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Status of two *Coreius* species in the Three Gorges Reservoir, China*

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Abstract Dam construction alters natural flow regimes which, in turn, cause significant changes in fish communities during and after impoundment. The construction of the Three Gorges Reservoir, from impoundment of the Changjiang (Yangtze) River, China, may have affected native fish species. Thus, the status of two lotic freshwater fish species, *Coreius heterodon* and *C. guichenoti*, were monitored in the Three Gorges Reservoir, including fish abundance, individual composition, growth, condition, and mortality. Data on both species were gathered from upstream, midstream and downstream areas of the reservoir and, where available, from studies published before and after dam construction. Lower abundance, slower growth, a less diversified age structure, poorer fish condition (indicated by hepatosomatic index) and higher mortalities were recorded in sites nearest the dam compared with upstream areas. Furthermore, after final impoundment, individual *Coreius* species inhabiting the area changed, with young individuals becoming more abundant, while upstream of the reservoir the two *Coreius* species became smaller at a given age. The results show that the status of the two *Coreius* species was subject to dramatic changes after impoundment.

Keyword: Three Gorges Reservoir; *Coreius* species; status; age profile; growth; impoundment

1 INTRODUCTION

In recent decades, a growing number of hydropower-generating facilities have been built around the world, with a consequent increase in dam construction, especially in Central and South America, Asia and Oceania (Gleick, 1993). In China, the number of dams has increased from 22 in 1950 to 88 605 in 2010 (Jia et al., 2010; MWR, 2011). Dams provide economic benefits that include hydropower (WCD, 2000), water supply regulation (Mugabe et al., 2003), flood control (Galat et al., 1998) and navigation (Thorp et al., 1994) among others; however, they now affect over half of all large, freshwater aquatic systems worldwide (Nilsson et al., 2005). River damming is broadly accepted as being responsible for the most significant and widespread impacts on freshwater environments (Dynesius and Nilsson, 1994).

Hydroelectric development has caused significant changes in fish fauna, including divergence of fish communities (Gehrke et al., 2002), reduced fish abundance (Cushman, 1985), decreased fish biodiversity (Paragamian, 2002), elimination of native species (Holmquist et al., 1998; Liermann et al., 2012) and loss of spawning habitats for migratory fish (Cambray et al., 1997). Simpler levels of species interactions and lower fish abundance have been observed in the upstream areas of dams (Katano et al., 2006). The impact of dams on fish population

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characteristics has been widely studied (Perera et al., 2013). However, previous investigations have mainly focused on the effects on population numbers (Rypel and Bayne, 2009). Decreases in riverine fish populations or even the extinction of riverine fish species have been reported in many rivers after impoundment (WCD, 2000; Jackson and Marmulla, 2001; Park et al., 2003; Xenopoulos and Lodge, 2006). Moreover, the ecological effects of the loss of migratory native fish species due to the damming of riverine ecosystems were more widespread than the bottom-up effects (Greathouse et al., 2006). In particular, a large part of the decline in productivity and reduction of fish growth has been attributed to the construction of dams (Paragamian, 2002).

The Three Gorges Dam (TGD), currently the largest hydroelectric dam in the world in terms of installed capacity, was completed recently (2012) in the upper Changjiang (Yangtze) River in China (Wu et al., 2003). It is also the largest reservoir in the world in terms of water capacity (about 40 km^3), total surface area (1 080 km^2) and total length (approximately 667 km) when the water level is at its maximum of 175 m above sea level (a.s.l.) (Fu et al., 2010). This provides an ideal location for investigating the effects of large dams on native fish populations.

Coreius heterodon (Bleeker, 1865) and *C. guichenoti* (Sauvage et Dabry, 1874) are two indigenous demersal and potamodromous (semi-migratory) cyprinid fish with similar food habits (He, 1980; Liu et al., 2012). In the Changjiang River, *C. heterodon* is primarily distributed in the mainstream and large tributaries of the middle reaches (Liu et al., 1990; Yan, 2005), while *C. guichenoti* is mainly distributed in the upper reaches (Liu et al., 1990; Ding, 1994). The spawning area of *C. heterodon* was mainly located in the Three Gorges Reservoir (TGR) area before impoundment (Anonymous, 1976; Xu et al., 1981; Liu et al., 1990), while that of *C. guichenoti* was located in the Jinsha and Yalong Rivers (Anonymous, 1976; Xu et al., 1981; Liu et al., 1990). The minimum age of sexual maturity of the two *Coreius* species is 3 years, and the spawning time extends from April to July when the water temperature is 18–22°C (Anonymous, 1976; Xu et al., 1981; Liu et al., 1990; Zhang, 2009). Eggs hatch while drifting downstream with the water flow (Liu et al., 1990). Larvae also grow while drifting downstream, and young and sub-adults migrate upstream for maturation and reproduction (Liu et al., 1990; Zhang, 2009). These two species have long been among the most valuable commercial fish in the Changjiang River (Liu and Cao, 1992; Wu et al., 2007). However, catches, especially of large individuals, have been declining since 1999 (SEPA, 2000–2006). According to 'self-organizing map' model predictions, *C. guichenoti* has a high probability of becoming extinct (Park et al., 2003). An understanding of the population characteristics of riverine fishes and an investigation of their life-history traits are essential for the implementation of appropriate conservation and management measures. The two *Coreius* species have been the subject of numerous studies in relation to, for example, growth characteristics (Zhou, 2010; Yang et al., 2011a), population dynamics (Yang, 2009), feeding habits (Liu et al., 2012), reproductive ecology (Liu et al., 1990; Cheng, 2008), genetic characteristics (Yuan et al., 2008; Xu and Milliman, 2009; Zhang and Tan, 2010) and prey dynamics (Yu et al., 1984; Tang et al., 2012). However, most studies were conducted before maximum impoundment (2010), and little is known about the potential impact of large-scaled impoundment on the status of these two species. Many fish are apparently resilient to river impoundment and may even thrive in these habitats (Chang et al., 1999; Han et al., 2008).

Although many studies have reported on the ecological impact of the TGD (Wu et al., 2004; Gao, 2007; Yang et al., 2012), most are limited to the riverine reaches downstream of the reservoir (Xie et al., 2007). Some studies have considered the impact on areas upstream from the dam, where damage can also be severe (Park et al., 2003; He et al., 2010; Perera et al., 2013). Nevertheless, most studies on the effects of the TGD have focused on changes in fish species composition and catch statistics (Gao, 2007). Our previous studies on the characteristics of the yellow catfish (*Peltobagrus fluvidraco*) population (Perera et al., 2013) indicated significant differences at three sites along the longitudinal profile of the TGR and suggested there was a need for further studies to evaluate the status of other native fish species after this major impoundment. The purpose of the current study was to evaluate large-scale spatial variations in the status and individual changes of two *Coreius* species over the longitudinal profile of the recently impounded TGR on the Changjiang River. The research provides an important case study on the ecological effects of large dams on migratory fish and the status of these two species after maximum impoundment. Our findings could be used to develop conservation strategies and improve management of

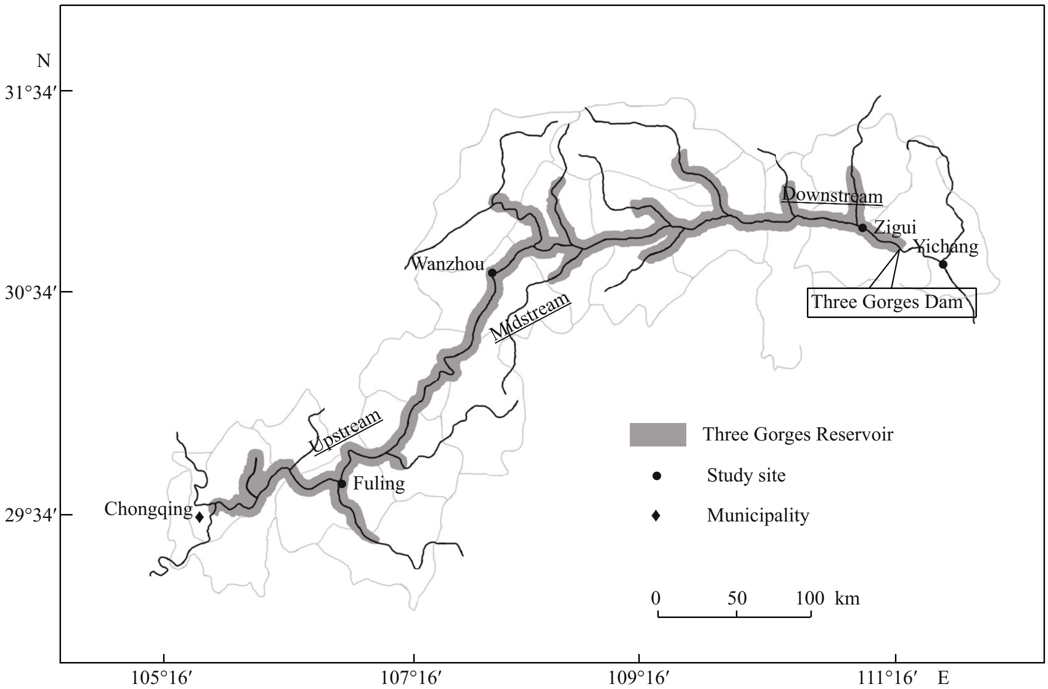

Fig.1 Sampling sites for *Coreius*. *heterodon* and *C. guichenoti* in the Three Gorges Reservoir, China

Fuling: upstream; Wanzhou: midstream; Zigui: downstream.

the two *Coreius* species, and also provide useful guidelines in this regard for other indigenous species.

2 MATERIAL AND METHOD

2.1 Study area

The first stage in the construction of the TGD was finished in 1997, and the dam was fully completed in 2009. The TGD, located in the upper reaches of the Changjiang River, is 185 m high. The storage capacity of the TGR was increased, in phases, from 135 m a.s.l. in 2003 to 156 m a.s.l. in 2006, and to 175 m a.s.l. in 2010, resulting in a final, maximum capacity of 39.3 billion m^3. Three sampling sites were chosen to collect the two *Coreius* species along the longitudinal axis of the TGR (Fig.1). Zigui, the downstream area, is located almost immediately adjacent to the dam (30°51′17.6″N, 111°00′04.4″E); Wanzhou, the midstream area, is located about 300 km from the dam (30°49′13.7″N, 108°23′46.6″E) and Fuling, the upstream area, is located ~500 km from the dam (29°42′48.5″N, 107°23′57.7″E). When the reservoir water level is at 135 m a.s.l., the depths (Lü et al., 2007), flow velocities (Zeng, 2006; Lü et al., 2007) and reservoir widths (unpublished data) at the downstream, midstream and upstream area were, respectively, approximately 100, 42 and 31 m, approximately 0.023, 0.280 and 0.705 m/s, and approximately 1.5, 0.9 and 0.7 km. The upstream area has a sandy bottom, while the midstream and downstream area have muddy bottoms (Liu, 2009). Very few benthic organisms, or none, have been recorded from the three sampling sites (Liu, 2009). The plant community in the water-level-fluctuating zone in the upstream area was dominated by herbaceous plants, but closer to the dam there is less species diversity of herbaceous plants (Xia, 2011).

2.2 Fish sampling and data collection

Coreius heterodon and *C. guichenoti* were sampled monthly using three-layer gillnets and long-lines between November 2010 and October 2011 at the three sites. Landings from five fishing boats were recorded at each location every month. The gill nets were 100–120 m in length and 10–20 m in height (three-layer multi-mesh gillnets with a central mesh size of 4–8 cm and outer mesh sizes of 10–20 cm). The long-lines were 2 km in length, with a baited hook every 4 m. Mealworms (*Tenebrio molitor*) or chironomid larva were used as baits. The gillnets and long-lines were deployed at twilight, and hauled and sampled for fish after 12 h. The total length (TL), standard length (SL) and body weight (*W*) of each captured specimen were measured to the nearest 1 mm and 0.01 g, respectively. The scales, gonads and livers were subsequently removed in the field.

The gonads and livers were weighed to the nearest 0.001g (W_G and W_L). Five to ten scales from the belly below the dorsal fin and lateral line were collected to determine their age. For age determination, the annual rings were counted and annuli diameter were recorded following the procedure of Yan (2005). The sex of each specimen was determined by visual inspection of the gonads. Following macroscopic evaluation of the ovaries, the *Coreius* specimens were classified into six groups according to the stage of development (Zheng and Xiong, 1993): Stage I (immature); Stage II (developing), Stage III (vitellogenesis), Stage IV (mature/spawning capability), Stage V (spawning/ actively spawning) and Stage VI (spent/regressing).

2.3 Data analysis

Hepatosomatic index (HSI), which serves as an indicator of the nutritional status of individual fish (Lloret et al., 2014), was expressed as liver weight (g) as a percentage of eviscerated body weight (g). HSI=100×(liver weight / body weight).

Length-frequency data with constant class size were modeled using the von Bertalanffy growth function (VBGF) using ELEFAN I (Electronic Length Frequency Analysis) as described in Zhuang and Cao (1999). ELEFAN I is a routine used to identify the best fit for the growth curve to a length-frequency dataset arranged sequentially (Pauly and David, 1981).

Le Cren's relative condition factor (K_n)—used as an indicator of body condition—was calculated as $K_n=W/W_e$, where W is the observed weight of the fish and W_e is the estimated weight, derived from W-L relationship representing all individuals in all samples (Lloret et al., 2014).

The instantaneous rate of total mortality (Z) for each year class sampled at each site was determined using two methods: (1) Hoenig Model: $Z_1=1/[c_1(t_{max}-t_c)]$, s.e.(Z)=SQR$(c_2Z^2)^{1/2}$, where c_1 and c_2 are functions of N (Hoenig and Lawing, 1982), t_{max} is the maximum age in years observed in a given stock and as an option, t_c is the mean age at first capture and N is the sample size from which t_{max} is estimated (Hoenig, 1983); (2) $Z_2=k(L_\infty-L_{mean})/(L_{mean}-L')$, where L_∞ is the asymptotic length measured from total length; k is the curvature parameter of the VBGF; L_{mean} is the mean length of the fish in a sample representing a steady-state population and L' is the cut-off length (Beverton and Holt, 1956). These estimates were averaged as the instantaneous total mortality rates ($Z=(Z_1+Z_2)/2$) (Yang et al., 2009; Maunder and Wong, 2011). The instantaneous rate of natural mortality (M) was determined using Pauly's M Equation (Pauly, 1980): $\log(M)=-0.0066-0.2790\log(L_\infty)+0.6543\log(k)+0.4634(T)$, where L_∞ is the asymptotic length measured from total length; k is the VBGF curvature parameter and T is the mean annual water temperature (18°C) of the habitat (Yang, 2009). The instantaneous rate of fishing mortality (F) was estimated from the relationship: $F=Z-M$, where Z and M are as defined above.

Mortality estimates and VBGF parameters were calculated using FiSAT II 1.2.2. Growth rates from the three sites were estimated from length-frequency data with constant class size separately for males and females. Power regressions of length-weight relationships were calculated for both species between sites and the exponent b-values have been estimated using the equation $W=a\mathrm{TL}^b$. Analysis of covariance (ANCOVA) was used to test difference in b-values between sexes and between sites. Differences in HSI between sites were evaluated using analysis of variance (ANOVA) with Tukey's post-hoc comparison test. The Mann-Whitney test was used to test differences in the Le Cren's condition index (K_n) and the total length of both species between sites. Cross-tabulation (χ^2 test) was used to test differences in the frequency of occurrence between sites. Differences were considered to be significant at $P<0.05$. Statistical analysis was performed using SPSS 16.0 (SPSS Inc., Chicago, IL, USA).

3 RESULT

3.1 *Coreius* stocks at different sites along the TGR

A total of 396 and 817 individuals of *C. heterodon* and *C. guichenoti* were collected, respectively, from the three sites along the TGR during our investigations. All fish were immature juveniles (Stage I) and/or young adults (Stage II). There were significant differences in the frequency of occurrence for both *C. heterodon* (χ^2=12.829, $P<0.05$) and *C. guichenoti* (χ^2=20.285, $P<0.05$) between sites. A 100% frequency of occurrence was recorded in the upstream area, but only 33.3% for *C. heterodon* and 8.3% for *C. guichenoti* were recorded in the downstream area (Fig.2).

3.2 Age and growth at different sites along the TGR

The TL of *C. heterodon* ranged 127–380 mm with a mean±SD of 218.2±46.2 mm in the upstream area (Fuling), 170–407 mm with a mean of 302.8±53.0 mm in the midstream area (Wanzhou) and 110–303 mm with a mean of 172.9±50.2 mm in the downstream area (Zigui) (Figs.3 and 4). TL of *C. heterodon* specimens collected from the downstream area was significantly smaller than those of from the midstream or upstream areas (Mann-Whitney test, $P<0.05$). TL of *C. guichenoti* ranged 85–322 mm with a mean value of 161.9±45.2 mm in the upstream area, 104–318 mm with a mean of 181.0±52.4 mm in the midstream area, but, in the downstream area, only one *C. guichenoti* specimen with a TL of 180 mm was recorded. The mean size of *C. guichenoti* specimens collected from the upstream area was significantly smaller than those of from the midstream area (Mann-Whitney test, $P<0.01$) (Fig.5).

The age structure of *C. heterodon* specimens collected from the three sites contained four age groups ranging from 1 to 4 years. However, the dominant age composition differed between the three sites: 3-year-old specimens dominated the midstream area, 1–2 year olds in the upstream area and 1 year olds in the downstream area (Fig.6a).

The age structure of *C. guichenoti* specimens collected from the upstream and midstream areas contained three age groups ranging from 1 to 3 years, with 1-year-old specimens dominating both areas. In the downstream area, only a single 2-year-old specimen was recorded over the 12-month research

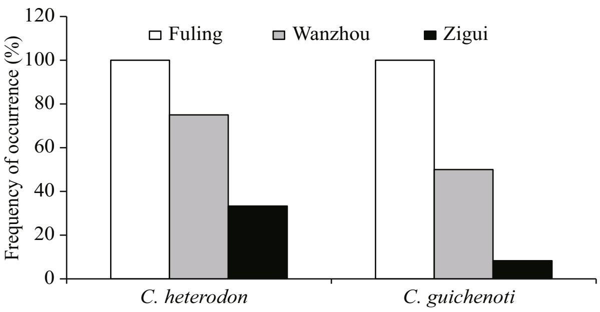

Fig.2 Frequency of occurrence of *Coreius heterodon* and *C. guichenoti* at different sites in Three Gorges Reservoir

Fuling: upstream; Wanzhou: midstream; Zigui: downstream.

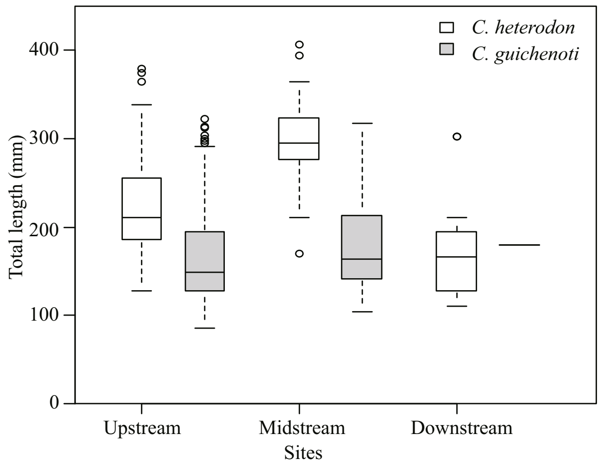

Fig.3 Box plots of total length of *Coreius heterodon* and *C. guichenoti* collected at three different sites over a 12-month period from November 2010 to October 2011

Upstream (mean TL±SD): 218.2±46.2 mm; Midstream: 302.8±53.0 mm; Downstream: 172.9±50.2 mm. Squares denote mean values; boxes denote quartiles and whiskers represent minimum and maximum total length. Circles represent outliers. Fuling: upstream; Wanzhou: midstream; Zigui: downstream.

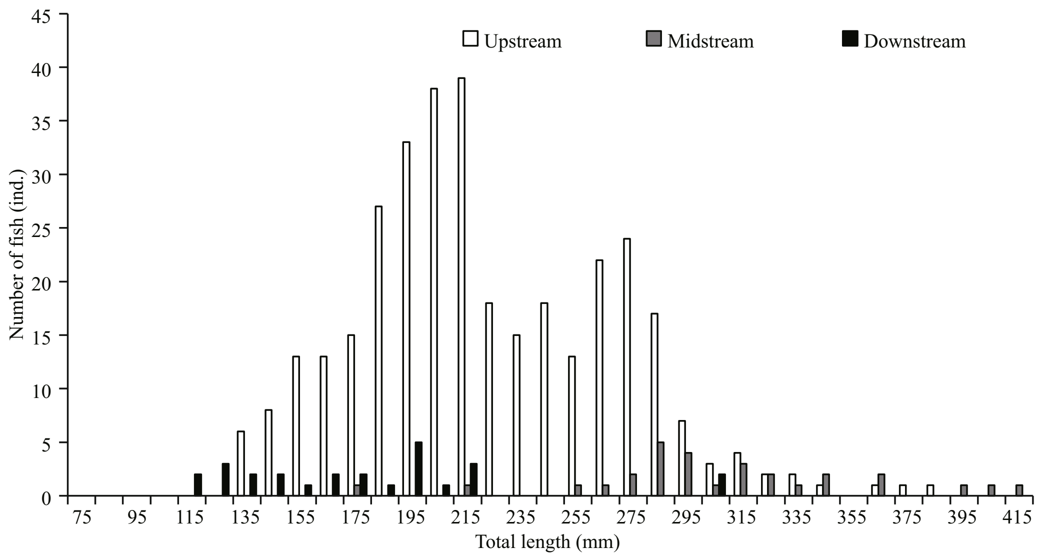

Fig.4 Total length distribution of *Coreius heterodon* at the three sampling sites in the Three Gorges Reservoir over a 12-month period from November 2010 to October 2011

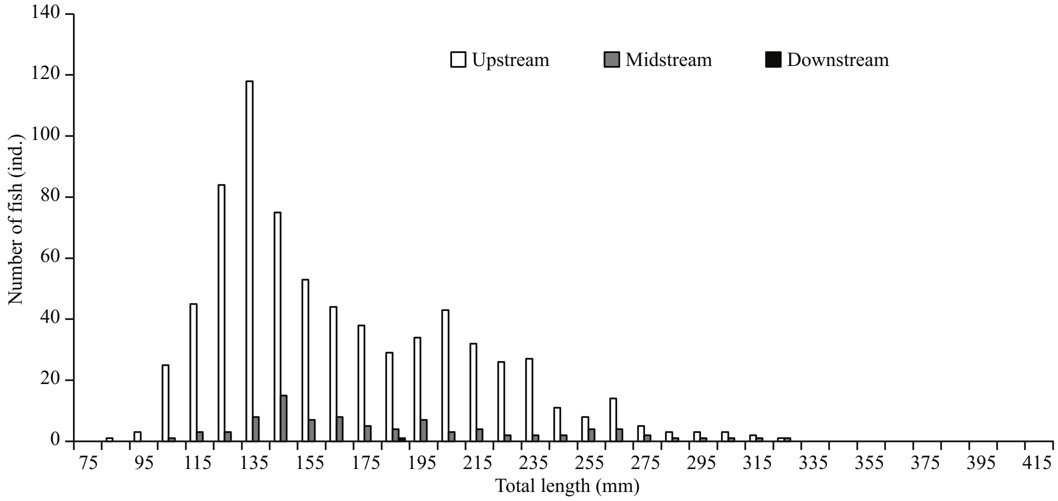

Fig.5 Total length distribution of *Coreius guichenoti* at three sampling sites in the Three Gorges Reservoir over a 12-month period from November 2010 to October 2011.

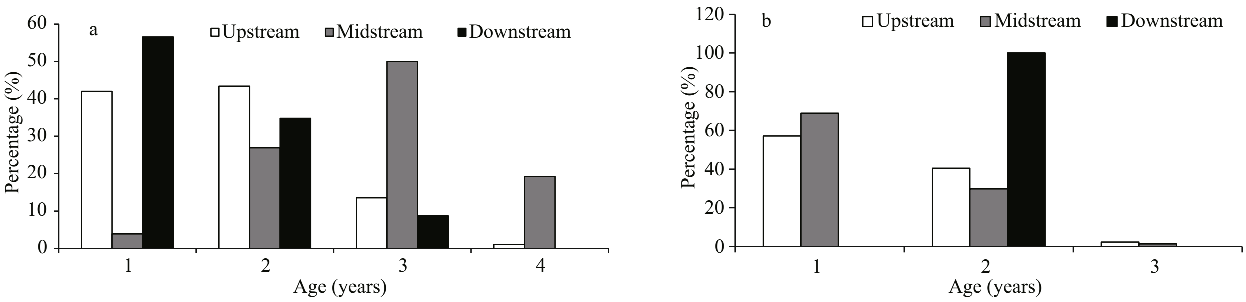

Fig.6 Age distribution of *Coreius heterodon* (a) and *C. guichenoti* (b) at the three sampling sites in the Three Gorges Reservoir over a 12-month period from November 2010 to October 2011

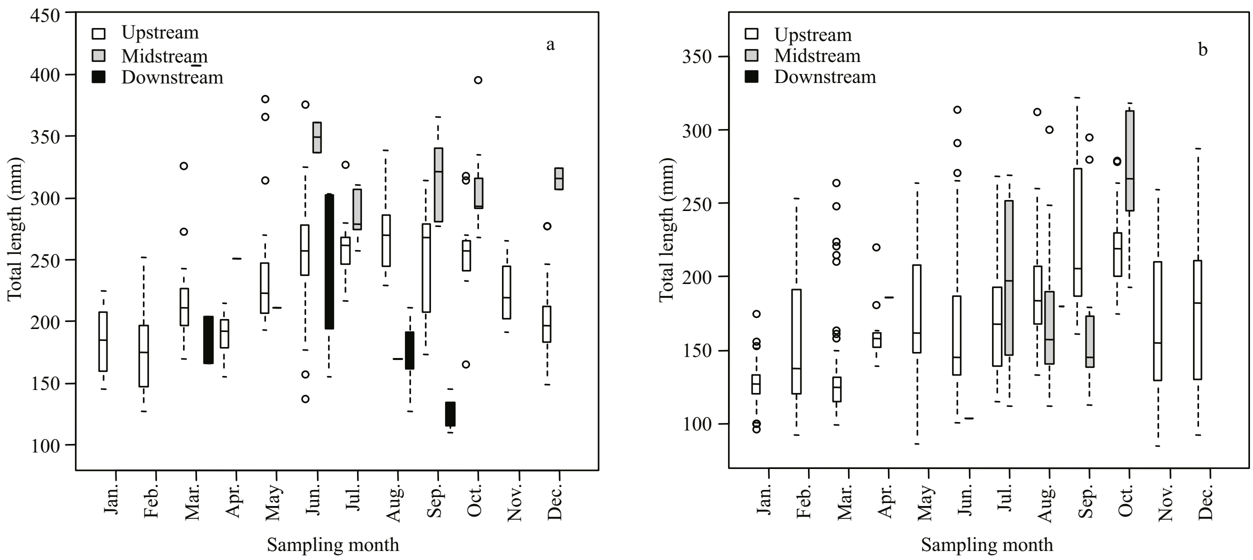

Fig.7 Total length of specimens of (a) *Coreius heterodon* and (b) *C. guichenoti* collected over a 12-month period from November 2010 to October 2011 at the three sampling sites in the Three Gorges Reservoir

Squares denote median, boxes denote quartiles and whiskers represent minimum and maximum total length. Circles represent outliers.

period of 2010–2011 (Fig.6b).

Monthly changes in total length (TL, mm) for the three sampling sites of *C. heterodon* and *C. guichenoti* are shown in Fig.7a and b, respectively. In both species, TL steadily increased from April to July, and decreased from August to December in the upstream

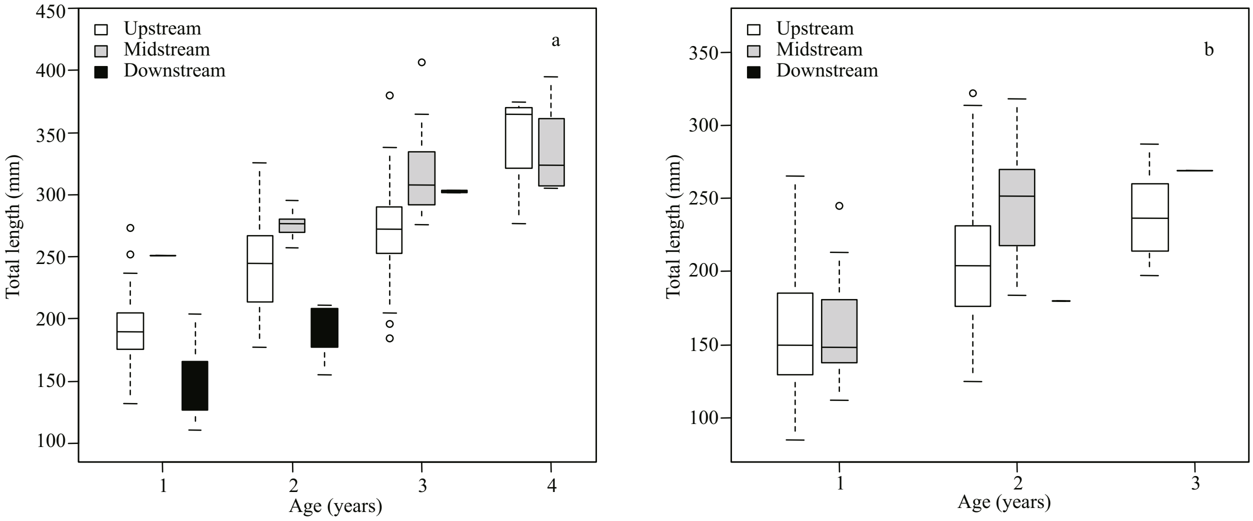

Fig.8 Total length of (a) *C. heterodon* and (b) *C. guichenoti* at different ages from the three sampling sites in Three Gorges Reservoir

Squares denote median, boxes denote quartiles and whiskers represent minimum and maximum total length. Circles represent outliers.

Table 1 Summary of the Von Bertalanffy growth parameters, Le Cren's condition index and HSI of *Coreius* sp. at three sites along the Three Gorges Reservoir

Locations	*C. heterodon*				*C. guichenoti*			
	L_∞ (mm)	k	K_n (mean±SD)	HSI (mean±SD)	L_∞ (mm)	k	K_n (mean±SD)	HSI (mean±SD)
Upstream	400.0	0.24	1.00±0.098[a]	2.05±1.26[a]	341.3	0.31	1.00±0.117[a]	2.97±1.45[d]
Midstream	431.5	0.09	1.00±0.109[a]	1.31±0.68[b]	341.3	0.15	1.01±0.099[a]	2.23±0.82[e]
Downstream	326.6	0.08	1.01±0.100[a]	0.84±0.44[c]	-	-	-	-

Different letters indicates significant differences (P<0.05).

site. The TL of *C. heterodon* at a given age in the downstream area was lower than those from the midstream or upstream areas (Fig.8). The proportion of large and older individuals of *C. heterodon* in the midstream area was greater than in the other sites, while the majority of large and older *C. guichenoti* individuals were collected in the upstream area.

Weight-length (W-L) relationships were first calculated individually for each sex. The individual W of both *C. heterodon* and *C. guichenoti* displayed no significant difference between the sexes (ANCOVA, P>0.05, TL as the covariate). Therefore, the data from females and males were combined, and the W-L relationship for each species was established. For *C. heterodon*, the W-L functions were W=1.55×10^{-6} TL$^{3.300}$, R^2=0.980, W=2.40×10^{-6}TL$^{3.222}$, R^2=0.966 and W=2.16×10^{-6}TL$^{3.241}$, R^2=0.988 in the upstream, midstream and downstream area, respectively. The b values (i.e. the exponents of TL) were significantly different between each two site (ANCOVA, P<0.01). For *C. guichenoti*, the W-L functions were W=1.19× 10^{-5}TL$^{2.944}$, R^2=0.981 and W=6.65×10^{-6}TL$^{3.065}$, R^2=0.986 in the upstream and midstream area, respectively. The b values were significantly different between the two sites (ANCOVA, P<0.01).

The final VBGF coefficient estimates for each site are summarized in Table 1. Growth rates at the three sites differed. The highest k values for *C. heterodon* and *C. guichenoti* were found in the upstream area, while the lowest were found downstream. *C. heterodon* showed the highest L_∞ in the midstream area and the lowest in the downstream site, while *C. guichenoti* displayed the same L_∞ in both the upstream and midstream areas.

Although there were no significant differences in K_n between the three sites for either species (P>0.05) (Table 1), significant differences in HSI between sites and species were found (Table 1). For the two species, the HSI of individuals collected from the upstream site was significantly higher than those of individuals collected from midstream (P<0.05). For *C. heterodon*, the HSI in the midstream site was significantly higher than in the downstream area (P<0.05).

Table 2 Age and standard length of *C. heterodon* from different periods and at different sampling sites in the Changjiang River

Sampling sites	Year		Standard length (mm) and percentage (%) at each age										Source
			1	2	3	4	5	6	7	8	9	10–13	
Mainstream and Hanjiang River	1973–1978	SL	139	192	277	328	371	393	407	444	464	470–529	[1]
		%	10.7	18.2	7.1	31.5	10.3	8.6	5.4	4.5	1.7	2.1	
Yibing to Jiangjin	1973	SL	216	251	291	328	405						[2]
		%	4	17	36	33	10						
Wanzhou to Wuling	1982	SL		208	286	309	329	361	398	430			[3]
		%		2.0	55.3	26.7	12.5	2.4	0.8	0.4			
Mudong	1992	SL	181	214	285	310	333	362	400				[4]
		%	3.2	22.3	41.5	19.1	9.6	3.2	1.1				
Mid and upper stream	1990–1995	SL	79	189	274	355	406	459					[5]
Mainstream	2003–2004	SL	162	193	263	300	354	383					[6]
		%	2.2	32.2	38.7	22.6	3	1.3					
TGR	2010–2011	SL	155	185	233	278							[7]
		%	56.7	31.7	8.7	2.9							

[1] Xu et al., 1981; [2] He, 1980; [3] Leng et al., 1984; [4] Diao and Zhou, 1994 ; [5] Zhuang and Cao 1999; [6] Yan, 2005; [7] Present study. Note: The years in the table represent sampling periods. SL: standard length.

Table 3 Age and standard length of *C. guichenoti* from different periods and at different sampling sites in the Changjiang River

Sampling sites	Year		SL (mm) and percentage (%) at each age							Source
			1	2	3	4	5	6	7	
Panzhihua to Yidu	2005–2007	SL	110	201	266	300	336	363	376	[1]
		%	18.3	35.4	28.4	9.9	6.1	1.6	0.5	
Chongqing and Yichang	2006–2007	SL	135	219	290	334	377			[2]
		%	63.4	26.1	8.4	1.7	0.3			
TGR	2010–2011	SL	120	156	199					[3]
		%	67.0	32.2	0.9					

[1] Cheng, 2008; [2] Yang, 2009; [3] Present study. Note: the years in the table represent sampling periods. SL: standard length.

3.3 Mortality rate estimation

The modeling process is size-related, and the precision of estimates is closely related to the ratio of sample size to the number of length classes in each sample (Gerritsen and McGrath, 2007). Therefore, we combined the length-frequency data of the three sampling sites to provide adequate results on mortality rates. Instantaneous total mortality rates Z of *C. heterodon*, estimated from Hoenig's and Beverton and Holt's methods were 1.951/year (Z_1) and 0.378/year (Z_2), respectively, with an average of 1.165/year. However, for *C. guichenoti*, these values of Z were 2.734/year (Z_1) and 0.696/year (Z_2), respectively, with an average of 1.715/year. Pauly's estimates of M for *C. heterodon and C. guichenoti* were 0.458 and 0.652/year, respectively. Estimates of F obtained from the average mortality for *C. heterodon and C. guichenoti* were 0.707/year and 1.063/year, respectively.

3.4 Historical changes in the *Coreius* sp. population structure

After the impoundment, the *C. heterodon* age structure contained four age groups with age-1 group accounting for 56.7% of the total. However, previous studies recorded between five and seven age groups in the Changjiang River (Table 2), with the age-3 and age-4 groups dominating, and the SL of each age group was larger than those recorded in our study. A similar situation was observed for *C. guichenoti*. Only three age classes (1–3) were recorded for *C. guichenoti* in our study, with age-1 group accounting for 67.0% of the total (Table 3). However, six age groups (age

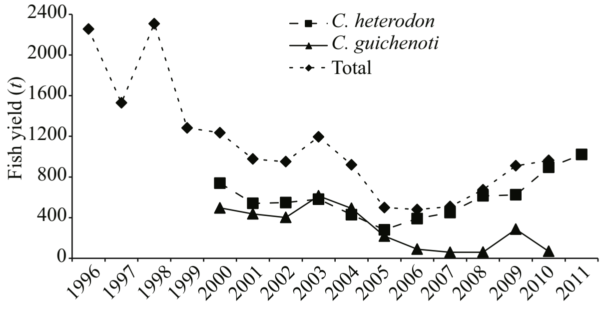

Fig.9 Dynamics of two *Coreius* species yield (*t*) in the TGR, 1996–2011

Total fish yield is presented as the sum of *C. heterodon* and *C. guichenoti*.

2–7) for *C. guichenoti* were recorded in midstream areas (Wanzhou) of the TGR in 2005–2007 (Cheng, 2008). This differs noticeably from previous studies, which detected between five and seven age groups in the TGR area prior to 2007 in the Changjiang River. Total yield of the two *Coreius* species sharply declined after impoundment (SEPA, 1997–2012), especially for *C. guichenoti* (Fig.9).

4 DISCUSSION

4.1 Status of *Coreius* sp, stocks in the TGR

The results of the present study show differences in abundance, age structure, growth, condition and mortality of the two *Coreius* species between upstream, midstream and downstream areas of the TGR, suggesting that the construction of the dam had a profound effect on the distribution of both these lotic species. Closer to the dam, a lower fish abundance was observed. Declines in the relative abundance of lotic-adapted species after dam construction have been observed and reported in many studies (Martinez et al., 1994; Zhong and Power, 1996). Lotic species may move upstream to habitats that are more lotic in character as a result of damming (Wu et al., 2007; Gao et al., 2010; Yang et al., 2012) and fish abundance has been found to decrease significantly with depth (Moranta et al., 1998). *Coreius* species release floating eggs in upstream areas of the Changjiang River, which then drift downstream with the current (Liu et al., 1990). A large proportion of eggs may sink because of lower flow velocities, resulting in low recruitment and consequent reduced abundance close to the dam (Zhong and Power, 1996). The Three Gorges area, prior to the construction of the dam, was the largest spawning ground of *C. heterodon* in the Changjiang River (Xu et al., 1981; Liu et al., 1990). However, in this study, no mature individuals were collected in the TGR, leading to the hypothesis that the reduction in older age groups and parental generation of the population could affect recruitment.

Closer to the dam, lower HSI values were observed. Changes in benthic communities after impoundment, resulting in variations in food supplies, could be the main reason for the phenomenon (Zhang et al., 2010). *C. heterodon* inhabits a limited area of the river for its whole life cycle, while *C. guichenoti* displays specific, migratory-like behavior (Luo et al., 2013). In *Coreius* species, the main component of the hepatopancreas is fat, which is used for energy storage (Ge et al., 2001). Thus, a high HSI is necessary in actively mobile, migratory species (e.g. *C. guichenoti*), which is consistent with our results. With dam construction in the upstream region of the Changjiang River, *C. guichenoti* experienced a loss of migratory pathways and even a change in migratory behavior (Luo et al., 2013), which could impinge on energy reserves.

4.2 Impact of TGD on population structure

Fish populations in non-regulated rivers normally have a larger number of age groups than those in regulated rivers (Torralva et al., 1997). After the final impoundment of the TGR, landings of *Coreius* were composed of young individuals, and each age group consisted of smaller-sized individuals than had been the case prior to impoundment. The shift towards a younger age structure in commercial landings could be a result of increased fishing pressure, hydropower development, environmental pollution (Yan, 2005; Cheng, 2008) or as a consequence of the ideal free distribution theory that populations increase with increasing habitat suitability while their size decreases (Blanchard et al., 2005).

The younger ages and smaller sizes recorded in the TGR may be explained as follows. First, the upstream area of the reservoir did not extend to Fuling and hydrological conditions remained basically unchanged when levels rose to 135 m a.s.l.; thus, the first phase of impoundment had little impact on *Coreius*. However, when water levels rose to 175 m a.s.l., the upstream area (Fuling) was flooded and environmental conditions changed greatly, with subsequent effects on *Coreius* populations. In the first-order tributaries within the upstream areas of the Changjiang River, *Coreius* species are mainly distributed in the Yalong, Jialing, Tuojiang, Minjiang and Wujiang Rivers (Anonymous, 1976; Ding, 1994; Yu et al., 2005). Cascade hydropower exploitation on these tributaries has blocked the migration paths of fish, and stocks of *Coreius* species have gradually declined in these areas (Jiang et al., 2007; Qing, 2010; Yang et al., 2011a, b; Zeng, 2012). Second, after final impoundment of the TGR, well-adapted lotic species or large individuals may have moved into the upper reaches of the river. This change in the age structure reflects to some extent how *Coreius* resources have been compromised in recent years.

Reservoir impoundment results in the loss of flowing-water habitats, changes in water temperature and water quality, variation in dissolved gases, sediment accumulation and the reduction of suitable spawning habitat (Walker, 1985; Wydoski and Hamill, 1991; Dadswell, 1996; Wang et al., 2014). Large reservoir impoundment may produce short-term variable flows during sluicing demand but constant flows otherwise, with a resulting lack of seasonal amplitude (Walker, 1985). Diffuse gradient hydraulic conditions formed after impoundment could affect fish behavior and delay downstream fish migration (Bednarek, 2001; Pelicice et al., 2014). Adaptation to changed environmental conditions could result in a decline in fish abundance and lower growth, via lost spawning grounds and delays in spawning time, as reported in carps in the Changjiang River (Wang et al., 2014). Increased water temperature due to dam construction may cause higher energy consumption and lower growth rates in fish (Luo and Wang, 2012). Therefore, the decrease in standard length at a given age of both *Coreius* species (Tables 2 and 3) in the TGR could be explained by changes in temperature. Invertebrate biomass and biodiversity were considerably depleted near the Thomson Dam, near Melbourne, Australia, associated with disturbed flows and siltation (Davey et al., 1982; Blyth, 1984). Therefore, altered benthic communities in the TGR could be another reason for this change, via bottom-up effects (Chen and Wise, 1999; Shao et al., 2008). Upstream of the reservoir, the two *Coreius* species have become smaller at a given age. It is difficult to determine if this represent a genetic change or phenotypic plasticity, although damming accelerates genetic differentiation in populations living above versus below a dam (Cheng, 2010; Zhang et al., 2010). Actually, a reduction in fish abundance may result in larger body sizes, because of less competition for food and space. Rick (1981) found that, in pink salmon (*Oncorhynchus gorbuscha*), a reduction in body size could present an evolutionary response to selection. The water temperature, depth and flow preferences of young and mature *Coreius* need to be determined in future studies to evaluate ecological suitability and conservation management strategies.

Our results on asymptotic length, L_∞, were similar to those from previous studies, showing that, for both species, values were lower than they had been before maximum impoundment (Zhuang and Cao, 1999; Chen et al., 2002; Zhou, 2010). The growth parameter, k, was lower for *C. heterodon* (Xu et al., 1981; Diao and Zhou, 1994; Chen et al., 2002) and higher for *C. guichenoti* (Yang et al., 2010, 2011a; Zhou, 2010) than it had been prior to the first stage of impoundment. Fish growth can be affected by hydrologic habitat (Rypel and Bayne, 2009), and the decrease in growth of the two *Coreius* species after damming in the TGR could be explained by changes in water temperature, as reported in whitefish (*Prosopium williamsoni*) after construction of the Libby Dam on the Kootenai River, Idaho, USA (Paragamian, 2002), and lower ecosystem productivity (Milbrink et al., 2011). The quantity, quality and size of food resources are often related to variations in population growth. One hypothesis that may explain the differences in growth rates is that, after impoundment of the TGR, benthic organisms failed to adapt to the new, deep-water environment, resulting in a lower biomass of available food which subsequently affected the growth of demersal fish. Any biological explanation for such a phenomenon remains to be clarified, but it may well be a specific feature of the *Coreius* population in the Changjiang River after impoundment. The gradual reduction in flow velocity from the upstream area of the reservoir towards the dam (SEPA, 2011) is demonstrated by the fact that the upstream area has the highest flow velocity and largest k value.

The largest and majority of older specimens of *C. heterodon* and *C. guichenoti* were collected in the midstream and upstream areas of the TGR, respectively, indicating that midstream was more suitable for the growth of *C. heterodon*, and upstream was more suitable for *C. guichenoti*. Food availability and abiotic factors influence regional and intraspecific variations in growth (Claramunt and Wahl, 2000; Neuheimer and Taggart, 2007), and the relatively lower fishing mortality may be another reason for the improved growth.

In the TGR, a higher natural mortality (M), lower total mortality (Z) and lower fishing mortality (F) were found for *C. heterodon* compared with values recorded before the first stage of impoundment (Chen et al., 2002), whereas, for *C. guichenoti*, Z and M

values were higher and the *F* value was slightly lower than in previous studies (Chen et al., 2002; Yang, 2009). Inappropriate habitat and lower growth rates influence mortality rates (Griffiths and Harrod, 2007). Higher temperatures caused higher metabolic rates, resulting in more frequent foraging, which increases the chances of encountering predators and indirectly affects mortality rates (Pauly, 1980). Fishing mortality rates have declined in recent years because of the enforcement of closed seasons and stricter fishery management. The exploitation rate ($E=F/Z$) for the two *Coreius* species was >0.5, which indicates a possible decline in stocks (Patterson, 1992). Therefore, these fishery management practices and policies need to be enforced for the long-term protection, conservation and stock restoration of these two *Coreuis* species.

4.3 Management implications

In the TGR, stocks of *Coreius* species have been in decline. After final impoundment of the TGR, the demographic structure of the *Coreius* populations inhabiting the area changed, with young individuals becoming more abundant and mature individuals progressively disappearing. The consequences of dam construction combined with the impact of commercial fishing leaves lotic populations, such as *Coreius* species, in a fragile situation that must be addressed urgently.

Long-term protection and conservation is required to rebuild the reproductive potential and age structure of *Coreius* populations, and aid in their recovery. It is recommended that fishery managers should consider the following points: (1) limit fishing effort. In particular, limit the number of fish hooks and set minimum landing sizes that are above the size-at-maturity of the species. This will ensure that immature and developing fish (which now dominate the populations in near-dam areas) will reach sexual maturity before capture; (2) ban fishing during breeding seasons, especially in the Jinsha River (upstream of the Changjiang River). The closed season should be extended and fishery surveillance increased to enforce these restrictions. At present, the closed season in the Changjiang River extends from February to April, which does not cover the breeding activities of *Coreius* sp., which take place between April and July (Cheng, 2008; Zhang, 2009). In addition, opening all sluice gates during the spawning season would be advantageous to migratory fish in terms of nursery grounds (Jutagate et al., 2007), as would the construction of fish passes on the Jinsha River so that migratory fish can access spawning grounds more easily (Gowans et al., 2003). Management of the fishery is clearly necessary for population recovery, but it is often insufficient. Habitat conservation also needs to be considered—the entire river system should be protected. In addition to rehabilitating environmental conditions, the fish fauna needs to be rebuilt in this region. In the 1950s, for example, paddlefish in the Missouri River were protected by a river habitat conservation directive (Elser, 1986). Artificial propagation is another possible rehabilitation measure. In the Changjiang River, *C. guichenoti* migrate to the Jinsha River to mature and reproduce; however, this migration path has been blocked by cascading hydroelectric dams. Therefore, stock enhancement appears to be the only, rapidly effective method for preventing collapse of the *C. guichenoti* population. Therefore, artificial propagation of *C. guichenoti* should be actively considered. Impoundment has adverse impacts on benthic organisms, but a reduction in peak flows may enhance the recovery of benthic fauna (Cowx et al., 1998). Thus, a new flow-management system could be introduced to reduce the adverse effects of damming on the benthos, which is the primary food resource of *Coreius* species (Xu et al., 1981; Liu et al., 2012). Finally, the status of these food resources within the reservoir, which play an important role in the condition of *Coreius* species, with consequences for growth, natural mortality and reproductive potential (Lloret et al., 2014), need to be properly evaluated because, at present, little is known about them.

5 CONCLUSION

The life-history traits of these two lotic species, *Coreius heterodon* and *C. guichenoti*, have been significantly affected by impoundment along the longitudinal profile of the Three Gorges Reservoir area. Lower abundance, slower growth, a less diversified age structure, poorer condition (indicated by the hepatosomatic index) and higher mortalities were recorded in areas nearest the dam compared with upstream areas. The results indicate that the two *Coreius* species were subject to dramatic changes after impoundment the Changjiang (Yangtze) River and creation of the reservoir. These changes could have resulted from alterations in habitat (with decreasing water flow rates), water temperature and food availability. Fishery management, conservation and restoration policies to rehabilitate the stock biomass of these species need to be implemented urgently.

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