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Reproductive biology of bream *Abramis brama* (L.) in the lower reaches of the Irtysh River, China*

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Abstract The reproductive biology of bream *Abramis brama* (L.) was studied from 546 fish collected from the lower reaches of the Irtysh River in Xinjiang, north-west China, from March to November 2013. The overall sex ratio (M/F) was 1.06:1, and was not significantly different from the theoretical 1:1 ratio (P>0.5). However, there was a dominance of males during the pre-spawning season (1.33 in March and 1.56 in April, P<0.5), while females were dominant during the peak spawning season (0.88 in June, P<0.5). The monthly variation in gonadosomatic index (GSI) and proportion of gonads at each macroscopic maturity stage, indicated that *A. brama* spawned once a year with peak spawning occurring from late May to June. The unimodal distribution of oocyte diameter each month indicated that *A. brama* is a single spawner, with a high degree of spawning synchronicity. The standard lengths (SL_{50}) and ages (A_{50}) at first maturity for males and females, were 178 and 204 mm, and 5.6 and 6.8 years, respectively. The mean absolute fecundity (AF) was 77 311 eggs per fish, and mean relative fecundity (RF) was 162 eggs per gram of body weight (BW). The AF of *A. brama* increased linearly with increasing of gonad weight (GW), eviscerated weight (EW) and standard length (SL), but was not significantly correlated with age. As, *A. brama* in the lower reaches of the Irtysh River reaches reproductive maturity relatively late in their life span, is mature for a short period and spawns in aggregations, this fish is vulnerable to overexploitation.

Keyword: reproductive biology; sex ratio; maturity; spawning period; fecundity; *Abramis brama*

1 INTRODUCTION

The common bream (*Abramis brama*) is a European freshwater fish species in the family Cyprinidae. It was introduced into Lake Balkhash in central Asia from the Ob River Basin in 1949, and gradually spread into Xinjiang Province, north-west China, along the Irtysh River and the Ili River. This species is now important in the commercial market and for recreational fishing in the lower reaches of the Irtysh River (Adakbek et al., 2003). Every year in spring, as the temperature rises and the river ice thaws, *A. brama* shoals in the lower reaches of the Irtysh River in China for breeding. The shoal is readily accessible to commercial and recreational fishermen. Recent studies indicate that this species is in decline, and has been classified as a near threatened fish on the IUCN Red List of Threatened Species (Freyhof and Kottelat, 2008). Hence, close attention should be paid to the conservation status of natural populations of *A. brama*.

Knowledge of the reproductive characteristics of exploited fish populations including sex ratio, size and age at first maturity, and the duration and periodicity of spawning and fecundity, are fundamental in the study of these populations. Understanding these characteristics is essential to

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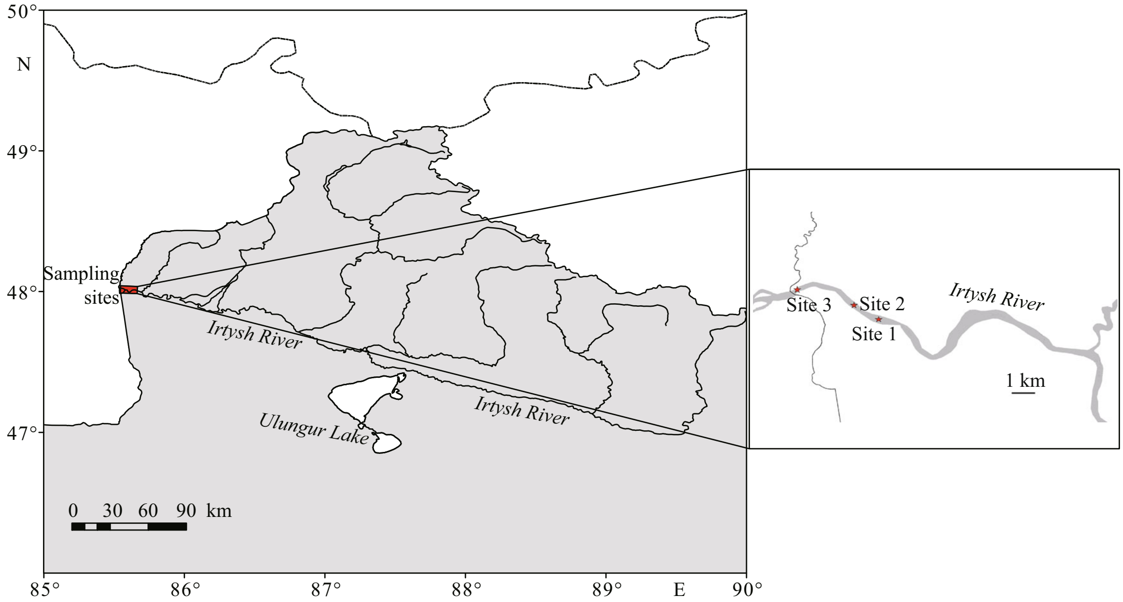

Fig.1 Location map showing sampling locations for *A. brama* in the lower reaches of the Irtysh River, China

quantifying reproductive capacity of both individuals and populations of a fish species (Murua et al., 2003). Artificial propagation of fish also requires an understanding of reproductive characteristics such as size and age at first sexual maturity, spawning period, fecundity and the environmental factors associated with reproduction (Cao et al., 2009). The information available on the reproductive biology of *A. brama* is incomplete. Descriptions of sex ratio, spawning period and patterns, size and age at maturity and fecundity have not been well documented. Furthermore, previous studies on the reproductive biology of *A. brama* have been conducted in Europe. To date, only minimum size and age at maturity of *A. brama* has been reported from Lake Ulungur, in China (Adakbek et al., 2003). There are no publications describing the reproductive biology of *A. brama* in the Irtysh River. The reproductive strategy of a fish species may vary temporally and spatially among stocks, in relation to biotic and abiotic environmental conditions (Cao et al., 2009). Therefore, comprehensive research on the reproductive biology of this species should be carried out to ensure the sustainable utilization of resources.

The objectives of this study were to describe the reproductive biology of *A. brama* inhabiting the Irtysh River by investigating: (1) the sex ratio, (2) spawning season and pattern, (3) size and age at first maturity and (4) absolute fecundity, relative fecundity and the relationships between absolute fecundity and ovary weight, eviscerated weight, standard length and age.

2 MATERIAL AND METHOD

2.1 Study site and sampling procedure

The headwaters of the Irtysh River originate on the southwestern slope of the Altai Mountains, and flow northwest through Lake Zaysan in Kazakhstan, meeting the Ishim and Tobol Rivers before merging with the Ob River near Khanty-Mansiysk in western Siberia (Russia), and terminating in the Arctic Ocean (Zhang et al., 2016a). The total river length is 4 248 km, of which 633 km runs through China. The Irtysh River Basin in China has a cold temperate continental climate. The winters are very cold and last for about six months (from mid-October to mid-March) with a mean water temperature of 0–3.0°C, while the summers are only about 45 days (from mid-June to early August) with a mean water temperature of 15–18°C. The vegetation along the river bank is rich, and is overwhelmed by rising waters during the flood season (April to June) each year (Zhang et al., 2016b).

A total of 546 *A. brama* individuals were collected using trammel nets (inner layer mesh size 10 cm and outer layer 23 cm), set gillnets (mesh size 2.5 cm) and a purse net (mesh size 1 cm) at three different sites in the lower reaches of the Irtysh River in China, from March to November 2013 (Fig.1, Table 1). At least 30 fish were collected each month. The standard length (SL) and fork length (FL) of fish were measured to the nearest 1 mm and body weight (BW) was measured to the nearest 0.01 g. After dissection of the body cavity, both the gonad weight (GW) and

Table 1 *Abramis brama* specimens collected from the lower reaches of the Irtysh River, China

Sampling sites	Data collected	Gears	Catch (*n*)	SL range (mm)	BW range (g)
Site 1 (48.01°N, 85.57°E)	2013.3–2013.11	Trammel nets; purse net	231	68–344	4.69–1 019.05
Site 2 (48.02°N, 85.55°E)	2013.3–2013.10	Trammel nets; set gillnets	188	92–336	15.05–950.90
Site 3 (48.03°N, 85.53°E)	2013.5–2013.8	Set gillnets	126	94–299	15.00–717.01

SL: standard length; BW: body weight; *n*: number.

Table 2 Macroscopic characteristics used for the determination of gonad developmental stages of *A. brama* (Brulé et al., 2003; Huo et al., 2013)

Classification	Stage	Macroscopic appearance	GSI mean±S.E. (sample sizes)
Immature	I	Sex cannot be identified macroscopically. Gonads relatively tiny and represented by two thread-like units. Whitish and translucent	0.28±0.02 (21)
		Female	
Early developing	II	Ovaries are easily recognized and ribbon-like, occupying much less than half of body cavity. Yellowish and opaque, vascularization starts to appear. Oocytes not visually discernible	0.99±0.06 (45)
Later developing	III	Enlarged ovaries, occupying almost half the body cavity. Yellow and well-developed vascularization. Opaque oocytes small and visible to naked eyes. Oocytes cannot be stripped from the ovaries membrane	2.74±0.29 (21)
Maturing	IV	Ovaries expand to fill most of the body cavity. Orange and superficial blood vessels appear on the wall of their inner parts. Full of large mature oocytes. Ovarian wall thin and flexible	8.60±0.61 (66)
Mature	V	Ovaries in maximum size and slightly soft, oocytes are expelled from the follicles and in a flow condition in the ovarian cavity. Orange. Oocytes are flowing freely when stripped or with a slight pressure on the abdomen	11.22±0.09 (20)
Spent	VI	The fishes have spawned. Ovaries significantly reduced in size. Brownish yellow. Flaccid, shrunk and blooded	1.31±0.09 (21)
		Male	
Early developing	II	Testes are easily recognized and ribbon-like, filling about 0.1 of the body cavity. Whitish grey and translucence. No visible vascularization	0.51±0.07 (18)
Later developing	III	Increased testes size, occupying about 0.2 of the body cavity. Whitish and opaque. Vascularization starts to appear	1.06±0.06 (79)
Maturing	IV	Testes larger, firm to touch, occupying about 0.3 of the body cavity. White or white-cream. Capillary distribution on the surface of the testes. Do not release sperm when stripped	1.81±0.07 (59)
Mature	V	Testes in maximum size, occupying about 0.4 of the body cavity. White-cream. Milt flowing freely when abdomen slightly compressed	2.06±0.20 (12)
Spent	VI	Significantly decreased in testes size. Carnation. Flaccid, shrunk and blooded	0.36±0.06 (16)

eviscerated weight (EW) were measured to the nearest 0.01 g, and the sex was identified macroscopically. Ovary and testes development were categorized into six stages based on macroscopic appearance (Table 2). A pair of lapillus were removed from each fish, rinsed in water to remove surrounding tissue and stored in labeled tubes for age determination.

2.2 Sex ratio

Sex ratio, expressed as male: female (M/F) was calculated monthly. Deviations from the expected 1:1 sex ratio were statistically tested using a Chi-square (χ^2) test (Zar, 1999).

2.3 Size and age at first maturity

The standard length (SL_{50}) and age (A_{50}) of fish at first sexual maturity were estimated based on 184 males (102–333 mm; ages 3–13 years) and 173 females (105–344 mm; ages 3–15 years). Gonad development of female and male *A. brama* were categorized into six stages based on macroscopic appearance according to Brulé et al. (2003) and Huo et al. (2013) (Table 2). Fish in stages IV–VI were considered to be sexually mature. SL_{50} and A_{50} for both sexes were estimated by fitting a logistic function to the proportion (P) of mature fish in 10 mm length classes (SL) and 1-year age intervals: $P=\{1+[e^{-r(X-b)}]\}^{-1}$, where P is the proportion of mature fish at SL or age; b is the SL or age at first maturity and r is a constant (Grandcourt et al., 2009). Age data were obtained through examination of growth rings on the lapillus.

Table 3 Standard length (SL) distribution of *A. brama* collected from the lower reaches of the Irtysh River, China, from March to November 2013

Standard length (mm)	Number of specimen		Total
	Male	Female	
100–120	6	4	10
120–140	4	7	11
140–160	2	4	6
160–180	13	7	20
180–200	19	15	34
200–220	37	20	57
220–240	54	32	86
240–260	29	24	53
260–280	14	38	52
280–300	4	11	15
300–320	1	4	5
320–340	1	5	6
340–360	0	2	2
Total	184	173	357

2.4 Spawning season and spawning pattern

Spawning season was determined by examining variation in the gonadosomatic index (GSI) and the proportion of gonads at each macroscopic maturity stage, each month. The GSI was calculated for each individual fish using the following formula: GSI=100GW×EW^{-1}, where GW is the gonad weight and EW is the eviscerated weight. Water temperature was measured twice a day (8:00 h and 20:00 h) in the Irtysh River and the mean values for each month were used in the analysis.

The monthly size-frequency distribution of oocytes was used to estimate the timing of spawning in *A. brama*. Two methods, histology and photography, were used to determine oocyte diameter. The first method involved subsampling ovaries at macroscopic maturity stages II, III, and VI (Table 2). The tissue was fixed in paraformaldehyde solution and processed using standard techniques for histology. Only oocytes sectioned through the nucleus were measured (Simon et al., 2012). Oocytes in early development were not sphere-like in cross-section, as they were squeezed by surrounding oocytes. Where this occurred the diameter of the longest axis crossing the nucleus of each oocyte was measured. Oocytes at a later developmental stage maintained their sphere-like shape, and the diameters were measured across oocytes with a nucleus. The size of oocytes at stages IV–V (Table 2) were measured using a second method. Ovaries were subsampled and fixed in 10% neutral buffered formalin, the oocytes were photographed (Leica EZ4D dissecting microscope) and measured to the nearest 1 µm in diameter, using image processing software (Image Pro Plus 6.0).

2.5 Fecundity

Fecundity of *A. brama* was calculated using the gravimetric method described by Bagenal and Braum (1978). The 64 ovaries from female *A. brama* at macroscopic stages IV–V collected from April to mid-June 2013 (before spawning) were subsampled, weighed with a precision of 0.01 g and fixed in 10% neutral buffered formalin. Fecundity was calculated as absolute fecundity (AF) and relative fecundity (RF) where AF=nGW/SW and RF=AF/BW, where n is the number of oocytes with yolk in the subsample, GW is the ovary weight, SW is the weight of the subsampled ovary and BW is the body weight. The relationships between AF and gonad weight, age, eviscerated weight and standard length were analyzed using regression analysis (Bagenal, 1978).

2.6 Statistical analysis

Data and images were analyzed and processed using Microsoft Excel 2007 (Microsoft, Redmond, WA, USA), SPSS 17.0 (IBM, Armnok, NY, USA), ArcGIS 10.2.2 (ESRI, Redlands, CA, USA) and OriginLab Origin V 8.5.1 (Originlab, Northampton, MA, USA). The difference in mean SL between males and females was determined using an independent sample t-test and tests for differences among monthly GSI values were determined using ANOVA followed by Tukey's post hoc test (Zar, 1999). The results are presented as means±S.E. and the significance level was set at 0.05.

3 RESULT

3.1 Size distribution and sex ratio

The distribution of sexes by size class showed that most specimens smaller than 260 mm (SL) were males, except for length classes 120–140 mm and 140–160 mm, while most fish larger than 260 mm (SL) were females. There were no males larger than 340 mm in length (Table 3). On average, females (235.22±3.72 mm) were significantly larger (SL) than males (217.77±2.84 mm; t-test, t=3.444, P<0.05).

A total of 546 individuals (173 females, 184 males

Table 4 Sex ratio of males to females (M/F) for *A. brama* collected from the lower reaches of the Irtysh River in China, from March to November 2013

Sampling month	Number of specimen		Sex ratio (M/F)	χ^2 -test
	Male	Female		
Mar.	20	15	1.33	$P<0.05$
Apr.	25	16	1.56	$P<0.05$
May	28	28	1.00	$P>0.05$
Jun.	22	25	0.88	$P<0.05$
Jul.	25	26	0.96	$P>0.05$
Aug.	21	21	1.00	$P>0.05$
Sep.	16	17	0.94	$P>0.05$
Oct.	14	13	1.08	$P>0.05$
Nov.	13	12	1.08	$P>0.05$
Total	184	173	1.06	$P>0.05$

and 189 indeterminate) were collected in this study. The overall sex ratio (M/F) was 1.06:1, not significantly different from the theoretical 1:1 ($P>0.05$; Table 4). However, the sex ratio (M/F) was 1.33 in March and 1.56 in April, strongly biased in favor of males ($P<0.05$). Conversely, the sex ratio (M/F, 0.88) was biased towards females in June ($P<0.05$). There were no significant differences from the expected 1:1 ratio in the remaining months ($P>0.05$).

Standard length (SL) has been used in most *A. brama* studies, but fork length (FL) has also been used by some authors. To compare the two dimensions, the relationship between SL and FL was examined. Fork length (FL) increased linearly with increasing SL and the best-fitted regression equation was FL=1.13 SL+3.00 (n=357, R^2=0.998).

3.2 Size and age at first maturity

SL_{50} and A_{50} were estimated by fitting a logistic function to the proportion (P) of fish that are reproductively mature as follows:

Size at 50% maturity

Male: $P=100\times(1+e^{(-0.12(SL-177.70))})^{-1}$ (n=184, R^2=0.998)

Female: $P=100\times(1+e^{(-0.10(SL-203.50))})^{-1}$ (n=173, R^2=0.998)

Age at 50% maturity

Male: $P=100\times(1+e^{(-1.47(Age-5.6))})^{-1}$ (n=184, R^2=0.992)

Female: $P=100\times(1+e^{(-1.37(Age-6.8))})^{-1}$ (n=173, R^2=0.998)

The estimated mean standard lengths (SL) at 50% maturity for males and females, were 178 mm (FL=204 mm) and 204 mm (FL=233 mm), respectively (Fig.2a), and the mean age at 50% maturity for males and females, were 5.6 and 6.8 years, respectively (Fig.2b). Observed minimum SL and age at maturity were 156 mm (FL=179 mm) age 4 years for males and 166 mm (FL=191 mm) age 5 years for females. All males above 195 mm SL (FL=223 mm) and age 7 years and all females above 235 mm SL (FL=269 mm) and 9 years were mature.

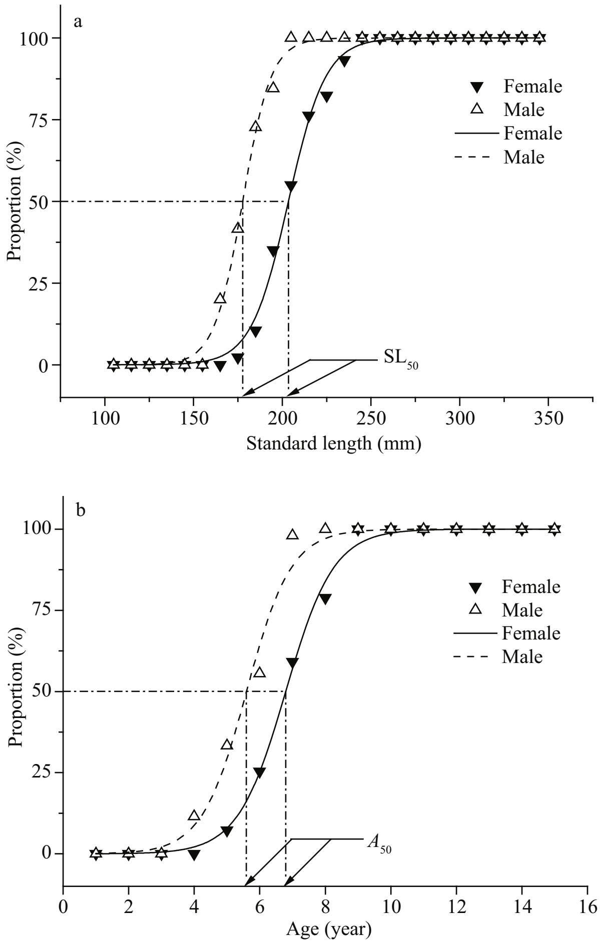

Fig.2 Logistic functions fitted to the proportion of reproductively mature *A. brama* by (a) standard length (in 10 mm size classes) and (b) age to the nearest year

Sample sizes for males are n=184 and for females n=173. Arrows indicate mean standard length (SL_{50}) and age (A_{50}) at first sexual maturity.

3.3 Spawning season and pattern

Monthly variation in GSI (Fig.3) and the proportion of gonads at each developmental stage (Fig.4) were used to estimate spawning times. *Abramis brama* showed the highest GSI (11.73% for females and 2.24% for males), and the highest percentage of mature stage gonads (56.8% for females and 46.6%

for males) in May. The GSI of both sexes showed a dramatic decline in June, stabilized at relatively low levels from June to September, and then exhibited an increasing trend from September to November (Fig.3). Spent individuals were only observed from late May through to early July, with the highest percentage (43.5% for females and 58.0% for males) occurring in June. Gonads of both sexes were mainly in developing stages (early and late) between July and November, and some gonads at the maturing stage were observed in October and November. There was no significant difference in GSI detected between the months March and November (P>0.05), but GSI in April was significantly higher than during March (P<0.05). Thus, the spawning period for *A*. *brama* in the Irtysh River was once each year from late May to June. Suitable water temperatures for reproduction of *A*. *brama* were 12–15°C (Fig.5).

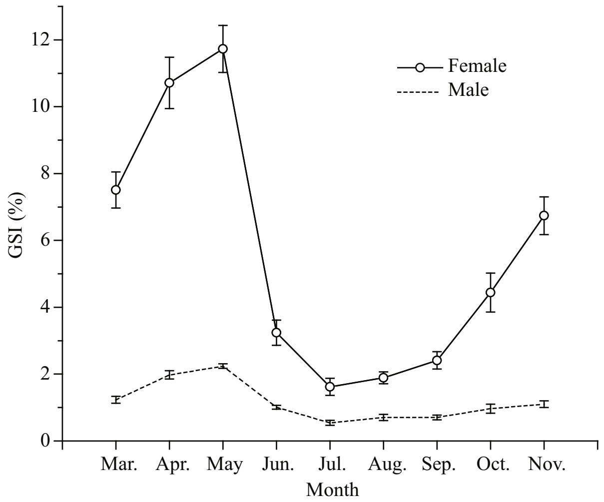

Fig.3 Monthly variation in the gonadosomatic index (GSI) of female and male *A. brama* collected from the lower reaches of the Irtysh River from March to November 2013

Values are expressed as means±standard error (S.E.).

Ovaries from 93 mature female *A*. *brama* were subsampled for oocyte diameter measurement. Monthly size-frequency distribution of oocytes are presented in Fig.6. There were two distinct phases during oocyte growth. The primary growth phase (PGP) included developing stages II and III (Table 2).

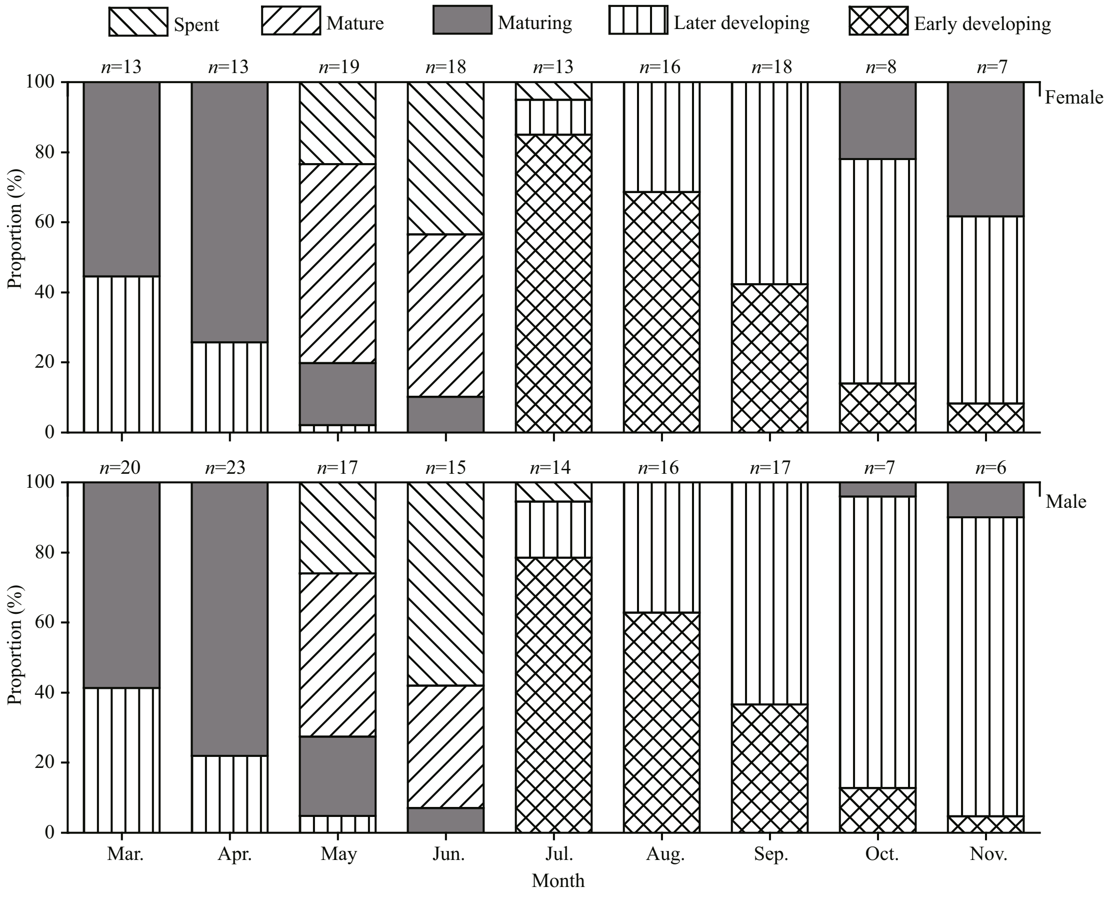

Fig.4 Monthly variation in the proportion of gonads at each macroscopic maturity stage for female and male *A*. *brama* from the lower reaches of the Irtysh River collected from March to November 2013

Numbers above bars show sample sizes.

Oocyte diameter in stage II oocytes ranged from 0.2–0.5 mm and in stage III oocytes ranged from 0.3–0.7 mm. The secondary growth phase (SGP) included stages IV, V and VI. Oocytes at stages IV and V were yolked, and ranged in diameter from 0.5–1.1 mm and 0.8–1.3 mm, respectively. At stage VI the diameters for oocytes dropped to 0.2–0.7 mm, with most in the 0.2–0.4 mm range (Fig.6). The period from late May to June was considered the spawning period. After spawning, gonads returned to stage II, and some developed to stage III until September. After that, the oocytes gradually developed to stage IV, with some remaining at stage III in November for overwintering. There was no significant difference in oocyte diameter distribution between November and March (P>0.05), however the size-distribution of oocytes in April was significantly higher than in March (P<0.05). Oocyte diameter had a unimodal distribution every month indicating that *A. brama* is a single spawner, and has a high degree of spawning synchronicity. Based on this, the estimated absolute fecundity is equal to the annual fecundity.

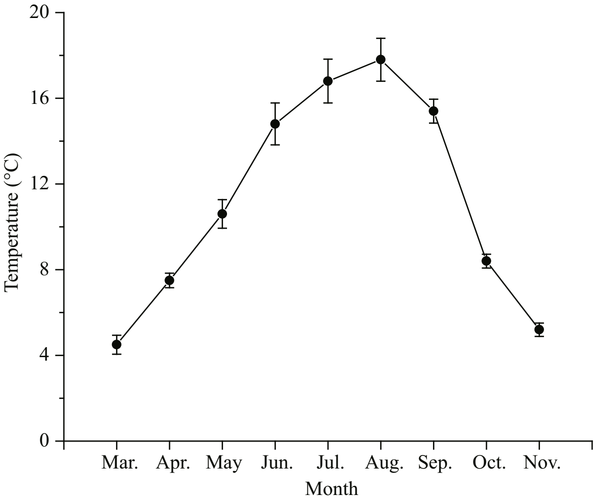

Fig.5 Monthly variation in the water temperature of the lower reaches of the Irtysh River between March and November 2013

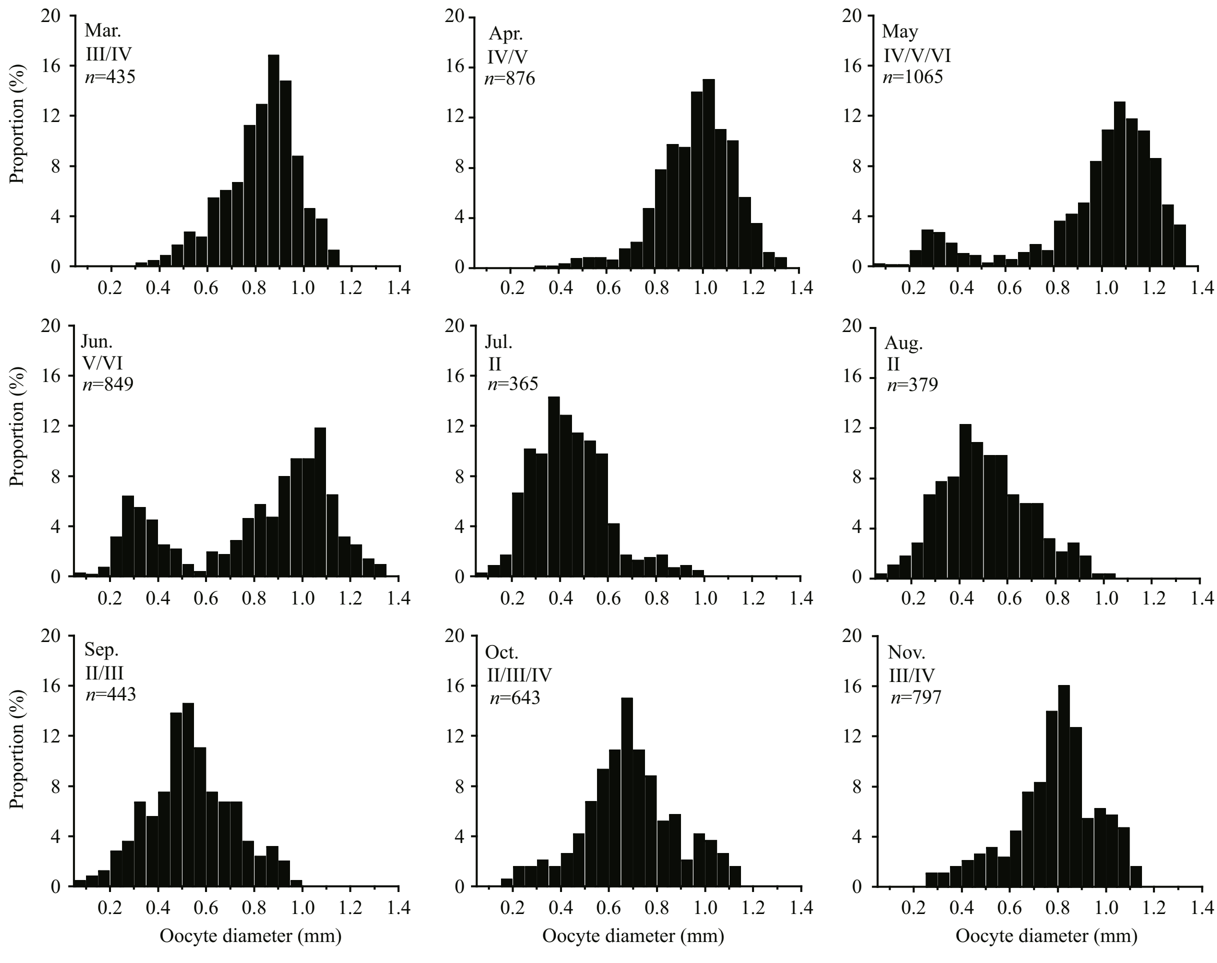

Fig.6 Oocyte size-frequency distributions indicating monthly variation in ovarian stages of mature female *A. brama* in the lower reaches of the Irtysh River between March and November 2013

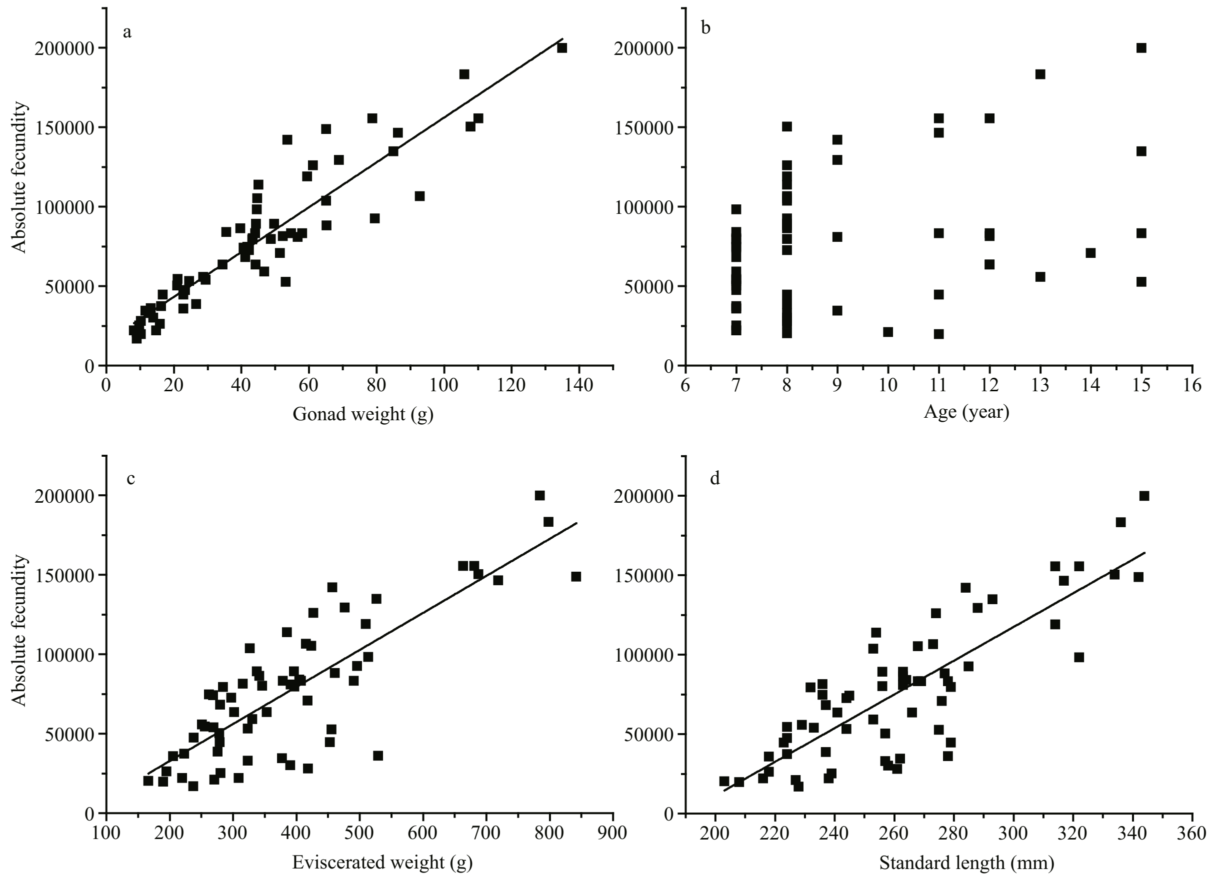

Fig.7 Relationships between absolute fecundity (AF) and (a) gonad weight (GM), (b) age, (c) eviscerated weight (EW) and (d) standard length (SL) for *A. brama*

3.4 Fecundity

Fecundity was estimated for 64 females that ranged from 203 to 344 mm SL. Absolute fecundity (AF) varied in a wide range from 16 853 to 199 747 eggs per fish, with a mean value 77 311 eggs per fish (S.D.=5 461), and RF ranged from 61 to 264 eggs/g with a mean value of 162 eggs/g (S.D.=7). The AF of *A. brama* increased linearly with increasing gonad weight (GW), eviscerated weight (EW) and standard length (SL), but was not significantly correlated with age (Fig.7). The best-fit regression equations were as follows:

AF and GW: AF=1 411.1 GW+1.5×10^4 (n=64, R^2=0.85),

AF and EW: AF=233.1 EW–1.4×10^4 (n=64, R^2=0.67),

AF and SL: AF=163.2 SL+1.5×10^4 (n=64, R^2=0.68).

4 DISCUSSION

The sex ratio of a population is one of the most important parameters in population ecology studies (Cao et al., 2009). The overall sex ratio of *Abramis brama* in the Irtysh River was close to the theoretical 1:1. However there was a change during the pre-spawning and spawning seasons; males predominated during the pre-spawning season (March–April), and females were predominant in June. During the non-spawning season, sex ratios did not differ significantly from 1:1 (July–November). The surplus of males during the spawning season may be considered an adaption to facilitate the preservation of females (Türkmen et al., 2002). This may be a reproductive strategy for *A. brama* in the Irtysh River. The predominance of males also occurs during the flood season, and a surplus of males and/or sperm may ensure a high fertilization rate, resulting in population growth. Differences in sex ratios were also found in *A. brama* at different sizes, with males being predominant among fish of a smaller size (<260 mm). The pattern of males predominating at early life stages has also been found in other freshwater fish (Simon et al., 2012). The difference in the size distribution of the sexes may be attributed to the earlier maturation of males, and a tendency towards slower growth and a higher mortality rate after maturation (Simon et al., 2012).

Reproductive strategies such as size and age at maturity and fecundity can directly influence the reproductive potential of a population (Beacham, 1983). In our study, males reached reproductive maturity at 204 mm FL, age 5.6 years and females were reproductively mature at 233 mm FL, age 6.8 years. The minimum size at reproductive maturity was 179 mm FL, age 4 years for males and 191 mm FL, age 5 years for females. All males above 223 mm FL and 7 years and all females above 269 mm FL and age 9 years were mature. The population of *A. brama* in the Irtysh River is characterized by relatively late maturation compared with this species at other locations. Valoukas and Economidis (1996) reported that all male *A. brama* in Lake Volvi, Greece larger than 135 mm FL, age 3 and female *A. brama* larger than 150 mm FL, age 4 were sexually mature. These are the smallest sizes at first maturity that have been recorded for an *A. brama* population. Adakbek et al. (2003) found the smallest mature female *A. brama* to be 178 mm FL and age 4 years in Ulungur Lake, China (similar in latitude to the Irtysh River). In the Międzyodrze waters in Poland, Neja and Kompowski (2001) found that the FL_{50} of female *A. brama* was 229 mm. The FL_{50} of female *A. brama* was 229 mm in Szczecin Lagoon and 252 mm in Lake Dąbie, in Europe (Kompowski, 1988). Lammens (1982) indicated that FL_{50} was 250 mm for males and 265 mm for females in Lake Tjeukemeer. Pawson et al. (2000) demonstrated that ecological factors (such as water temperature and food availability) greatly influence the sexual maturity of fish. Differences in the size of fish at first maturity are linked to stock units, but may also be influenced by study methods (Neja and Kompowski, 2001).

Many freshwater fishes in the temperate zone spawn in late spring and early summer (Peter and Crim, 1979). The results of this study indicated that *A. brama* is a single spawner with a short spawning season from late May to June, with a high degree of spawning synchronicity. This result is consistent with most previous studies on this species in other geographical areas (Kompowski, 1982; Neja and Kompowski, 2001; Adakbek et al., 2003; Adámek et al., 2004). However, Valoukas and Economidis (1996) reported that the spawning season of *A. brama* in Lake Volvi began in April. In addition, Targońska et al. (2014) found that *A. brama* had two kinds of reproductive strategies, and may spawn once or several times per year. Kompowski (1982) indicated that a higher water temperature would be expected to bring about an early spawning of *A. brama*. In another study, the reproductive activities of this species were completed in June when environmental conditions became suitable (high water temperatures, rich source of food, and stable water environment) for embryonic development (Domagała et al., 2015). This could be considered an adaptation to the riverine conditions in Sinkiang.

The gonad development of many late spring and early summer spawning freshwater fishes begins in fall and continues into spring, following a relatively long period of gonadal quiescence after spawning in relation to environmental factors (Peter and Crim, 1979). The pattern of gonad development in *A. brama* varied among studies and did not always follow this predicted pattern. Neja and Kompowski (2001) reported that the gonads of *A. brama* in Międzyodrze started to develop in early winter, and continued throughout the winter until spawning in late spring. Valoukas and Economidis (1996) found that the gonads of *A. brama* in Lake Volvi started to develop in September, but this development was interrupted during the winter months, and the greatest growth was recorded during March and April. Our study also showed that the gonadal development of *A. brama* in the Irtysh River started in September, was interrupted during the winter months and showed remarkable growth in April. This strategy of delayed onset of gametogenesis may be advantageous for *A. brama* to allow recovery from spawning and leave energy for growth. Further, the ceasing of gonad growth during the winter months may represent an adaptation to the local aquatic environment, due to low food availability and low water temperatures during the winter months in the Irtysh River.

The absolute fecundity (AF) of *A. brama* in the Irtysh River was 77 311 eggs per fish, and the relative fecundity (RF) was 162 eggs per gram of fish body weight. The AF obtained in this study was low compared with previous studies. The AF of *A. brama* in Lake Tjeukemeer was 101 531 eggs (Lammens, 1982), and in River Sow and Trent (UK) was 204 826 and 426 058 eggs per fish, respectively (Adámek et al., 2004). The maximum size of *A. brama* in the Irtysh River is the smallest recorded (Zhang et al., 2016a). A low supply of food resources may explain the small size of fish, and may be the reason for the low fecundity of *A. brama* in the Irtysh River. Wootton

(1999) found that absolute fecundity shows a tendency to increase with fish size and weight, so the effect of body size and weight on fecundity should be eliminated in comparative studies. However, due to the lack of RF data from other studies, it was difficult to compare results. Furthermore, comparisons among studies may be biased by differences in study locations, differences in time, and by differences in the methods used (Gundersen et al., 2001).

5 CONCLUSION

Management of many exploited fish populations is based on the biological characteristics of the fish (Hilborn and Walters, 1992). Based on our study, the reproductive biology characteristics of *A*. *brama* identified in the lower reaches of the Irtysh River can be summarized as follows: maturation occurring relatively late in their life span, a short spawning season, and aggregation-spawning. This renders this species vulnerable to exploitation. More restrictive harvest regulations, such as a seasonal fishery closure (April to June) and catch size limits (SL>250 mm), may prevent overexploitation of these stocks, and thereby provide better spawning opportunities to ensure the sustainable utilization of this species.

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