

REGULAR PAPER

Age and growth of black seabream *Acanthopagrus schlegelii* (Sparidae) in Hong Kong and adjacent waters of the northern South China Sea

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Age and growth of the black seabream *Acanthopagrus schlegelii* (family Sparidae) from the northern South China Sea (NSCS) were studied by reading growth rings in sectioned sagittal otoliths. Ring formation frequency was determined to be annual by using marginal increment analysis. The von Bertalanffy growth function parameters were estimated as: $L_{\infty} = 43.7$ cm L_5 ; $K = 0.22$ year; $t_0 = -1.59$ years. Functional males are significantly younger than functional females, with sexually transitional individuals between the modal ages of males and females supporting protandry in this species. Males become sexually mature within 1 year and 50% age at sex change is at 2 years. The maximum age recorded for both males and females sampled was 9 years which is lower than for conspecifics elsewhere and may reflect high fishing pressure in the study area when compared with conspecifics in other areas or could reflect latitudinal effects. Otolith mass was significantly and positively related to age, providing a cheap and quick alternative method for approximating age. *Acanthopagrus schlegelii* is a relatively fast-growing and rapidly maturing species attaining a similar asymptotic length to conspecifics. A need for fishery management is indicated to protect both young juveniles and older adults, especially females, to increase reproductive output and safeguard fishery production.

KEYWORDS

growth curve, marginal increment analysis, otolith mass, Protandry, sexual pattern, VGBF

1 | INTRODUCTION

The study of age and growth is important for understanding life cycles of fishes, and, in the case of commercially important species, is often important for management and conservation planning. Age at sexual maturity, along with study of demographic structure, can be used to better understand life history or to evaluate responses of exploited species to fishing as well as provide information for fishery resource monitoring and management (Jennings *et al.*, 1998; Trippel, 1995). In the case of potentially hermaphroditic species, such as in the Sparidae, a family that includes both protogynous and protandrous functional sex change, an understanding of the age of maturity, sex change and of longevity is important for diagnosing sexual pattern and for better understanding the possible evolutionary significance of hermaphroditism.

Seabreams (family Sparidae) are important for commercial and recreational fisheries in many temperate and sub-tropical regions. The

total reported global capture production of sparids increased from 132,652 to 418,438 t from 1950, when records began, until 2015 (FAO, 2017). According to FAO data, in the north-west Pacific Ocean, particularly East Asia (*i.e.* China, Taiwan, Korea and Japan), sparid catches fluctuated between 38,700 and 52,204 t until the 1990s, then increased dramatically to 200,726 by 2015; the contribution of this region to global sparid catches increased from about 20% in the 1950s to about 50% in the 2000s.

A recent IUCN Red List assessment of the global conservation status of all 151 sparids determined 8.6% to be Threatened (*i.e.* Vulnerable (VU), Endangered (EN) or Critically Endangered (CR)) and 7.9% to be Near Threatened (NT). The major threat to threatened species is overfishing, combined with insufficient fishery management (Cheung & Sadovy, 2004; Law, 2017; Sumaila & Cheung, 2015), associated with species-specific characteristics of large maximum body size, longevity and slow turnover rates (Comeros-Raynal *et al.*, 2016).

Notably, 19 species (*i.e.* 6.0% of all sparids globally) were determined to be Data Deficient (meaning that they could not be assessed for their conservation status) because of limited biology information or due to their uncertain taxonomic status. These outcomes indicate that more research is needed on the biology and fisheries of this group of fishes and that some species are already in need of management. An understanding of age and growth is an important aspect of their biology.

In the northern South China Sea (NSCS), including Hong Kong and adjacent waters, 11 species of sparid (7.3% of species globally) occur in coastal fisheries. Although most are listed as Least Concern (*i.e.* of no or little conservation concern) globally according to IUCN categories and criteria, several indicators suggest that commercially important sparids in the region are overfished, as shown by declining catches and sizes, and in need of management based on fishermen interviews, literature review and on catch data reconstruction (Law, 2017). However, the biology and fisheries of sparids in this region are poorly understood.

Situated just to the south of the Tropic of Cancer, Hong Kong is tropical but experiences a sub-tropical climate. The annual mean bottom seawater temperature ranges from 16.7°C in February and 27.1°C in September, as estimated from monthly average data recorded 1997–2016 at one of the major fishing grounds of sparids in Hong Kong (station TM7 in Tolo Channel, Hong Kong; Environmental Protection Department, 2018).

In this study, the age and growth of black seabream *Acanthopagrus schlegelii* (Bleeker 1854) from the NSCS was examined by using sectioned otoliths (sagittae). *Acanthopagrus schlegelii* is distributed in the coastal waters of the north-west Pacific Ocean (Vietnam, China, Taiwan Korea and Japan), with Hong Kong towards the southern limit of its range (Buxton *et al.*, 2014). It is common in regional capture fisheries and mariculture operations (Law, 2017). *Acanthopagrus schlegelii* belongs to the family Sparidae, which is well-known for the diversity and complexity of its sexual patterns, including gonochorism and sequential hermaphroditism (*i.e.* adult sex change in both directions) (Atz, 1964; Buxton & Garratt, 1990; Sadovy de Mitcheson & Liu, 2008). *Acanthopagrus schlegelii* is a monogynous protandric species and the 50% length of sex change is 29.1 cm L_S (Law & Sadovy de Mitcheson, 2017; Sadovy de Mitcheson & Liu, 2008). Wu *et al.* (2010) found 30–50% of functional males changing to functional females at 3–4 years old and Masuda *et al.* (1984) found most fish becoming female by 5 years of age. The species is listed as Least Concern on the IUCN Red List (Buxton *et al.*, 2014). Despite the economic importance of this species, which gains high prices in local retail markets, however, there is very little information on its age and growth in the field. Studies in Japan recorded a maximum 50 cm standard length (L_S) (Masuda *et al.*, 1984) and longevity of 28 years in Japan (Yamashita *et al.*, 2015). A maximum age of 15 years was recorded in an aquarium-held fish (Buxton *et al.*, 2014). Individuals attained between 25–30 cm L_S at 3 years in captivity (Tsui, 2005). Since age and growth within a species can vary across its geographic distribution, both in response to fishing pressure and according to different biotic and abiotic factors (Paul & Tarring, 1980; Choat & Robertson, 2002), a study of this aspect of biology of the NSCS stock is needed to improve understanding of the species and for management planning.

2 | MATERIALS AND METHODS

2.1 | Sampling and otolith processing

At least 30 fish were collected monthly from wet markets in Hong Kong, supplemented with samples from government trawler surveys (smaller samples), between November 2011 and December 2012 inclusive. Additional market sampling was conducted to supplement certain size classes. It was not possible to sample the species directly from the field due to low accessibility in local waters. Fish were measured fresh for standard length (L_S , cm). Functional sex was determined using histology from a separate study (Law & Sadovy de Mitcheson, 2017). Sagittal otoliths were extracted, cleaned with 75% ethanol and stored in a dry keeper before processing. The left otolith was weighed (0.0001 g) unless broken and mounted on a glass slide using Crystalbond 509 (www.agarscientific.com) for sectioning. The otolith was ground by a Gemmasta GF4 faceting machine (www.shell-lap.com.au) along the dorso-ventral plane until a thin section (c. 100 μ m) through the nucleus was produced. Sections were then mounted on glass slides and observed under a light microscope with transmitted light.

2.2 | Age and growth

Otoliths showing clear growth rings were used for ageing. The number of opaque rings was counted blind on two occasions to minimize possible reader bias (Campana, 2001). In case of disagreement, a second reader counted the rings until consensus was reached; if no consensus, the samples were discarded. Age and growth data were considered together with reproductive data from a separate study (Law & Sadovy de Mitcheson, 2017).

The precision of ageing was determined by calculating the c.v. of 100 randomly chosen specimens according to (Chang, 1982), with a target of less than 5%, based on the recommendation of Campana (2001): $C.V._j = 100 \left\{ \sqrt{\left[\frac{\sum_{i=1}^R (X_{ij} - \bar{X}_j)^2}{(R-1)} \right]} \right\} (\bar{X}_j)^{-1}$ where c.v._j is the age precision estimate for the *j*th fish; X_{ij} is the *i*th age determination of the *j*th fish; \bar{X}_j is the mean age estimated of the *j*th fish; *R* is the number of times each fish was aged.

Growth rate was estimated by fitting length and age data from successfully aged specimens into a generalized von Bertalanffy Growth Function (VBGF; von Bertalanffy, 1938) by $L_t = L_\infty (1 - e^{-K(t-t_0)})$, where L_t is fish length at age *t*, L_∞ is the mean asymptotic fish length; *K* is the growth coefficient and t_0 = theoretical age at zero length. Growth coefficient (*K*) and mean asymptotic length (L_∞) were calculated to describe the growth characteristics of the species.

2.3 | Validation of frequency of ring formation

Marginal increment analysis (MIA) is commonly used as an indirect validation method to examine the formation frequency of growth rings in otoliths and other hard structures. The marginal increment is the distance between the dorsal or ventral margin and the outermost edge of the last completed opaque zone (Figure 1). The marginal

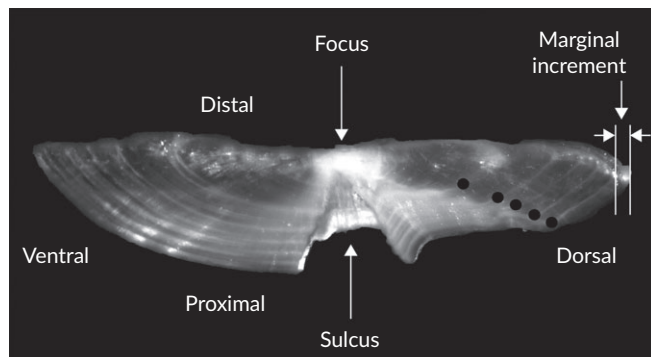


FIGURE 1 Section of the sagittal otolith of a 33.7 cm standard length *Acanthopagrus schlegelii*. Fish was taken in April 2013 and was aged at 5 years. ●, The outer edge of an annual pair or transparent and opaque rings

increment ratio (R_{MI}) can be calculated by dividing the marginal increment by the width of the last complete growth ring by $R_{MI} = (O_R - O_{Rn}) / (O_{Rn} - O_{Rn-1})$, where O_R is the radius from the otolith focus to the dorsal or ventral margin; O_{Rn} is the radius from the focus to the distal edge of last opaque growth ring and O_{Rn-1} is the radius from the focus to the distal edge of the second opaque growth ring. The ratio was tested against the fitness of the models suggested in (Okamura *et al.*, 2013) to determine likely periodicity of ring formation (*i.e.* zero, one or two cycles annually). Since the width between the first ring and the settlement mark was far larger than the widths between successive rings, the analysis was only conducted for individuals of at least 2 years old to avoid possible errors by using the widths between settlement mark and first ring. This latter distance is usually considerably wider than the width between subsequent rings.

2.4 | Ageing by otolith mass

Both left and right otoliths were cleaned, dried and weighed separately to the nearest 0.0001 g, if intact. Mean otolith mass (O_M) was calculated for later analysis. To investigate the possibility of using otolith mass for ageing *A. schlegelii* a regression was constructed between mean otolith mass and age (t) as read from sectioned otoliths by growth ring counts. Otolith mass were used to obtain estimated age and mass data rounded up to the nearest age integer to produce discrete age classes (Worthington *et al.*, 1995). Estimated ages less than 1 year were categorized as age class 0⁺.

2.5 | Age back-calculation

Age back-calculation, commonly used in fish ageing studies, is a technique involving measurement of a hard structure, such as an otolith section, to estimate the body length of the fish at different ages prior to capture based on a calibrated mathematical equation. This procedure enables back-dating of key physiological stages (such as larval settlement) which is particularly useful when early-life stage individuals are rarely available and also allows for detailed investigation of life history, such as growth-rate changes throughout a lifetime, which is related to the total mortality (*i.e.* fishing mortality and natural mortality; Shima & Sweaer, 2009; Vigliola & Meekan, 2002; Wilson *et al.*, 2009). Age-back-calculation was conducted by using Fraser-Lee

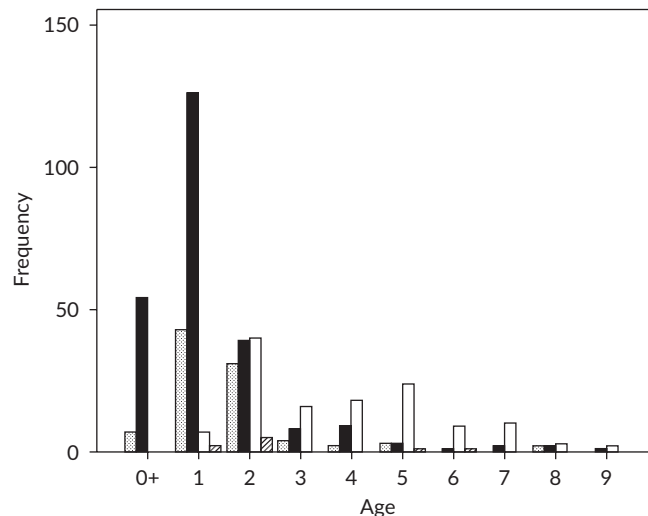


FIGURE 2 Age frequency distribution of *Acanthopagrus schlegelii* of different sexual status examined histologically ($n = 503$): □, bisexual inaction; ■, male; ▒, female; ▨, transitional

(FL) method. Parameters were fitted to the equation as follows: $L_i = a + (O_{Ri}[L_c - a])O_{Rc}^{-1}$, where L_i is the length of the fish at the time of i th ring formed, L_c is the length of the fish at the time of being captured, O_{Ri} is the otolith radius at the time of i th ring formed, c is the otolith radius at the time of being captured and a is the intercept of regressing fish length on otolith radius.

3 | RESULTS

3.1 | Age and growth

Opaque rings of 503 otoliths (*i.e.* 96.5% of total samples) were counted. The precision of ageing was represented by a c.v. of 1.6%. The ages of the samples ranged from 0⁺ to 9 years old (Figure 2). Functional males and females ranged from 0 to 9 years and 1 to 9 years, respectively, with sexually transitional individuals between 1 to 6 years. Females were significantly older than males, bisexual

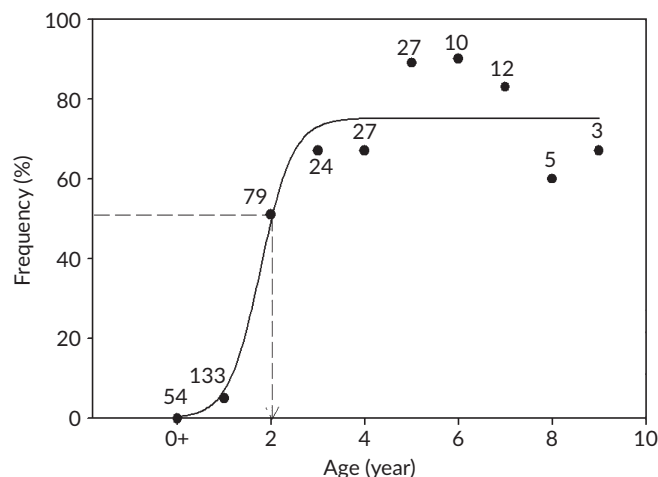


FIGURE 3 Female *Acanthopagrus schlegelii* age-frequency distribution: Age = $1.7762 - 0.3434 (\ln(75.1375[\% \text{female}]^{-1}) - 1)$, $r^2 = 0.90$, $p < 0.001$. Individual sample sizes are shown; $\Sigma n = 374$

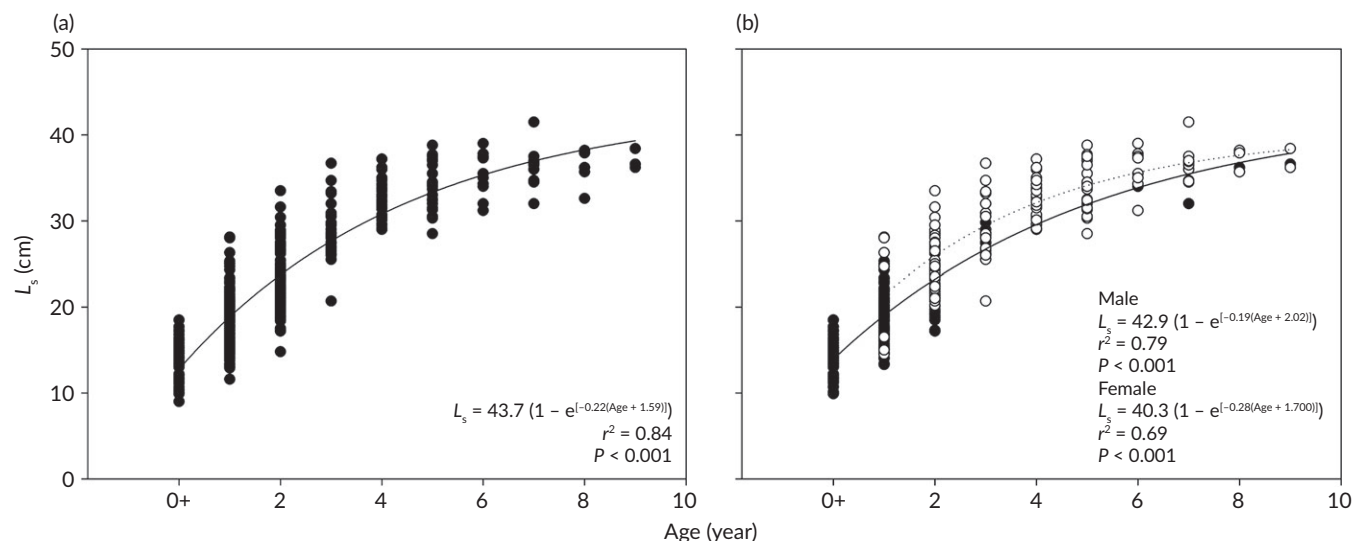


FIGURE 4 von Bertalanffy growth curves fitted to standard length (L_s) data for (a) male and female *Acanthopagrus schlegelii* combined ($n = 503$) and (b) males ($n = 245$) and females ($n = 129$) separately. Bisexual inactive and transitional individuals were excluded

inactive (i.e. gonads containing both male and female immature germ cells) and transitional (i.e. those undergoing change from functional male to functional female phase) individuals (ANOVA: $F_{3, 471} = 73.58$, $p < 0.001$, Student–Newman–Keuls (SNK) *post-hoc* test), but several older males were also found. The 50% age at sex change was determined as 2 years by using regression between percentage of female and age (3 parameter sigmoid regression: $a = 75.1735$, $b = 0.3434$, $x_0 = 1.7762$, $r^2 = 0.90$, $p < 0.001$; Figure 3).

VBGFs were generated for both pooled sexes and separate sexes. The combined sex curve (including bisexual inactive and transitional fish) is relevant because this species is a monogynic protandrous hermaphrodite. The VBGFs are $L_\infty = 43.7$ cm L_s , $K = 0.22$ years and $t_0 = -1.59$ years (Figure 4(a)). VBGFs were also generated separately for each sex after excluding bisexual inactive and transitional individuals to describe the growth pattern of the species by functional sex (Figure 4(b)). A significant difference between male and female curves was found using the likelihood-ratio test according to Kimura (1980)

using the fishmethods package R (www.r-project.org): $\chi^2 = 42.66$, d. f. = 3, $p < 0.001$, but there were no differences in growth parameters.

3.2 | Marginal increment analysis

A unimodal pattern in marginal increments was observed when the monthly R_{MI} was plotted suggesting that opaque rings form annually from May to July (Figure 5) and that ring pairs (opaque plus translucent) are deposited annually. The results were statistically supported by the low Akaike information criterion (AIC) used for fitting the model for annual-ring formation (AIC values for models testing zero, one and two rings formed per year were 321.6, 292.7 and 323.0, respectively). There is no significant relationship between R_{MI} and the bottom seawater temperature recorded in 2012 at station TM7 in the Tolo Channel, one of the major fishing grounds of sparids in Hong Kong (Pearson correlation -0.532 , $p > 0.05$).

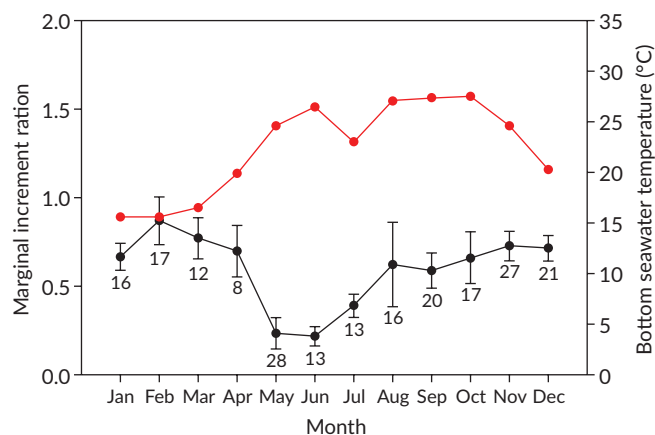


FIGURE 5 Monthly marginal increments (\bullet ; mean \pm s.e.; sample sizes shown) of sectioned *Acanthopagrus schlegelii* otoliths ($n = 201$) and monthly bottom seawater temperature (\bullet) in Tolo Channel, Hong Kong (Station TM7) in 2012 (Environmental Protection Department, Hong Kong SAR, 2017)

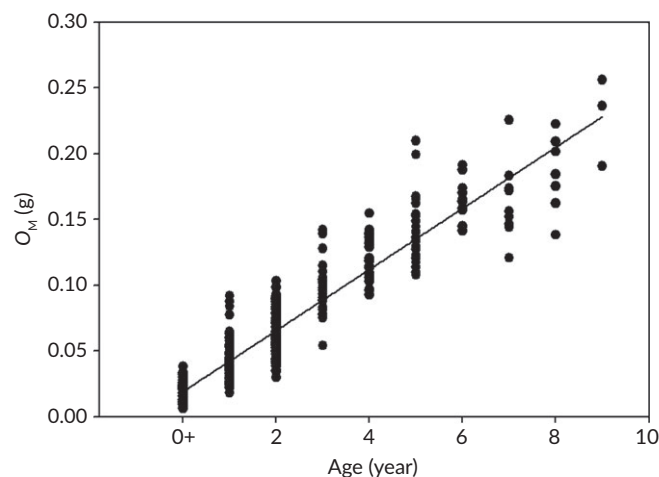


FIGURE 6 Otolith mass (O_M)–age relationship of *Acanthopagrus schlegelii*: $y = 0.0232x + 0.0191$, $r^2 = 0.88$, $p < 0.001$, $n = 468$

TABLE 1 Comparison of age determination by otolith ring reading and otolith mass (O_M) of *Acanthopagrus schlegelii* ($n = 468$)

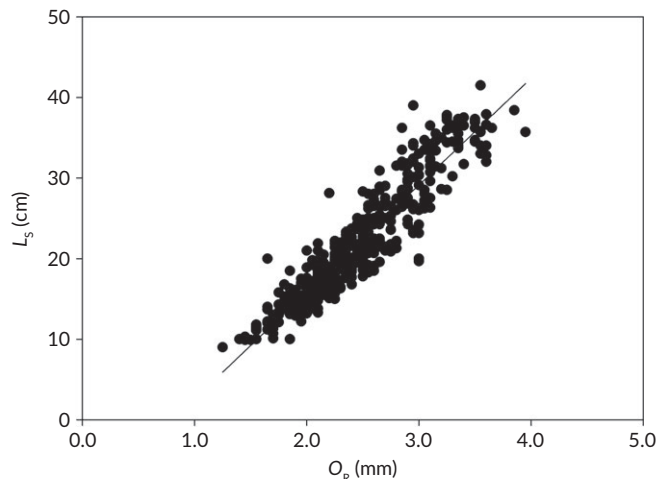
<i>n</i>	O_M (g)		Age (years)		Agreement (%)	c.v. (%)	Bias (years)
	Mean \pm s.d.	Range	True	Range			
63	0.0214 \pm 0.0069	0.0062–0.0381	0	0–1	87	295	0.10
179	0.0398 \pm 0.0121	0.0179–0.0918	1	0–3	64	58	–0.13
109	0.0640 \pm 0.0159	0.0296–0.1032	2	0–4	50	35	–0.03
27	0.0989 \pm 0.0176	0.0752–0.1418	3	2–5	52	22	0.52
27	0.1205 \pm 0.0162	0.0925–0.1546	4	3–6	44	16	0.37
27	0.1405 \pm 0.0247	0.1076–0.2096	5	4–8	37	20	0.19
11	0.1651 \pm 0.0155	0.1414–0.1913	6	5–7	45	11	0.18
11	0.1683 \pm 0.0329	0.1206–0.2256	7	4–9	27	22	–0.55
7	0.1888 \pm 0.0309	0.1382–0.2225	8	5–9	43	18	–0.71
3	0.2275 \pm 0.0337	0.1903–0.2560	9	7–10	33	16	–0.33

3.3 | Otolith mass and age

Otolith mass (O_M) was positively and significantly correlated with age according to linear regression (ANOVA $F_{1,462} = 3,392.07$, $p < 0.001$, $r^2 = 0.88$; Figure 6) although variation of O_M within age classes was high, especially for older individuals. Comparison of age determination between otolith growth ring readings and O_M were made and the percentage of agreement and c.v. calculated (Table 1). Both percentage of agreement and c.v. decreased with increasing age. The estimate of age based on otolith rings was significantly different from that using O_M (Student's t -test $t = 6.328$, d.f. = 926, $p < 0.05$), however the bias in ages as determined by annual ring counts and O_M were not consistent among age groups.

3.4 | Age back-calculation

In the Fraser-Lee model, $a = 10.685$ from the regression between L_S and otolith radius (ANOVA $F_{1,446} = 2,821.08$, $p < 0.001$; Figure 7). Mean lengths-at-age estimated by back-calculation were compared among age groups (Table 2). Lee's phenomenon, which means individuals with slower growth rate suffer less mortality when young, was not observed from this set of results. This estimation of length at previous ages was similar to the length 4 | at ages of the true samples.

**FIGURE 7** Relationship between standard length (L_S) and otolith radius (O_R) in *Acanthopagrus schlegelii*: $y = 13.268x - 10.685$, $r^2 = 0.86$, $p < 0.001$, $n = 448$

4 | DISCUSSION

Acanthopagrus schlegelii from Hong Kong and adjacent waters has a similar faster growth rate and shorter longevity compared with conspecifics elsewhere and other similar-sized congeners globally. While mean asymptotic lengths of many species of *Acanthopagrus* Peters 1855 are similar (i.e. c. 30–50 cm), recorded longevity in sparids elsewhere is much longer, ranging from 16–31 years (Table 3). According to the literature, *A. schlegelii* attains its maximum length faster compared with the large congener *Acanthopagrus berda* (Forsskal 1775), but at a rate similar to others of comparable mean asymptotic length (Table 3). *Acanthopagrus butcheri* (Munro 1949) and *Acanthopagrus morrisoni* (Iwatsuki 2013), were recorded to 31 and 25 years respectively in Australia (Hall *et al.*, 2004; Potter *et al.*, 2008).

Large natural differences in growth rate and longevity among congeners, even those of similar maximum lengths, can occur for several possible reasons including the latitudinal differences and effect of fishing. For example, Choat and Robertson (2002) summarized the growth patterns of several reef-associated genera within two families, Acanthuridae in the Great Barrier Reef and Scaridae (subfamily Scarinae) in Panama and found that growth parameters, such as estimated maximum ages and growth coefficients, spanned wide ranges even within a single genus. Similar patterns were revealed for two genera of Scarinae from Micronesia (Taylor & Choat, 2014). Other than natural differences, fishing can also affect growth patterns. For example, size and bag limits were implemented for *Acanthopagrus* spp. in Western Australia for decades to control fishing effort (DFWA, 2016), evidently increasing survival rates of smaller fish and overall longevity (Sarre & Potter, 2000).

In *A. schlegelii* differences in growth patterns are indicated across locations. For example, asymptotic lengths for both sexes (i.e. 43.7 cm L_S) were smaller in this study than those recorded in Japan (i.e. 50 cm L_S ; Masuda *et al.*, 1984); maximum age recorded for *A. schlegelii* found in this study (9 years) was much less than that of those in Tokyo Bay, Japan (28 years; Yamashita *et al.*, 2015) (Table 3), while growth rates for individuals in Hong Kong were higher than those following restocking of the species in Hiroshima Bay, Japan (Gonzalez & Umino, 2009), which is further north than Hong Kong (Table 4). Length at age for individuals of 3–7 years of age in local waters were significantly larger than those in Japan.

TABLE 2 Mean back-calculated standard length (L_S) at age for *Acanthopagrus schlegelii* in Fraser–Lee model ($n = 380$)

Age	n	L_S at capture (cm) (mean \pm s.d.)	Age (years)								
			1	2	3	4	5	6	7	8	9
Mean back-calculated L_S (cm)											
1	179	18.2 \pm 2.9	17.3								
2	105	23.6 \pm 3.3	20.6	22.7							
3	21	28.2 \pm 3.1	23.0	25.7	27.5						
4	25	32.2 \pm 2.2	25.0	28.1	30.0	31.2					
5	27	33.6 \pm 2.4	25.4	28.2	30.3	31.7	32.9				
6	9	35.7 \pm 2.8	26.3	29.4	31.6	33.2	34.2	35.2			
7	7	36.5 \pm 2.5	26.3	29.4	31.5	32.6	33.9	35.3	36.0		
8	4	36.4 \pm 1.0	24.2	28.2	29.2	31.8	32.8	34.0	34.8	35.8	
9	3	37.1 \pm 1.2	24.4	28.1	30.3	31.9	33.3	34.5	35.2	35.8	36.5
Back-calculated weighted mean L_S (cm)			20.1	25.1	29.8	31.8	33.3	34.9	35.5	35.8	36.5
Growth increment (cm)				5.0	4.7	2.0	1.5	1.6	0.6	0.3	0.7
L_S at age of true samples (cm, mean \pm s.d.)			18.4 \pm 2.9	23.6 \pm 3.3	29.1 \pm 2.9	32.2 \pm 2.2	34.1 \pm 2.4	35.5 \pm 2.5	36.6 \pm 1.9	36.6 \pm 1.8	37.1 \pm 1.2

A difference in growth patterns between the populations at the two extremities of *A. schlegelii* distribution is consistent with the temperature–size rule (TSR) proposed for ectothermic teleosts, which shows increased growth rates, greater longevity and larger asymptotic lengths at higher than lower latitudes due to temperature differences (Atkinson, 1994; Conover, 1992). Examples of this rule have been noted in both tropical species, such as for certain acanthurids (Choat & Robertson, 2002), lutjanids (Cappo *et al.*, 2013; Piddocke *et al.*, 2015) and scarinids (Choat *et al.*, 2003) as well as temperate species such as *Odax pullus* (Forster 1801) and *Notolabrus fucicola* (Richardson 1840) (Trip *et al.*, 2014). The magnitude and direction of the growth pattern variation is based on a prediction of the influence on metabolic rate of the fish from ambient temperature (Clarke, 2003; Munch & Salinas, 2009; Portner & Farrell, 2008).

Apart from intrinsic factors possibly controlling growth–pattern latitude, extrinsic factors may also be involved. Fishery effects could have resulted in loss of larger and older fish, which may have affected rates of sexual maturation and growth (Jennings *et al.*, 1998; Trippel, 1995). *Acanthopagrus schlegelii* is probably overfished already due to

insufficient management in the NSCS, according to fisher interviews, and considering that a large proportion of landed fish are juveniles (Law, 2017; Sumaila & Cheung, 2015). Further studies on the demography of this species by latitude (or under different temperature conditions) and according to different fishing conditions are needed to understand the factors associated with growth rate and longevity differences observed.

In *Acanthopagrus schlegelii*, females were significantly older than males, bisexual inactive and transitional individuals, consistent with the assessment of monogynic protandric hermaphroditism for this species (Law & Sadovy de Mitcheson, 2017). However, the data also suggest that sex change is not closely associated with age because the age range of transitional individuals was broad (1–6 years) with a very few individuals remaining functional males up to the maximum age observed. However, while the oldest male and female both attained 9 years in this study, it is possible that older fishes have been lost under heavy exploitation in this region. Since older fishes are most likely to be females, loss of the largest and oldest fishes through fishing would have differentially affected the female segment of the population.

TABLE 3 von Bertalanffy growth parameters and maximum recorded length of six *Acanthopagrus* spp

Species	L (cm)	K	t_0 (years)	t_{max} (years)	Location	Reference
<i>A. australis</i>	–	–	–	22	Southeast Australia	Gray <i>et al.</i> , 2000 in Iwatsuki <i>et al.</i> 2015
<i>A. australis</i>	29.5	0.51	–0.32		East Australia	Pollock, 1982
<i>A. vagus</i>	50.0 (L_F)	0.08	–3.00	16	South Africa	James <i>et al.</i> , 2003
<i>A. bifasciatus</i>	32.5 (L_F)	0.23	–2.20	21	Sothorn Arabian Gulf	Grandcourt <i>et al.</i> 2004
<i>A. butcheri</i>	41.2 (L_T)	0.23	–0.83	31	Southwest Australia	Potter <i>et al.</i> , 2008
<i>A. butcheri</i> (σ + φ)	40.2 (L_F)	0.07	–4.09	21	Southeast Australia	Morison <i>et al.</i> , 1998
Male	38.2 (L_F)	0.07	–3.70	21		
Female	54.5 (L_F)	0.04	–5.21	16		
<i>A. morrisoni</i>	41.9 (L_T)	0.32	0.08	25	Shark Bay, Australia	Hall <i>et al.</i> , 2004
<i>A. schlegelii</i>	–	–	–	28	Tokyo Bay, Japan	Yamashita <i>et al.</i> , 2015
<i>A. schlegelii</i> (σ + φ)	43.7 (L_S)	0.22	1.59	9	Hong Kong	This study
Male	42.9 (L_S)	0.19	–2.02	9		
Female	40.3 (L_S)	0.28	–1.70	9		

Note. K = annual growth coefficient; L_∞ = asymptotic length; L_F = fork length; L_S = standard length; L_T = Total length; t_0 = theoretical age at $L_T = 0$; t_{max} = maximum age recorded in study.

TABLE 4 Length at age of the populations of *Acanthopagrus schlegelii* in Hiroshima Bay (Gonzalez & Umino, 2009) and in Hong Kong (this study)

		Hiroshima Bay, Japan (34° N, 132° E)		Hong Kong (22° N, 114° E)	
		(Annual SST range 10.0–25.3°C)		(Annual SST range 16.9–27.6°C)	
Age (years)	n	1983 (Before restocking)	2000 (After restocking)	2012–2014	
		L_F (cm)	L_F (cm)	n	L_F (cm)
		Mean \pm s.d.	Mean \pm s.d.		Mean \pm s.d.
0 ⁺				69	16.0 \pm 2.5
1				194	21.1 \pm 3.3
2				117	27.2 \pm 3.8
3	52	26.5 \pm 1.8	15 27.1 \pm 2.3	28	33.1 \pm 3.7
4	22	30.1 \pm 2.5	57 27.8 \pm 1.9	30	37.1 \pm 2.5
5	22	31.8 \pm 2.8	27 29.0 \pm 2.7	31	38.3 \pm 3.1
6	9	32.9 \pm 3.2	35 30.8 \pm 2.4	11	40.5 \pm 2.8
7	5	35.0 \pm 3.1	6 31.3 \pm 1.4	11	41.1 \pm 2.5
8				7	40.9 \pm 2.1
9				3	42.6 \pm 1.3

Note. Annual sea surface temperature (SST) ranges were obtained from the Hong Kong observatory (www.hko.gov.hk) and Japan oceanographic data Centre (www.jodc.go.jp).

Growth patterns between sexes were similar as there were no significant difference in growth parameters in *A. schlegelii*. In other protandrous species, on the other hand, such as *Lithognathus mor-myrrus* (L. 1758) (Lorenzo *et al.*, 2002; Türkmen & Akyurt, 2003) and *Pagellus acarne* (Risso 1827) (Pajuelo & Lorenzo, 2000), males attain greater asymptotic length and have higher growth rates than females. The reasons why *A. schlegelii* is unlike other studied sparids in this respect is not known. One possible explanation is that larger older fish are absent in the study population may obscure any size–sex differences which become apparent only in older, larger, fish. It is possible that large males can gain advantage in competition for mating with a female over smaller males (Law & Sadovy de Mitcheson, 2017), thus males continue to increase in size even if they do not change sex. The mating pattern of the species, however, is not known.

Relationships between age and otolith mass have been successfully developed for both temperate (Cardinale *et al.*, 2000; Pawson, 1990) and tropical species (Lou *et al.*, 2005, 2006; Pilling *et al.*, 2003) and that the relationship between otolith mass and age could be both population specific and dependent on abiotic and biotic factors (Lou *et al.*, 2006; Pawson, 1990; Worthington *et al.*, 1995). In this study, a positive significant relationship was found between otolith mass and age similar to that found in other sparids, such as *A. butcheri* (Morison *et al.*, 1998) and *Chrysophrys auratus* (Forster 1801) (Morison *et al.*, 1998). While the c.v. increased in older age groups (possibly due small incremental variability between otolith mass and age over time only becoming apparent in older fish), otolith mass could be a simple and cost-effective method of determining a general age–size relationship, especially among younger fish and useful for stock assessment provided it is used only for the population studied in the same location and if the relationship is calibrated regularly (Lou *et al.*, 2006; Pawson, 1990).

Variation in otolith mass with L_S within the same age group, particularly for larger and older fish, could be due to cumulative effects over time (as suggested above) or result from uncoupling of somatic and otolith growth as observed in various fish species. For example, otoliths can continue to grow even after somatic growth has slowed down, or even ceased, which means that a slow-growing individual may have a larger or heavier otolith compared with a fast-growing individual of the same size (Fey, 2006; Francis *et al.*, 1993; Mosegaard *et al.*, 1988; Secor & Dean, 1992; Templeman & Squires, 1956). Size-selective mortality has been suggested as the main reason for the Lee phenomenon, whereby fast-growing individuals are more susceptible to size-selective fisheries if they enter the fishable stock earlier than those that grow more slowly (Francis, 1990). However, Lee's phenomenon is not evident based on the results from the age back-calculation in *A. schlegelii*. Overall, as for a number of other fishes, we cannot account for the differences in otolith mass particularly among older fish.

The relatively fast growth and early sexual maturation of *A. schlegelii* in the study region may account for its apparent resilience to fishing pressure (Cheung *et al.*, 2005), compared with many other similar sized species in the regional multi-species fishery (Law, 2017). While a stock assessment is needed to determine whether *A. schlegelii* in the study area is overfished, the apparent rarity of old individuals sampled in this study and shorter longevity compared with the same species in other parts of its range suggest the possibility of growth overfishing (Beverton & Holt, 1957). If this is the case, management is needed to improve yield and increase economic value and spawning biomass (Birkeland & Dayton, 2005). Older, larger, fish may have a greater adaptive ability to adverse environmental conditions compared with smaller younger fish (Ottersen *et al.*, 2006), while maintaining a more natural age structure could reduce fluctuations in abundance and increase biological stability (Anderson *et al.*, 2008) including under climate change (Sumaila *et al.*, 2011). In this protandric species, larger and older individuals are predominantly females, which are naturally fewer in a protandrous species (*i.e.* low female–male ratio) (Law & Sadovy de Mitcheson, 2017). These larger fish are likely to be targeted in fisheries because larger fish typically bring more revenue to fishers. Unmanaged removal of larger individuals (*i.e.* usually older and predominantly female in this species) would further reduce the naturally low female-to-male ratio and reproductive output; larger females are more fecund than smaller females. Fishery management options including slot limits (minimum and maximum to protect both juveniles and larger females), temporal and, or spatial closure of fisheries in spawning and nursery grounds and control of fishing effort.

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