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Marine and Freshwater Research
https://doi.org/10.1071/MF19315

Stock-specific assessment of precise age and growth in the long-whiskered catfish *Sperata aor* from the Ganges River

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Abstract. Sustainable management of the long-whiskered catfish *Sperata aor* (Hamilton, 1822) in the Ganges River justifies precise stock-specific information on age and growth. The aim of the present study was to estimate the age and growth of three stocks, namely Narora–Kanpur, Varanasi and Bhagalpur, of *S. aor* from the Ganges River. Among the hard structures chosen for analysis, vertebrae provided precise age estimates up to 9 years of age in all the three stocks of *S. aor* based on average percentage error. Edge analysis of vertebrae and marginal increment ratio analysis of sectioned otoliths showed annulus formation once per year during April–June. The von Bertalanffy growth rates showed significant differences between the sexes and among the stocks. The growth coefficient k (0.24–0.30 year^{-1}) showed rapid growth relative to asymptotic length (L_∞) in all three stocks. The growth performance index was nearly the same for all three stocks. The results of the present study can be used in formulating scientifically sound management policies in view of anthropogenic threats to the populations of *S. aor* from the Ganges River.

Additional keywords: age estimation, age validation, calcified structures, growth pattern, von Bertalanffy growth function.

Received 7 October 2019, accepted 21 February 2020, published online 25 March 2020

Introduction

The long-whiskered catfish *Sperata aor* (Hamilton, 1822) is a demersal fish species that is distributed in Pakistan, India, Nepal, Bangladesh and upper Myanmar (Talwar and Jhingran 1991). Although *S. aor* is a riverine species, it is also well adapted to lacustrine conditions. The juveniles of this species primarily feed on insects, whereas the adults are piscivorous. Ramakrishniah (1992) reported that *S. aor* from Nagarjunasagar Reservoir, India, attains first maturity at a length of 57.3 cm and age of 4 years. The spawning season of this species varies regionally in India between March and August, with peak spawning occurring in April and June in the Ganges River (Saigal and Motwani 1964). Captive breeding, larval rearing and organised culture techniques are yet to be standardised at a commercial scale for most catfishes, including *S. aor* (Rahman *et al.* 2005); therefore, market availability depends entirely on capture fisheries. In the past, the fish was caught from the middle and lower regions of the Ganges, but due to a shift in its distribution pattern it is now also reported from the upper region (Sarkar *et al.* 2012). This shift may be because of variations in hydrology and an increase in water temperature by ~1.5°C, possibly due to climate change in the upper stretch of the Ganges River (Vass *et al.* 2009; Sarkar *et al.* 2012). Currently, no harvest management plan, area-based regional management plan and *ex situ* conservation strategies are in place (Rema Devi and Raghavan 2011). In India and Bangladesh, *S. aor* is reported as vulnerable primarily because of habitat loss, overexploitation, pollution, destruction of breeding grounds and the effects of climate change (Lakra *et al.* 2010; Mollah 2015). Populations of *S. aor* are also facing extreme threat due to the effects of dams, barrages and dense human settlements along the Ganges River (Khan and Nazir 2019). Therefore, in view of the anthropogenic threats to the fishes of the Ganges River, effective management and conservation strategies should be prepared as a priority for the target fish species (Nazir and Khan 2017). *S. aor* in the Ganges River has been recently reported as three distinct stocks (Nazir and Khan 2017; Khan and Nazir 2019).

Ageing precision is a valuable means of assessing the relative ease of estimating fish age from a particular ageing structure or assessing the reproducibility of an individual's age estimations (Campana 2001). The most suitable ageing structure may vary from species to species; therefore, the selection of a hard structure for age and growth estimation is crucial (Quist *et al.* 2007; Abecasis *et al.* 2008). Furthermore, the process of estimating fish age from hard structures incorporates two major sources of error: the error inherent in the hard structure itself and the error associated with interpretation of growth increments (Campana 2001). The inherent error associated with the hard structure can be assessed but not controlled, whereas the interpretation error can be both assessed and controlled

Fig. 1. Map showing the sites where *Sperata aor* were collected along the Ganges River.

(Morison *et al.* 2005). Ageing errors may have a considerable effect on the understanding of population dynamics, with severe consequences for scientifically sound management strategies (Campana 2001; Koenigs *et al.* 2013). Therefore, ageing errors should be reduced wherever possible by including an age validation method (Beamish and McFarlane 1983).

Age, growth rate and mortality rate are the most influential life history characteristics that regulate the productivity of fish populations (Campana and Thorrold 2001). Age estimates are used to determine fishery age compositions, which can determine total mortality and add age structure to population models. Growth estimates from length-at-age models can be used to estimate other life history parameters, such as natural mortality and longevity. The von Bertalanffy growth function (VBGF) is the most frequently used of all length-at-age growth models in fisheries, and its parameters, such as the growth coefficient k and asymptotic length L_{∞}, are beneficial in describing general fish growth (Chen *et al.* 1992; Quinn and Deriso 1999; Cope and Punt 2007). Further, the VBGF allows for easy comparisons of growth among populations or between sexes and provides parameter estimates that can be used in the Beverton–Holt yield-per-recruit model (Pauly 1998).

The Ganges River emerges from the 'Gaumukh' ice cave (30°92′N, 79°08′E) in the Garhwal Himalayas at an altitude of 4100 m, flows ~2525 km and then ultimately drains into the Bay of Bengal (Fig. 1). The basin of Ganges River is the fifth largest in the world, draining an area of $\sim 1.08 \times 10^6$ km^2; ~80% of the Ganges basin is located in India (Trivedi 2010). The Ganges basin hosts ~265 fish species, including commercially important fishes such as Indian major carp, large catfish, featherbacks, murrels and mahaseer (Talwar and Jhingran 1991; Sinha and Khan 2001). In India, the Ganges River and its major tributaries are controlled by several barrages, mainly diverting water for the irrigation of agricultural fields, thereby resulting in loss of fish biodiversity (Payne *et al.* 2004; Sarkar *et al.* 2012).

The paucity of precise information on basic biological parameters, such as age and growth, impedes the proper management of vulnerable *S. aor*. Therefore, the objectives of the present study were to: (1) identify the most appropriate ageing structure for estimating precise age of stocks of *S. aor* by evaluating and comparing age estimates from different hard structures (otoliths, vertebrae, opercular bones and pectoral spines); (2) validate the estimated age; and (3) assess stock-specific growth using the VBGF equation.

Materials and methods

Sampling

S. aor were collected (twice yearly) from the four sampling stations across the Ganges River, namely Narora (28°11′N, 78°23′E), Kanpur (26°27′N, 80°20′E), Varanasi (25°31′N, 83°01′E) and Bhagalpur (25°27′N, 87°02′E; Fig. 1). Between 2013 and 2016, 557 *S. aor* individuals were captured from all sites. For age validation, fish samples were collected monthly from the Narora site from January to December 2015. The fish samples from the Narora and Kanpur sites were combined because they represent a single stock (Nazir and Khan 2017; Khan and Nazir 2019); therefore, for ageing precision and growth estimation, 251 samples from the Narora–Kanpur stock, 155 from the Varanasi stock and 151 from the Bhagalpur stock were analysed. Fish length (total length (TL)) was recorded fro each individual to the nearest millimetre and converted to centimetres before final analysis. The fish samples were then transported to the laboratory on ice. The sex of each individual fish was determined externally on the basis of the presence of a papilla in the vent region and by visual examination of gonads under a stereo zoom microscope.

In the laboratory, the hard structures (otoliths, vertebrae, opercular bones and pectoral spines) were removed from each individual. The hard structures were prepared following standard protocols (Phelps *et al.* 2007; Ding *et al.* 2011; Leonardos and Tsikliras 2011; Khan *et al.* 2016) and subsequently each hard structure (whole or thin sectioned) was examined under a stereo zoom microscope (SMZ745T; Nikon, Tokyo, Japan). Moreover, each hard structure was analysed independently by two readers (AN and MAK) without knowledge of fish size, date and location of capture or age estimates from other hard structures of the same fish.

Sex ratio

An exact binomial ratio test was performed to determine whether the sex ratio differed significantly from parity in all three *S. aor* stocks.

Preparation of hard structures

Otoliths (lapillus) were studied for age estimation by placing them in water or 95% ethanol. Otoliths with unclear annuli were ground using 600-grit CarbiMet 2 Abrasive Discs (Buehler Ltd, Lake Bluff, IL, USA) to make the annuli more distinct. The other otolith of a pair was prepared for thin sectioning (~0.5 mm) using an IsoMet low-speed saw (Buehler Ltd, Lake Bluff, IL, USA) according to the protocol of Khan *et al.* (2016). The thin sections were polished using wet 1200-grit CarbiMet 2 Abrasive Discs and subsequently examined.

Vertebrae (4th–10th) were placed in boiling water for ~5–10 min and then cleared of attached tissue. After cleaning, each vertebra was immersed in 95% ethanol for 30 min, followed by 30% hydrogen peroxide for 10–15 min (Ding *et al.* 2011).

Opercular bones were detached using a scalpel and were then placed in boiling water for 2–3 min to remove any extraneous tissue. A bristle brush was used to remove the tissue that boiling water did not loosen (Phelps *et al.* 2007). Cleaned opercular bones were then placed in 95% ethanol for ~5 min before being dried at room temperature for 2–3 days.

Pectoral spines were disarticulated and all the attached tissue was cleaned. Pectoral spines were sectioned using an IsoMet low-speed saw and the sections were soaked in a 70% acetic acid solution for ~30 s to make the annuli clear and then rinsed with distilled water (Leonardos and Tsikliras 2011).

Data analysis

Precision and validation of age estimates

The age estimates obtained from the hard structures were compared by calculating the average percentage error (APE). The APE was derived using the formula of Beamish and Fournier (1981) as follows:

$$\mathrm{APE}_j = \frac{1}{R}\sum_{i=1}^{R}\frac{X_{ij} - X_j}{X_j} \times 100$$

where X_{ij} is the ith age determination of the jth fish, X_j is the mean age estimate for the jth fish and R is the number of times each fish is aged.

APE is a better measure of precision than percentage agreement; it is sensitive to age disagreement and the magnitude of the difference in age assignment between readers (Beamish and Fournier 1981). Relationships between the hard structure exhibiting precise age estimates and the other alternative hard structures were estimated by Pearson correlation analysis. Moreover, regression analysis was performed to estimate the slope, which shows the deviation in age estimates from the alternative structures in relation to the hard structure exhibiting precise age estimates (Phelps *et al.* 2007).

Edge analysis (EA) and marginal increment analysis (MIA) were conducted to validate that an annulus is formed annually and to determine the periodicity of annulus formation (Campana 2001; Okamura and Semba 2009; Blackwell and Kaufman 2012; Porta and Snow 2017). For EA, each vertebra was assigned to one of the two edge types (translucent or opaque). Monthly changes in edge type were analysed to determine the annual periodicity of the translucent and opaque zones (Campana 2001; Ma *et al.* 2011). The marginal increment ratio (MIR) was obtained using MIA (Beamish and McFarlane 1983; Smith 2014). The MIR from each sectioned otolith was estimated using the following formula:

$$\mathrm{MIR} = (R - R_{\mathrm{n}})/(R_{\mathrm{n}} - R_{\mathrm{n}-1})$$

where R is the radius (the distance between the focus and the otolith edge), R_{n} is the distance between the focus and the last complete band and $R_{\mathrm{n}-1}$ is the distance between the focus and the penultimate complete band (Lessa *et al.* 2006; Smith 2014). Monthly mean MIR values were plotted to elucidate periodic trends in annulus formation (Lessa *et al.* 2006).

Growth analysis

The VBGF was fitted to length-at-age data obtained from the age readings of the most suitable hard structure with least-squares procedure by means of non-linear regression. The VBGF equation is represented as:

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right]$$

where L_t is the length of fish at time t (hereafter age), L_∞ is the asymptotic mean length, k is the growth rate and t_0 is the hypothetical age at zero length.

The L_∞ may be overestimated because of the restricted length range of the collected samples, especially large individuals; therefore, it is quite common to fix t_0 to zero and only estimate k and L_∞. The fixing of t_0 to zero may constrain L_∞ to a value closer to the maximum size range sampled and may give a better model fit. Likelihood ratio tests were performed to test for significant differences in growth between stocks and sexes (Kimura 1980). The parameters of the von Bertalanffy growth equations were estimated separately for the three stocks and between sexes for the age estimates obtained from the most suitable hard structure.

The growth performance index (ϕ) was calculated to compare the growth performance of different populations or stocks of the target species based on von Bertalanffy growth parameters (Munro and Pauly 1983):

$$\phi = \log_{10}(k) + 2\log_{10}(L_\infty)$$

Calculations and statistical analyses were performed using Microsoft (Redmond, WA, USA) Excel, SPSS ver. 23.0 (IBM SPSS Statistics, Chicago, IL, USA) and PAST ver. 3.16 (Natural History Museum, University of Oslo, Oslo, Norway; see https://folk.uio.no/ohammer/past/, accessed 16 September 2019; Hammer *et al.* 2001).

Results

Sex ratio

The overall sex ratio of female to male *S. aor* for all three stocks from the Ganges River was 1 : 0.9, which was not significantly different from unity ($P = 0.165$ for Narora–Kanpur stock, $P = 0.261$ for Varanasi stock and $P = 0.329$ for Bhagalpur stock).

Age estimation

Vertebrae provided precise age estimates in all three stocks of *S. aor* based on the lowest APE (Table 1). Correlation analysis showed the age estimates were similar between vertebrae and sectioned otoliths in all three stocks ($r > 0.98$; $P = 0.000$; see Supplementary Material fig. S1, available at the journal's website). Overall, when vertebrae ages were compared with otoliths, opercular bones and pectoral spines, the APE was lowest (1.68% for Narora–Kanpur, 1.71% for Varanasi and 1.63% for Bhagalpur) between vertebrae and sectioned otoliths with a slope >0.97.

Relative to vertebrae age, the age estimates from opercular bones, whole otoliths and pectoral spines exhibited lower precision than did sectioned otoliths in all three stocks of *S. aor*. Ages estimated from opercular bones, whole otoliths and pectoral spines diverged slightly from vertebrae ages ($r = 0.56$–0.98; $P = 0.000$; see fig. S1). Slopes ranged from 0.96 to 0.98 and APE ranged from 2.85 to 5.76%, thereby indicating that ages estimated from these three structures differed slightly from those estimated from vertebrae.

The summary data of the samples collected and the mean value of age estimates from the hard structures for all three *S. aor* stocks are presented in Table 2. Overall, vertebrae showed the highest mean age value, whereas the lowest value was found for sectioned pectoral spines. The three *S. aor* stocks exhibited a similar trend of variation in mean value of age estimates from different methods.

Validation of age estimates

The proportion of translucent edges on vertebrae increased regularly from March to July (reaching 100%) and retained a high level in August and September, then decreased from October to November, and stayed at a lower level between December and February (Fig. 2*a*). In February, the edge was opaque for 91% of fish. These results suggest that the change from an opaque to translucent zone in vertebrae occurred once a year from March to June.

Table 1. Comparison of age estimates based on average percentage error between two readers and among hard structures for the three stocks (Narora–Kanpur, Varanasi, Bhagalpur) of *Sperata aor*

Hard structure	Average percentage error		
	Narora–Kanpur	Varanasi	Bhagalpur
Between readers			
Vertebrae	1.41	1.45	1.39
Sectioned otoliths	1.88	1.92	1.94
Opercular bones	3.51	3.47	3.43
Whole otoliths	4.64	4.57	4.64
Sectioned pectoral spines	6.87	7.18	6.92
Between structures			
Vertebrae–sectioned otoliths	1.68	1.71	1.63
Vertebrae–opercular bones	2.85	2.89	2.94
Vertebrae–whole otoliths	3.56	3.53	3.58
Vertebrae–sectioned pectoral spines	5.67	5.76	5.73

Table 2. Summary data of the samples collected and mean value of age estimates of the three stocks (Narora–Kanpur, Varanasi, Bhagalpur) of *Sperata aor*

Stock	Total length (cm)			Mean age estimate (years)				
	Minimum	Maximum	Mean	Vertebrae	Sectioned otoliths	Opercular bones	Whole otoliths	Sectioned pectoral spines
Narora–Kanpur	13.1	90.1	48.57	4.72	4.57	4.41	4.03	3.97
Varanasi	12.5	89.1	48.65	4.77	4.61	4.44	4.05	3.98
Bhagalpur	12.7	85.4	48.94	4.73	4.58	4.40	4.02	3.95

For sectioned otoliths, the MIR increased gradually from June to April, with a maximum MIR of 0.494 observed in April. Subsequently, the MIR was low between May and June, with a minimum MIR of 0.193 in May (Fig. 2*b*). The MIR results suggest that annulus formation (i.e. transition from an opaque to translucent zone) occurred between April and June.

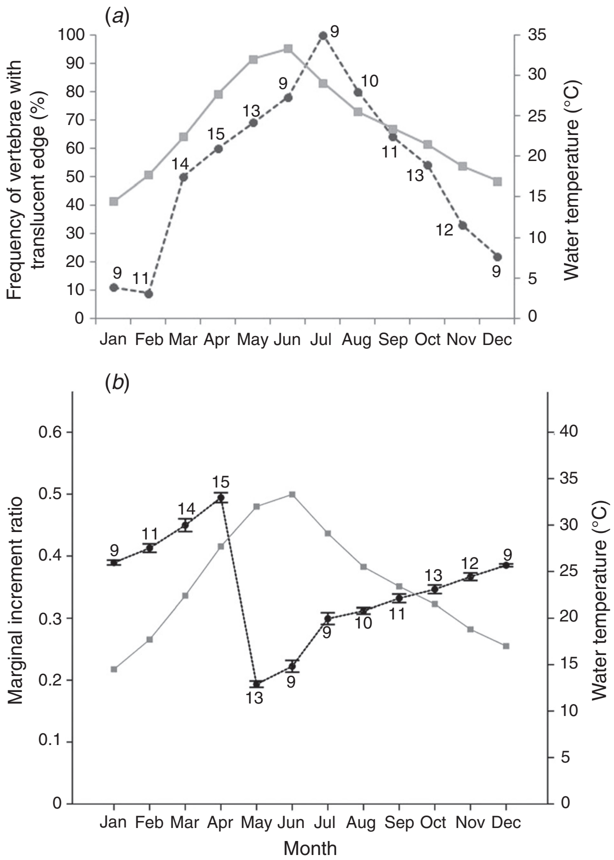

Fig. 2. (*a*) Frequency of *Sperata aor* vertebrae with translucent edge (circles). (*b*) Mean (± s.d.) monthly changes in the marginal increment ratio for *Sperata aor* sectioned otoliths (circles). The grey line in (*a*) and (*b*) represents monthly water temperature (squares). Numbers next to symbols indicate the number of samples.

Growth estimation

The von Bertalanffy growth model was fit using the ages estimated from vertebrae. The von Bertalanffy growth parameters of the three *S. aor* stocks are presented in Table 3. Likelihood ratio tests showed significant differences in growth between the sexes ($\chi^2 = 16.88$, $P = 0.037$) and among stocks ($\chi^2 = 11.39$, $P = 0.048$). The fitted von Bertalanffy growth model for both males and females of the three *S. aor* stocks are shown in Fig. 3. The growth performance index (ϕ) of both sexes and the three stocks is given in Table 3.

Discussion

In the present study, of the different hard structures used for age estimation in *S. aor*, vertebrae provided precise age estimates based on the lowest APE value. In addition, the age readers reported consistently unambiguous and distinct annuli on vertebrae up to an age of 9 years. However, these results should be taken with caution owing to the lack of much older fish. The paucity of much older fish samples may be due to overexploitation of *S. aor* stocks and, at present, no published information is available on the potential of the species for exploitation. Li and Xie (2008) reported vertebrae as the best ageing structure for age determination in Siluriformes fishes on account of the ease of processing and the regularly formed, clear rings. Sectioned otoliths also provide clearer annuli, thereby requiring less time and effort on the part of readers to estimate age compared with whole otoliths. Interpretation of annuli on whole otoliths is very difficult due to the presence of false rings (Morales-Nin 1992), which are regularly deposited and correspond to crucial stages of the life cycle, such as sexual maturity (Colloca *et al.* 2003). In the present study, both readers underestimated age when using whole otoliths compared with vertebrae, sectioned otoliths and opercular bones. Several studies have reported that the use of whole otoliths can lead to age underestimation compared with sectioned otoliths (Abecasis *et al.* 2006; Khan *et al.* 2016). Khan *et al.* (2016) further reported that using whole otoliths of *S. aor* in older individuals may underestimate age because the annuli are not clear due to the curvature of the edge and the zones along the edge becoming crowded and difficult to differentiate. In the present study, annual rings on opercular bones were poorly

Table 3. von Bertalanffy growth parameters and growth performance index (ϕ) of the three stocks (Narora–Kanpur, Varanasi, Bhagalpur) of *Sperata aor* from the Ganges River using the vertebrae method of age estimation

Data for asymptotic length (L_∞) and the growth coefficient k are given as the mean ± s.e.m.

Stock	Sex	L_∞ (cm)	k	φ
Narora–Kanpur	Male	96.5 ± 2.5	0.26 ± 0.04	3.38
	Female	95.8 ± 2.7	0.24 ± 0.03	3.34
	Combined	96.5 ± 1.8	0.24 ± 0.02	3.35
Varanasi	Male	92.4 ± 3.1	0.26 ± 0.03	3.35
	Female	91.2 ± 3.6	0.26 ± 0.03	3.33
	Combined	92.3 ± 1.9	0.25 ± 0.02	3.33
Bhagalpur	Male	89.1 ± 2.6	0.30 ± 0.06	3.38
	Female	88.6 ± 2.0	0.29 ± 0.05	3.36
	Combined	89.2 ± 1.1	0.29 ± 0.04	3.36

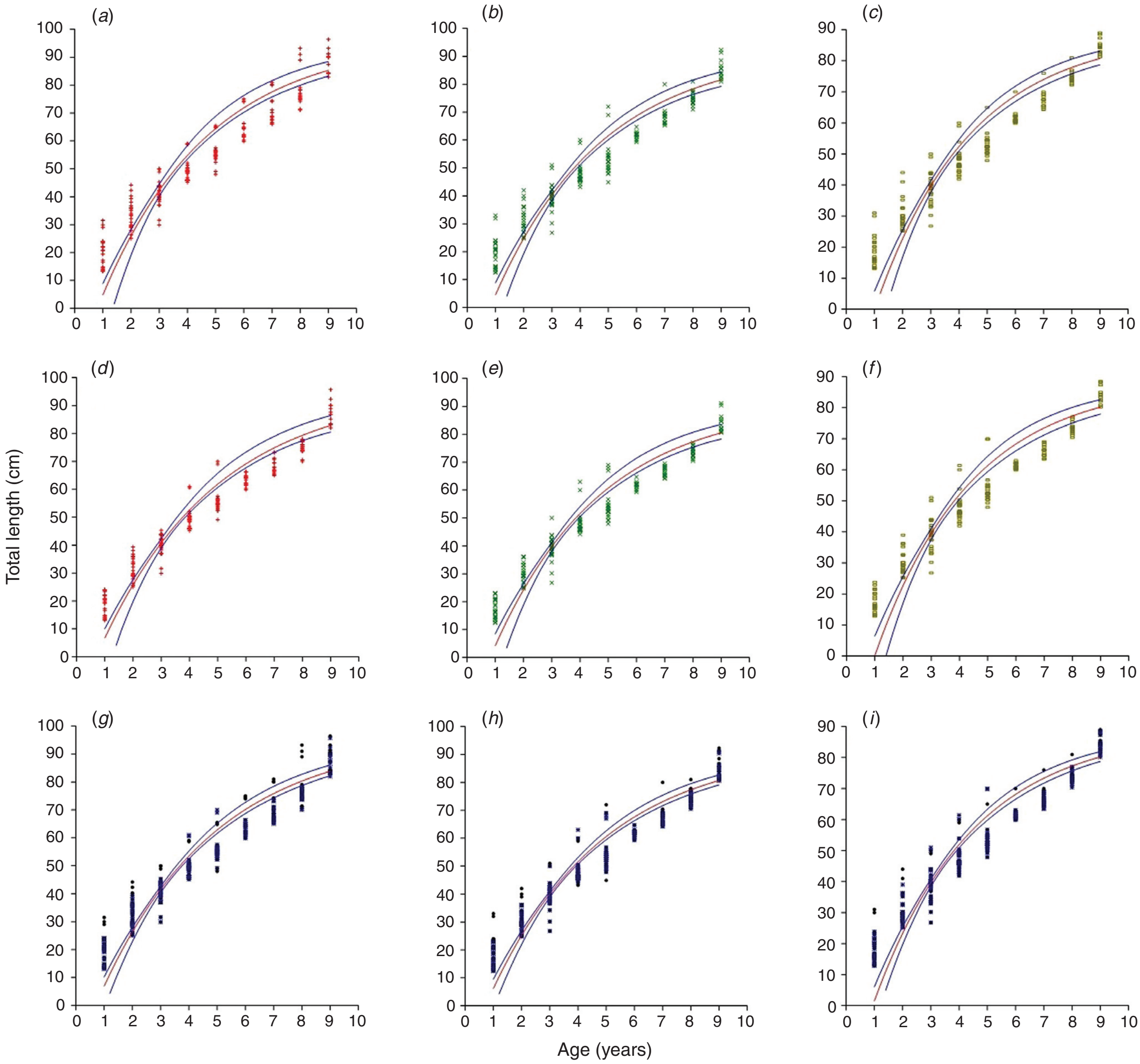

Fig. 3. von Bertalanffy growth curves (middle lines) with 95% confidence intervals (above and below the growth curves) for (*a–c*) male and (*d–f*) female *Sperata aor* and (*g–i*) the sexes combined for stocks from (*a*, *d*, *g*) Narora–Kanpur, (*b*, *e*, *h*) Varanasi and (*c*, *f*, *i*) Bhagalpur along the Ganges River.

defined, inconsistent and difficult to follow across the structure, making age reading very difficult. The opercular bones may underestimate age because the root of the opercular bone is thick and this thickness fans out into a spongy tissue, which often results in less identifiable first and/or second annuli (Ma *et al.* 2011; Zhiming *et al.* 2018). The annuli were less clear in sectioned pectoral spines, and our observations agree with those of earlier researchers, namely that the pectoral spines may consistently underestimate age because the nucleus may be reabsorbed and replaced by a hole (vascularisation) and so the lumen of the pectoral spine increases with age and conceals initial growth increments (Clay 1982; Quick and Bruton 1984; Singh Kohli 1989; McFarlane and King 2001).

Validation of the age estimates in *S. aor* and the periodicity of annulus formation was checked by EA of vertebrae and MIA of sectioned otoliths. Both these methods provide corroborating information on annulus formation. However, the factors governing the timing of annulus formation in *S. aor* need to be investigated. It is well known that water temperature is one of the most important environmental factors affecting fish growth and thereby opaque and translucent zone formation on hard structures (Das 1994; Wright *et al.* 2002). In the present study, the mean water temperature was <20°C during the period November–February at the selected sites along the Ganges River. Moreover, in May and June the mean water temperature was >30°C and so could have changed the metabolic activity of the fish species. This may have resulted in the beginning of a translucent zone; however, this requires further investigation, possibly in future studies. Further, food availability and reproductive activity are other factors affecting annulus formation (Morales-Nin and Ralston 1990; Wright *et al.* 2002; Bustos *et al.* 2009; Zhou *et al.* 2017). Saigal and Motwani (1964) reported March–August as the breeding season for *S. aor*, with peak spawning occurring in April and June, in the Ganges River, and this seems to be synchronous with annulus formation. Further studies are required to prove these assumptions and to study the physiological and environmental factors, as well as their interactions, that regulate annulus formation.

The growth coefficient k was ≤ 0.30 year^{-1} for all three stocks in this study, and it can therefore be inferred that the selected fish species shows rapid growth relative to asymptotic length (L_∞). Further, the species showed overall good growth in the Ganges River compared with the Nagarjunasagar Reservoir, India (Ramakrishniah 1988). Growth differed not only between sexes, but also among the stocks of the selected species. Several factors, such as genetic variability among the stocks (Nazir and Khan 2017) and variations in water quality among stretches of the Ganges River (Nazir and Khan 2019), may be responsible for the observed differences in growth. Other factors, such as food availability and fishing pressure, may have also led to changes in the length and age of individuals from different sites (de Santana and Minte-Vera 2017). The growth performance index ϕ was nearly the same for all three stocks of target fish species. In the present study, the mean value of ϕ was 3.35, which is less than the 3.70 reported for *Sperata seenghala* from the Indus River (Memon *et al.* 2017) and indicates that the growth of *S. aor* is relatively slower than that of *S. seenghala*. In general, the growth of a fish species can be affected by several factors, such as water temperature, food availability, fishing mortality and different stocks (Murie and Parkyn 2005). Therefore, it is essential to understand the effects of these factors on the growth of different stocks of selected fish species.

In conclusion, vertebrae should be used for precise age and growth estimation up to the age of 9 years in *S. aor* from the Ganges River. Annulus formation on the hard structures is governed by several factors, such as temperature, food availability and spawning season. Moreover, annulus formation coincides with both high temperature and the peak spawning season of the target fish species. Therefore, further studies should be undertaken to investigate the individual or combined effects of these factors on annulus formation. Rapid growth relative to asymptotic length was found for all three stocks in this study, and the growth rate varied significantly between sexes and among stocks of *S. aor*. The information generated by the present study can be used with greater confidence to understand the life history characteristics of fish stocks to prevent extirpation of stocks and to make sustainable use of this important fishery resource. Furthermore, we recommend studying other life history characteristics of stocks of *S. aor* in the Ganges River to develop science-based management strategies.

Conflicts of interest

The authors declare that they have no conflicts of interest.

Declaration of funding

This study was funded by the Science and Engineering Research Board, Department of Science and Technology, New Delhi (Project number: SR/SO/AS-40/2012).

Acknowledgements

The authors thank Prof. W. Ahmad, Chairperson, Department of Zoology, Aligarh Muslim University (Aligarh, India) for providing the necessary facilities for this study. Aafaq Nazir gratefully acknowledges financial assistance from the Science and Engineering Research Board, Department of Science and Technology, New Delhi. The authors also thank two anonymous reviewers for their useful comments that improved the presentation and quality of the manuscript.

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Handling Editor: Jacob Johansen