to the large aggregation of adult *A. sinensis* below GZD and other refuges reaches identified in the present study. For example, the minimum flow and water depth needed to assure fish could move and live in these place, channel dredging ought to be avoided within the spawning ground in order to prevent destruction of the river bottom in this critically important area and fishing activities should be banned during all of the year. Also, passage routes for adult *A. sinensis* should be protected during the season when adult *A. sinensis* are present. Due to the busy boat navigations and abundant fisheries in the passage routes, protection of adult *A. sinensis* is difficult. It is suggested that adult *A. sinensis* in some important reaches, like the fishing areas [*e.g.* Longzhou (1545 rkm) and Yuexin (1500 rkm) (Yangtze Aquatic Resources Survey Group, 1988)] can be given some protection like supervision of fishing, banning the use of illegal fishing gear, and prohibiting anchoring ships and building of ports and docks. It is imperative to make all attempts to ensure *A. sinensis* complete their normal migrations and movements in the Yangtze River, preventing adverse effects from human activities.

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References

Ban, X. & Li, D. M. (2007). Ecological hydrological influence of large water conservancy projects on *Acipenser Sinensis* in Yangtze River. *Engineering Journal of Wuhan University* **3,** 10–13 (in Chinese).

Bemis, W. E. & Kynard, B. (1997). Sturgeon rivers: an introduction to acipenseriform biogeography and life history. *Environmental Biology of Fishes* **48,** 167–183.

Benson, R., Turo, S. & McCovey B. Jr. (2007). Migration and movement patterns of green sturgeon (*Acipenser medirostris*) in the Klamath and Trinity rivers, California, USA. *Environmental Biology of Fishes* **79,** 269–279.

Boreman, J. (1997). Sensitivity of North American sturgeons and paddlefish to fishing mortality. *Environmental Biology of Fishes* **48,** 399–405.

Chen, X. H. (2004). Studies on the developments of embryo and gonad at early stages of Chinese sturgeon, *Acipenser sinensis*. PhD Thesis, College of Life Science, Zhongshan University, Guangzhou, China.

Chen, Z. Y., Chen, D. C., Xu, K. Q., Zhao, Y. W., Wei, T. Y., Chen, J., Li, L. Q. & Watanabe, M. (2007). Acoustic Doppler current profiler surveys along the Yangtze River. *Geomorphology* **85,** 155–165.

Conte, F. S, Doroshov, S. I., Lutes, P. B. & Strange, E. M. (1988). *Hatchery Manual for the White Sturgeon Acipenser transmontanus Richardson with Application to Other North American Acipenseridae.* Oakland, CA: University of California Press.

Deng, Z. L., Yu, Z. T., Xu, Y. G., Zhou, C. S. (1985). Age determination and population structure of spawning Chinese sturgeon (*Acipenser sinensis* Gray). *Acta Hydrobiologica Sinica* **9,** 99–111 (in Chinese).

Du, H., Wei, Q. W., Zhang, H., Liu, Z. G., Wang, C. Y. & Li, Y. H. (2011). Bottom substrate attributes relative to bedform morphology of spawning site of Chinese sturgeon *Acipenser sinensis* below the Gezhouba Dam. *Journal of Applied Ichthyology* **27,** 257–262.

Fernandes, S. J., Zydlewski, G. B., Zydlewski, J. D., Wippelhauser, G. S. & Kinnison, M. T. (2010). Seasonal distribution and movements of shortnose sturgeon and Atlantic sturgeon in the Penobscot River Estuary, Maine. *Transactions of the American Fisheries Society* **139,** 1436–1449.

Fox, D. A., Hightower, J. E. & Parauka, F. M. (2000). Gulf Sturgeon Spawning Migration and Habitat in the Choctawhatchee River System, Alabama–Florida. *Transactions of the American Fisheries Society* **129,** 811–826.

Heublein, J. C., Kelly, J. T., Crocker, C. E., Klimley, A. P. & Lindley, S. T. (2009). Migration of green sturgeon, *Acipenser medirostris*, in the Sacramento River. *Environmental Biology of Fishes* **84,** 245–258.

Ke, F. E. & Wei, Q. W. (1992). Estimating the population structure and resource of spawning Chinese sturgeon. *Freshwater Fisheries* **4,** 7–11 (in Chinese).

Kieffer, M. & Kynard, B. K. (1993). Annual movements of shortnose and Atlantic sturgeons in the Merrimack River, Massachusetts. *Transactions of the American Fisheries Society* **122,** 1088–1103.

Kieffer, M. C. & Kynard, B. (2012). Pre-spawning and non-spawning spring migrations, spawning, and effects of river regulation and hydroelectric dam operation on spawning of Connecticut River shortnose sturgeon. In *Life History and Behaviour of Connecticut River Shortnose and Other Sturgeons* (Kynard, B., Bronzi, P. & Rosenthal, H., eds), pp. 73–113. Norderstedt: Demand GmbH.

Kynard, B. (1997). Life history, latitudinal patterns, and status of the shortnose sturgeon, *Acipenser brevirostrum*. *Environmental Biology of Fishes* **48,** 319–334.

McDowall, R. M. (1987). The occurrence and distribution of diadromy among fishes. *American Fisheries Society Symposium.* **1,** 1–13.

McDowall, R. M. (1988). *Diadromy in Fishes: Migrations Between Freshwater and Marine Environments.* London: Croom Helm.

McDowall, R. M. (1992). Diadromy: origins and definition of terminology. *Copeia* **1992,** 248–251.

Paragamian, V. L., Wakkinen, V. D. & Kruse, G. (2002). Spawning locations and movement of Kootenai River white sturgeon. *Journal of Applied Ichthyology* **18,** 608–616.

Parsley, M. J., Anders, P. J., Miller, A. I. & Beckman, L. G. (1992). Factors affecting white sturgeon spawning and recruitment in the Columbia River downstream from McNary Dam. In *Status and Habitat Requirements of the White Sturgeon Populations in the Columbia River Downstream from McNary Dam* (Beamesderfer, R. C. & Nigro, A. A., eds.), pp. 61–79. Portland, OR: Oregon Department of Fish and Wildlife, National Marine Fisheries Service, US Fish and Wildlife Service and Washington Department of Fisheries.

Parsley, M. J., Popoff, N. D., Wright, C. D. & Leeuw, B. K. (2008). Seasonal and diel movements of white sturgeon in the lower Columbia River. *Transactions of the American Fisheries Society* **137,** 1007–1017.

Qiao, Y., Tang, X. C., Brosse, S. & Chang, J. B. (2006). Chinese Sturgeon (*Acipenser sinensis*) in the Yangtze River: a hydroacoustic assessment of fish location and abundance on the last spawning ground. *Journal of Applied Ichthyology* **22,** 140–144.

Wang, C. Y., Kynard, B., Wei, Q. W., Du, H. & Zhang, H. Spatial distribution and staging-spawning habitat suitability for adult Chinese sturgeon at Gezhouba Dam, Yangtze River: Effects of river alternations. *Journal of Applied Ichthyology* (in press).

Watanabe, Y., Wei, Q. W., Yang, D. G., Chen, X. H., Du, H., Yang, J., Sato, K., Naito, Y. & Miyazaki, N. (2008). Swimming behavior in relation to buoyancy in an open swimbladder fish, the Chinese sturgeon. *Journal of Zoology* **275,** 381–390.

Wei, Q. W. (2003). Reproductive behavioral ecology of Chinese sturgeon (*Acipenser sinensis* Gray) with its stock assessment. PhD Thesis, Institute of Hydrobiology, Wuhan, China (in Chinese).

Wei, Q. W., Ke, F. E., Zhang, M. J., Zhuang, P., Luo, D. J., Zhou, Y. Q. & Yang, W. H. (1997). Biology, fisheries, and conservation of sturgeons and paddlefish in China. *Environmental Biology of Fishes* **48,** 241–255.

Wei, Q. W., Yang, D. G., Ke, F. E., Kynard, B. & Kiefefer, M. (1998). Technique of ultrasonic telemetry for Chinese Sturgeon, *Acipenser sinensis*, in Yangtze River. *Journal of Fisheries of China* **22,** 211–217 (in Chinese).

Wei, Q. W., Kynard, B., Yang, D. G., Chen, X. H., Du, H., Shen, L. & Zhang, H. (2009). Using drift nets to capture early life stages and monitor spawning of the Yangtze River Chinese sturgeon (*Acipenser sinensis*). *Journal of Applied Ichthyology* **25,** 100–106.

Yang, D. G., Kynard, B., Wei, Q. W., Chen, X. H., Zheng, W. D. & Du, H. (2006). Distribution and movement of Chinese sturgeon, *Acipenser sinensis*, on the spawning ground located below the Gezhouba Dam during spawning seasons. *Journal of Applied Ichthyology* **22,** 145–151.

Yangtze Aquatic Resources Survey Group (1988). *The Biology of the Sturgeons and Paddlefish in Changjiang and their Artificial Propagation.* Chengdu: Sichuan Scientific and Technical Press (in Chinese).

Yi, Y. J., Wang, Z. Y. & Yang, Z. F. (2010). Two-dimensional habitat modeling of Chinese sturgeon spawning sites. *Ecological Modelling* **221,** 864–875.

Zhang, H. (2009). Abiotic environment for natural reproduction of Chinese sturgeon (*Acipenser sinensis*). PhD Thesis, College of Fishery, Huazhong Agriculture University, Wuhan, China (in Chinese).

Zhang, H., Wei, Q. W., Yang, D. G., Du, H., Zhang, H. J. & Chen, X. H. (2007*a*). An observation on water current profiles of spawning of *Acipenser sinensis* down-ward Gezhouba Dam. *Journal of Fishery Sciences of China* **14,** 183–191 (in Chinese).

Zhang, H., Wei, Q. W., Yang, D. G., Du, H., Zhang, H. J. & Chen, X. H. (2007*b*). Topography research on spawning grounds of *Acipenser sinensis* below Gezhouba Dam. *Acta Ecologica Sinica* **27,** 3945–3955 (in Chinese).

Zhang, H., Wei, Q. & Du, H. (2008). A bedform morphology hypothesis for spawning areas of Chinese sturgeon. *Environmental Biology of Fishes* **84,** 199–208.

Zhang, H., Wei, Q. W., Kynard, B., Du, H., Yang, D. G. & Chen, X. H. (2011). Spatial structure and bottom characteristics of the only remaining spawning area of Chinese sturgeon in the Yangtze River. *Journal of Applied Ichthyology* **27,** 251–256.

