



Age and growth of Cape stumpnose *Rhabdosargus holubi* (Pisces: Sparidae) in the Eastern Cape, South Africa

MW Farthing, NC James & WM Potts

To cite this article: MW Farthing, NC James & WM Potts (2016) Age and growth of Cape stumpnose *Rhabdosargus holubi* (Pisces: Sparidae) in the Eastern Cape, South Africa, African Journal of Marine Science, 38:1, 65-71, DOI: [10.2989/1814232X.2016.1156577](https://doi.org/10.2989/1814232X.2016.1156577)

To link to this article: <https://doi.org/10.2989/1814232X.2016.1156577>



Published online: 04 Apr 2016.



Submit your article to this journal [↗](#)



Article views: 92



View Crossmark data [↗](#)



Citing articles: 1 View citing articles [↗](#)

Age and growth of Cape stumpnose *Rhabdosargus holubi* (Pisces: Sparidae) in the Eastern Cape, South Africa

MW Farthing^{1*}, NC James² and WM Potts¹

¹ Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa

² South African Institute for Aquatic Biodiversity, Grahamstown, South Africa

* Corresponding author, e-mail: matthew.farthing.rsa@gmail.com

Rhabdosargus holubi is a small (maximum weight = 2.4 kg) yet important fishery species in the estuaries of the south-east coast of South Africa. Little is known of its biology and specifically its growth rate, which is essential for sustainable management of the fishery. We examined and counted the opaque zones in the sectioned otoliths of 134 *R. holubi* to determine its age and growth parameters. The otoliths from two recaptured fish marked with oxytetracycline confirmed that one opaque zone was deposited annually. The species reached a maximum age of 18 years and growth was adequately described by a von Bertalanffy growth function of the form: $L_t = 358.1 (1 - e^{-0.24(t+0.77)})$ mm fork length. There were no significant differences between any of the male and female growth parameters (likelihood ratio test: $p = 0.3$). The growth was slow (omega index: $\omega = 86.56$); however, despite this, the unique life history of *R. holubi* may provide a degree of resilience to heavy fishing pressure in estuaries.

Keywords: estuarine fishery, growth ring validation, marine conservation, otoliths

Introduction

Rhabdosargus holubi (Steindachner, 1881) is a small (maximum size = 450 mm total length; Heemstra and Heemstra 2004) sparid that is distributed along the south-east coast of Africa from St Helena Bay, South Africa, to Maputo, Mozambique (Götz and Cowley 2013). Spawning occurs in the nearshore marine environment primarily during winter, specifically May–August in KwaZulu-Natal (KZN) (Wallace 1975) and July–February in the South-Eastern Cape (Whitfield 1998). Individuals reach 50% sexual maturity at approximately 150 mm standard length (SL) in the Eastern Cape (Whitfield 1998). The early life stages are transported by the south-westward-flowing Agulhas Current, and recruit as post-flexion larvae and early juveniles into estuaries during late winter and early summer (Blaber 1974). The warm temperatures and high nutrient levels in estuaries favour fast growth (Blaber 1973a), and fish spend their first year of life in these environments, migrating back out to sea after reaching approximately 120 mm SL. Some individuals remain trapped in closed estuaries, where they may reach sizes greater than 200 mm SL (James et al. 2007a).

Rhabdosargus holubi is the dominant estuarine-dependent marine teleost species recorded in permanently open and temporarily open/closed estuaries in the warm-temperate region, which spans the south, south-east and east coast of South Africa (Harrison 2005). The species is also an important component of the linefishery in many South African estuaries (10–15.6% by number) (Pradervand and Baird 2002), particularly in Eastern Cape estuaries (Cowley et al. 2003). These figures underestimate the presence of *R. holubi*, as most individuals making use of estuaries are

young, feeding predominately on filamentous macroalgae and diatom flora, and are generally too small to be caught with hook and line (De Wet and Marais 1990). James et al. (2007b) showed that *R. holubi* made up 34–92% of the annual seine-net catch in the East Kleinemonde Estuary. *Rhabdosargus holubi* is also important in the KZN shore-based linefishery, representing 4.6% of the total landed catch (Dunlop and Mann 2012).

On account of their importance to recreational and subsistence fisheries, Sparidae have been the focus of many age and growth studies (e.g. Smale and Punt 1991; Chale-Matsau et al. 2001; Brouwer and Griffiths 2004). Understanding the age and growth of a species, as well as the factors influencing this relationship, is of principal importance in fisheries management. It is thought that the slow growth, long life and high residency commonly exhibited by sparids increase their susceptibility to overexploitation (e.g. Buxton and Clarke 1991). Consistent with this, *R. holubi* is estuarine-dependent, long-lived and relatively slow-growing, suggesting that it may be vulnerable to exploitation. This is especially concerning given the continued degradation of estuaries along the eastern seaboard of South Africa (Götz and Cowley 2013) and the high fishing pressure in estuaries (Cowley et al. 2013). Little information has been published on the age and growth of *R. holubi*. Cohort analysis conducted in the East Kleinemonde Estuary by Cowley (1998) showed growth of c. 10 cm SL during the first year. However, cohort analysis in slow-growing species with a protracted spawning season and variable recruitment (into a temporary open/closed estuary) may give imprecise

estimates of growth (Campana et al. 2001). Blaber (1973b) used otoliths to age *R. holubi* in the West Kleinemonde Estuary, but only juveniles were aged and the difficulty in distinguishing opaque zones limited the study's success. Within the genus *Rhabdosargus*, Griffiths et al. (2002) investigated the age and growth of *R. globiceps* using sectioned otoliths, with a good level of success. Radebe et al. (2002) aged *R. sarba* using sectioned otoliths and validated the age estimates using oxytetracycline (OTC) marking. Our study used similar methods to determine the age and growth of *R. holubi* in the Eastern Cape, with a view to developing a preliminary understanding of an increasingly important fishery species sampled in the epicentre of its distribution.

Material and methods

Rhabdosargus holubi individuals were collected opportunistically, using hook and line, seine-nets and spearfishing, from the permanently open Kowie and Kariega estuaries, from the inshore coastal zone around Port Alfred, and from the enclosed Marina Martinique system, located near Jeffreys Bay, in the Eastern Cape, South Africa (Figure 1; Table 1). The following data were recorded for each fish: total weight (g), fork length (FL, mm) and sex, where possible. The sagittal otoliths were removed and later were processed as described by Secor et al. (1991) and sectioned transversely. The number of opaque zones between the nucleus and otolith edge were enumerated by three independent readers using a dissecting microscope at between 10x and 40x magnification. In cases where only two of the three readers agreed, the modal count was accepted. If all three readers disagreed, the otolith was rejected.

In addition, 30 individuals (285–345 mm FL) were captured using a seine-net (75 m x 2 m) for validation of growth ring periodicity. These fish were tagged and injected intramuscularly with High-Tet 12™ oxytetracycline at c. 0.1 ml OTC kg⁻¹, according to the methods of Potts and

Cowley (2005), and released into the Marina Martinique system during March and June in 2012. Marina Martinique is an artificial saltwater impoundment, isolated from the ocean except for water that is pumped from the inshore surf zone into the system. During May 2013, two tagged individuals were recaptured using the same gear.

The otoliths from these recaptured specimens were processed in dark conditions illuminated only by a red light-source to avoid degradation of the OTC. Sections were then examined under fluorescent light using a compound microscope at 40x magnification. The opaque zones between the highlighted OTC band and the edge of the otolith were enumerated. Once photographed, the same sections were then exposed to normal light conditions for the purpose of ageing.

A general, three-parameter von Bertalanffy growth function (VBGF) was fitted to the observed length-at-age data for *R. holubi* using an iterative least squares procedure with Microsoft Excel Solver™:

$$L_t = L_\infty (1 - e^{(-K(t-t_0)})}$$

where L_∞ is the theoretical asymptotic length at age t , K is the growth coefficient and t_0 is the theoretical age at zero length. Models were fitted to the observed length-at-age data for each sex, and then to the pooled sample, which included juvenile and unsexed fish (Table 1). A parametric residual resampling procedure (PRRP, $n = 250$ resamples), or 'bootstrap' (Efron 1981), was employed to estimate the error in the model parameters. A likelihood ratio test (LRT) (Kimura 1980), was performed to test for differences between the model parameters for each sex. Comparing two K parameters without context of L_∞ is poor practice, as they are inversely correlated (Knight 1968). To avoid this, Gallucci and Quinn (1979) developed the omega (ω) growth index, which describes growth as a function of K and L_∞ . Age estimate reproducibility was described using the index average percentage error (IAPE) as described by Beamish and Fournier (1981):

$$100 \left[\frac{1}{n} \sum_{j=1}^n \left(\frac{1}{R} \sum_{i=1}^R \left| \frac{X_{ij} - X_j}{X_j} \right| \right) \right]$$

where n is the number of fish aged, R is the number of times each fish was read, X_j the average age calculated for the j th fish from all readings and X_{ij} is the i th reading for the j th fish.

Table 1: Number of *Rhabdosargus holubi* sampled according to sex and location

Sex	Location				<i>n</i>
	Kowie	Kariega	Marina Martinique	Surf zone, Port Alfred	
Males	22	28	10	1	61
Females	15	24	11	2	52
Unsexed	12	–	–	1	13
Juveniles	2	6	–	–	8
<i>n</i>	51	58	21	4	134

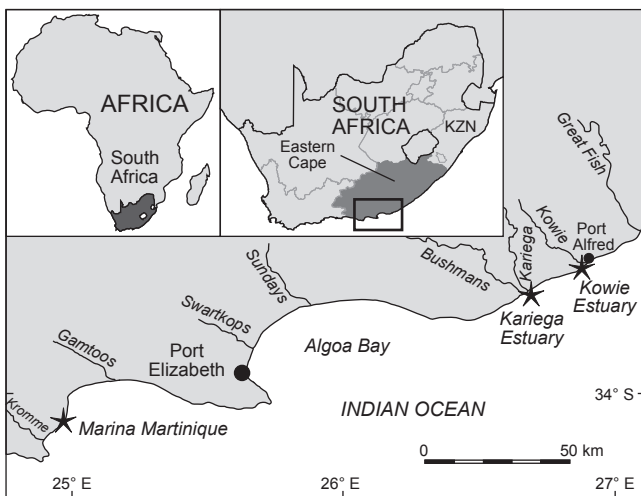


Figure 1: Map showing sampling locations (stars) within the Eastern Cape, South Africa

Results

The majority of individuals caught in the study ranged between 100 and 149 mm FL, with only one individual <50 mm FL (Figure 2). The number of individuals between 250 and 299 mm was relatively low compared with the number of individuals collected in the 300–349 and 350–399 mm size classes (Figure 2).

Sectioned otoliths from *R. holubi* showed clear, discernible growth rings, which comprised broad hyaline zones and narrow opaque zones. Growth rings were clearly visible, particularly in older fish (Figure 3). Of the 134 sectioned otoliths, agreement was reached by all three readers for 53%, while two of the three agreed for the remaining 47%. Despite this, the reproducibility of age estimates for *R. holubi* was relatively low (IAPE = 12.6%), particularly in the younger age classes (0–2 years: IAPE = 16.7%). There was a positive correlation between reproducibility and age, with reproducibility increasing with age (3–12 years: IAPE = 5.3%; 13–18 years: IAPE = 1.2%).

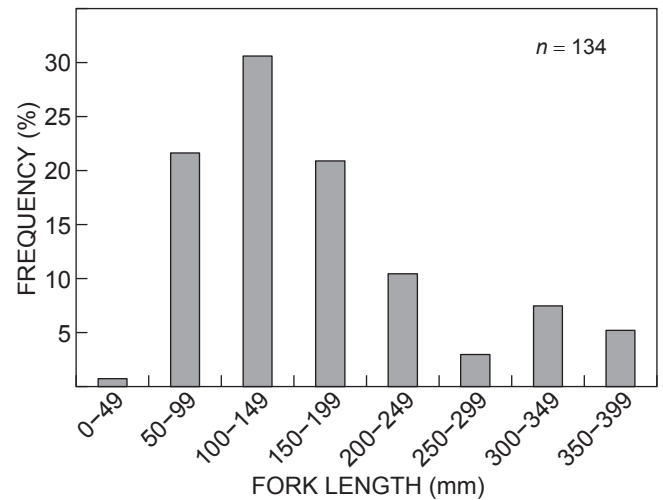


Figure 2: Fork length percentage frequency of *Rhabdosargus holubi* sampled

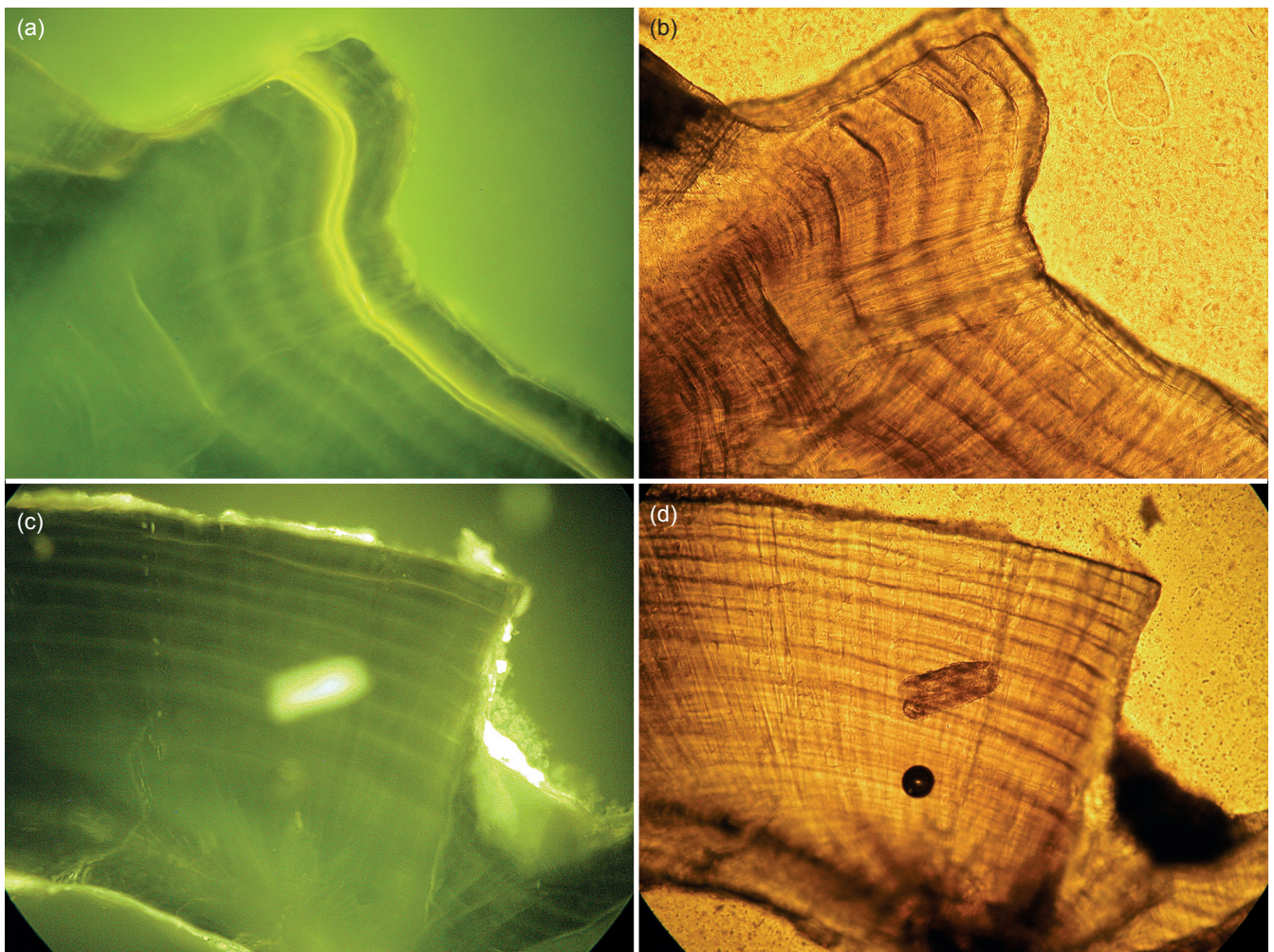


Figure 3: Photomicrographs of sectioned otoliths removed from recaptured *Rhabdosargus holubi* specimens: 285 mm FL individual viewed under (a) fluorescent and (b) normal light, and 345 mm FL individual viewed under (c) fluorescent and (d) normal light

Table 2: Mean, standard error (SE), coefficient of variation (CV), lower (LCI) and upper confidence interval (UCI) obtained from parametric residual resampling procedures performed on the von Bertalanffy growth function (VBGF) generated for male, female and pooled samples of *Rhabdosargus holubi*

Model	Parameter	VBGF	Mean	SE	CV (%)	LCI (95%)	UCI (95%)
Females	L_{∞} (mm)	392.5	386.77	12.47	3.22	365.12	411.71
	K (y^{-1})	0.17	0.19	0.02	12.58	0.15	0.24
	t_0 (years)	-1.24	-1.20	0.30	24.75	-1.80	-0.69
Males	L_{∞} (mm)	343.94	344.40	12.26	3.56	323.09	368.44
	K (y^{-1})	0.26	0.28	0.05	18.18	0.19	0.39
	t_0 (years)	-0.83	-0.84	0.39	46.36	-1.76	-0.27
Pooled	L_{∞} (mm)	358.1	346.86	10.87	3.13	328.38	369.06
	K (y^{-1})	0.24	0.26	0.04	16.21	0.18	0.34
	t_0 (years)	-0.77	-0.90	0.37	41.32	-1.71	-0.31

Clear fluorescent bands appeared in the sectioned otoliths from both of the specimens recaptured after approximately one year at liberty (Figure 3). One individual (285 mm FL) was recaptured after 312 days at liberty. Two OTC bands were visible from an initial (21 March 2012) and second tagging event (26 June 2012) (Figure 3a). The second OTC band appeared shortly after an opaque zone, with one opaque zone visible between the fluorescent band and the otolith edge (Figure 3a, b). The other individual (345 mm FL) was at liberty for 405 days, after being marked during the first tagging event only (21 March 2012). In both individuals there was a single opaque zone visible between the fluorescent OTC band(s) and the otolith edge, with hyaline zones present before and after (Figure 3). Therefore, because a single opaque zone was deposited over a period of 312 or 405 days, this validates the annual periodicity of growth ring deposition.

The fitted VBGF used to describe the observed length-at-age data for both males ($L_t = 343.9(1 - e^{-0.26(t+0.83)})$) and females ($L_t = 392.5(1 - e^{-0.17(t+1.24)})$) provided biologically realistic L_{∞} values based on the maximum size of specimens examined (Table 2, Figure 4). Despite the apparent difference in L_{∞} (Table 2), an LRT showed that the L_{∞} of females was higher, but not significantly ($p = 0.06$), than that of males, which relates well to the maximum size of fish collected from each sex (females = 372 mm FL; males = 310 mm FL). The 250 PRRP iterations for each sex overlapped when the estimated L_{∞} was plotted as a function of its respective K , when t_0 was plotted as a function of its respective L_{∞} , and when K was plotted as a function of its respective t_0 , which suggests similarity. These findings were supported by the results of the LRT, which showed no significant differences between the VBGF for each sex ($p = 0.3$).

The pooled model ($L_t = 358.1(1 - e^{-0.24(t+0.77)})$), which included juveniles and unsexed fish, provides a description of the growth of *R. holubi* (Table 2, Figure 4). Growth was relatively rapid for the first five years and then slowed, with one fish of 372 mm FL attaining an age of 18 years (Figure 4). The high coefficients of variation (CV), estimated by the PRRP, for all three models (pooled, male and female) suggested that there was relatively high variability among the model parameters (Table 2, Figure 4). The highest CV values were observed for the t_0 parameter (Table 2).

Discussion

Otoliths of *R. holubi* were relatively easy to read when compared to those of other sparids (e.g. *Polysteganus undulosus*; Chale-Matsau et al. 2001), and did not require complex preparation such as burning, baking or polishing. The relatively high IAPE (12.6%) could probably be attributed to the high proportion of 0- and 1-year-old fish under study. Age estimation in younger fish has been shown to have a lower reproducibility (e.g. Richardson 2010), and in our study the IAPE for 0- to 2-year-old fish was high (16.7%) compared with 1.2% for 13- to 18-year-old fish. This pattern is due to the rapid early growth of younger fish that generally promotes broad and less-defined growth rings (Campana and Thorrold 2001). Older fish in our study were consequently much easier to age, as the progression of narrowing growth rings could be tracked from the nucleus to the edge of the otolith, and back to the nucleus. Richardson (2010) found the same trend, with reproducibility increasing with the size and age of *D. capensis*. Similarly, Blaber (1973b), who studied young *R. holubi* only, experienced difficulty interpreting the growth zones in the otoliths.

This study is the first to use OTC-marking validation for *R. holubi*. OTC validation is considered the most robust form of age validation, but is often undermined by the low probability of recapture (Potts and Cowley 2005). The unique opportunity for recapture provided by the enclosed Marina Martinique system allowed the annuli to be validated, and the results confirmed that one opaque and one hyaline zone were deposited per annum. Although it is acknowledged that the environmental conditions in the marina do not necessarily mimic those of the coastal ocean, the conditions are very similar to those found in the temporarily open/closed estuarine environments that *R. holubi* inhabits. Our results are in support of the assumption of Blaber (1973b) that opaque zone deposition in *R. holubi* is annual, which is similar to other sparids from the region (e.g. Smale and Punt 1991; Chale-Matsau et al. 2001; Brouwer and Griffiths 2004; Potts and Cowley 2005).

Marina Martinique provided the opportunity to study several large and old specimens trapped in the system, which was beneficial because age and growth studies are often hampered by poor representation of the largest and oldest individuals. However, this may also contribute heavily

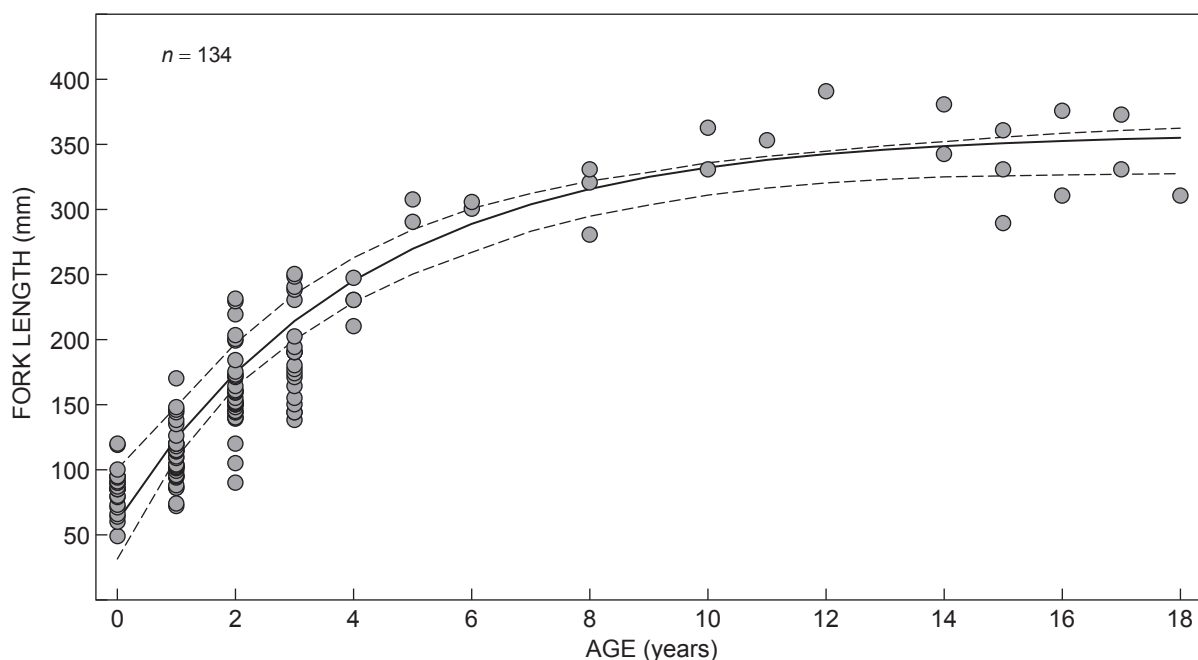


Figure 4: Von Bertalanffy length–age relationship for the pooled sample of *Rhabdosargus holubi*, which included juvenile and unsexed individuals, with 95% confidence intervals

to the abnormality of residual distribution during the PRRP, with young fish having low residuals and older fish large residuals, without graduation in between. This is highlighted by the estimated standard error of the 250 theoretical fits of the male and female models obtained from the PRRP. The SEs were high (Table 2) compared to those for other sparids such as *Sarpa salpa* (van der Walt and Beckley 1997) and variation was better explained using the coefficient of variation (CV), which assesses variation in the context of the mean. The CVs ranged between 3.2% and 46.4% in our study, which exceeds the range of 1–5% estimated in studies of other sparids (e.g. van der Walt and Beckley 1997; Kallianiotis et al. 2005). However, it should be noted that the highest CV values were observed for the t_0 parameter, which may be due to the high proportion of 0-year-old fish sampled, which would contribute to the variability in the earliest stage of the VBGF growth curve. This is supported by the wide confidence interval in the 0-year-old age class (Figure 4). This variation is compounded by the relatively fast growth of *R. holubi* in its first year, with the 0-year-old fish included in this sample ranging from 49 to 120 mm FL. Therefore, although the parameters were more variable than those of the closely related *S. salpa* (van der Walt and Beckley 1997), particularly in the case of t_0 , the L_∞ and K parameters for all models exhibited low to moderate levels of variation (Table 2).

Differences in age and growth between sexes is common in sparids (Pajuelo and Lorenzo 2001), whereby females reach a larger body size than males in order to maximise egg production, and thereby invest heavily in gonadal growth (Sadovy 2001). However, in group-spawning, rudimentary hermaphrodites, males often exhibit similar investment in reproduction, with little difference in the gonadosomatic index between sexes (Buxton and Garratt 1990; Sadovy

1996; Richardson 2010). Although the reproductive style of *R. holubi* is unknown, both *R. globiceps* (Griffiths et al. 2002) and *R. sarba* (Hughes et al. 2008) exhibit rudimentary hermaphroditism, so it is therefore likely that *R. holubi* is also a rudimentary hermaphrodite. The similar growth rates for males and females in our study supports this assumption, because the growth of group-spawning, rudimentary hermaphroditic sparid species is not normally sexually dimorphic (Buxton and Garratt 1990).

The pooled length–age model showed that *R. holubi* is slow-growing and long-lived, reaching a maximum age of 18 years. Initial growth was fairly rapid compared to that of other sparids (e.g. *Diplodus capensis* and *Diplodus hottentotus* [Mann 1992]; *Rhabdosargus globiceps* [Griffiths et al. 2002]), with fish attaining 124 mm FL in their first year, concurring with growth estimates by Blaber (1973b) and Cowley (1998) for the species. Growth continues relatively rapidly for the first five years and then slows, with individuals attaining 315 mm FL by year 8 and 354 mm FL by year 18 (Figure 4). Despite its slow growth, *R. holubi* appears to grow more rapidly than a similar-sized, warm-temperate sparid such as *Diplodus capensis* (Mann 1992) (Table 3). Within the genus *Rhabdosargus*, the growth and longevity (18 years) of *R. holubi* are comparable to the predominately cool-temperate *R. globiceps* (Griffiths et al. 2002) and the mainly subtropical *R. sarba* (Radebe et al. 2002) (Table 3). Owing to the poikilothermic nature of fishes, environmental temperature has a significant effect on their body temperature, and thereby affects metabolic activity (Bullock 1955). Pauly (1980) showed that temperature greatly affects all three VBGF parameters of 175 fish stocks worldwide. Bourlière (1957), cited by Liu and Walford (1966), presented evidence that decreasing temperature correlated with long life and slow growth of various poikilothermic vertebrates.

Table 3: Von Bertalanffy growth function parameters, maximum age and omega index for *Rhabdosargus holubi* and several other similar sparids

Species	L_{∞} (mm)	K (y^{-1})	t_0 (years)	Max. age (years)	ω
<i>Rhabdosargus holubi</i>	358.06	0.24	-0.77	18	86.56
<i>Rhabdosargus globiceps</i> ¹	342	0.24	-0.55	21	82.08
<i>Rhabdosargus sarba</i> ²	715	0.16	0.99	16	114.4
<i>Diplodus capensis</i> ³	309.44	0.25	1.05	21	77.36

¹ Griffiths et al. (2002)² Radebe et al. (2002)³ Mann (1992)

The distribution of *R. holubi* overlaps with both *R. globiceps* and *R. sarba*, and as such the growth of *R. holubi* may vary across its distribution.

The slow growth, long life and estuarine dependence exhibited by *R. holubi* suggest it may be vulnerable to exploitation in the estuaries of eastern South Africa due to high fishing pressure (Cowley et al. 2013) coupled with habitat degradation (Götz and Cowley 2013). However, as adult *R. holubi* are seldom captured in the surf zone of the Eastern Cape, and the herbivorous (De Wet and Marais 1990) and small juveniles are mostly inaccessible to anglers before they recruit into the estuarine fishery, it is likely that this species is fairly resilient to exploitation. Although *R. holubi* is susceptible to fishing in estuaries after recruitment into the fishery (at around 75 mm FL), its rapid growth at this time ensures that this phase is short, given that it leaves the estuary at a size of about 124 mm FL, at an age of 1 year. Therefore, the impacts of the heavy subsistence and recreational angling effort in estuaries are reduced by this life-history strategy. Growth continues fairly rapidly in the surf-zone habitat, where this species reaches 50% maturity at 150 mm SL in the Eastern Cape (Whitfield 1998). This equates to a size of 176 mm FL (Marais and Baird 1980) and represents 2 years of age, using the growth rates estimated here. Early adult fishes continue growing rapidly until they are approximately 5 years old (Figure 4), at 268 mm FL, after which the primary energy investment of the large fish is dedicated to gonadal growth (Buxton and Garratt 1990). These larger individuals that occupy the surf zone have essentially escaped the major fishing effort and, although targeted particularly in KZN (Dunlop and Mann 2012), are able to contribute to reproductive output. Despite the apparent resilience of *R. holubi* to exploitation, conservation of important estuarine habitats is still critical for the success of this and many other estuarine-dependant species, such as *Lithognathus lithognathus* Cuvier, which are targeted heavily by recreational shore anglers (Bennett 1993; Whitfield 1998).

In summary, this study is the first to validate the periodicity of ring deposition in the otoliths of *R. holubi*, and it has provided the first age and growth information of the species beyond their first year of life. Our results concur with those of other work on this species, and show *R. holubi* to be a slow-growing, long-lived sparid, which attains a maximum age of 18 years. Despite these characteristics, the unique life history of *R. holubi* may provide a degree of resilience to heavy fishing pressure in estuaries. Based on the similar growth of males and females, it is possible that *R. holubi*, like others in the genus, is a group-spawning, rudimentary hermaphrodite. However, this can

only be confirmed using an appropriate multimethod study (Richardson et al. 2011; Winkler et al. 2014). Future studies should aim to (i) ensure better representation in the 200–299 mm FL length class, (ii) sample across the distribution of *R. holubi*, and (iii) incorporate a range of estuary types (i.e. temporarily open/closed estuaries) to obtain a comprehensive understanding of age and growth.

Acknowledgements — The Rhodes University Research Council provided funding for this study. The Marina Martinique Home Owners Association and particularly Morne Strydom are thanked for their assistance during the study. We thank Martin Davies, Zyangani Chirambo, Nicholas Schmidt, Bernard Erasmus, Roy Bealey, Nicholas Ridder, Adrian Stander, Ryan Harrison, Megan Mulcahy, Mathew Goddard and Ryan Van Zeeventer for assistance in the field.

References

- Beamish RR, Fournier DA. 1981. A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Science* 38: 982–983.
- Bennett BA. 1993. Aspects of the biology and life history of white steenbras *Lithognathus lithognathus* in southern Africa. *African Journal of Marine Science* 13: 83–96.
- Blaber SJM. 1973a. Population size and mortality of juveniles of the marine teleost *Rhabdosargus holubi* (Pisces: Sparidae) in a closed estuary. *Marine Biology* 21: 219–225.
- Blaber SJM. 1973b. The ecology of juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae). PhD thesis, Rhodes University, South Africa.
- Blaber SJM. 1974. The population structure and growth of juvenile *Rhabdosargus holubi* (Steindachner) (Teleostei: Sparidae) in a closed estuary. *Journal of Fish Biology* 6: 455–460.
- Brouwer SL, Griffiths MH. 2004. Age and growth of *Argyrozona argyrozona* (Pisces: Sparidae) in a marine protected area: an evaluation of methods based on whole otoliths, sectioned otoliths and mark-recapture. *Fisheries Research* 67: 1–12.
- Bullock TH. 1955. Compensation for temperature in the metabolism and activity of poikilotherms. *Biological Reviews of the Cambridge Philosophical Society* 30: 311–342.
- Buxton CD, Clarke JR. 1991. The biology of white musselcracker *Sparodon durbanensis* (Pisces: Sparidae) on the eastern Cape coast, South Africa. *South African Journal of Zoology* 10: 285–296.
- Buxton CD, Garratt CA. 1990. Alternative reproductive styles in seabreams (Pisces: Sparidae). *Environmental Biology of Fishes* 28: 113–124.
- Campana SE, Thorold SR. 2001. Otoliths, increments and elements: keys to a comprehensive understanding of fish populations. *Canadian Journal of Fisheries and Aquatic Sciences* 58: 30–38.
- Chale-Matsau JR, Govender A, Beckley LE. 2001. Age, growth and retrospective stock assessment of an economically extinct

- sparid fish, *Polysteganus undulosus*, from South Africa. *Fisheries Research* 51: 87–92.
- Cowley PD. 1998. Fish population dynamics in a temporarily open/closed South African estuary. PhD thesis, Rhodes University, South Africa.
- Cowley PD, Childs AR, Bennett RH. 2013. The trouble with estuarine fisheries in temperate South Africa, illustrated by a case study on the Sundays Estuary. *African Journal of Marine Science* 35: 117–128.
- Cowley PD, Wood AD, Corroyer B, Nsubuya Y, Chalmers R. 2003. A survey of fishery resource utilization on four Eastern Cape estuaries (Great Fish, West Kleinmond, East Kleinmond and Kowie). Report to the Eastern Cape Estuaries Management Programme, Institute of Natural Resources, University of KwaZulu-Natal.
- De Wet PS, Marais JFK. 1990. Stomach content analysis of juvenile Cape stumpnose *Rhabdosargus holubi* in the Swartkops Estuary, South Africa. *South African Journal of Marine Science* 9: 127–133.
- Dunlop SW, Mann BQ. 2012. An assessment of participation, catch and effort in the KwaZulu-Natal shore-based marine linefishery, with comments on management effectiveness. *African Journal of Marine Science* 34: 479–496.
- Efron B. 1981. Nonparametric estimates of standard error: the jackknife, the bootstrap and other methods. *Biometrika* 68: 589–599.
- Gallucci VF, Quinn TJ. 1979. Reparameterising, fitting and testing a simple linear growth model. *Transactions of the American Fisheries Society* 108: 14–25.
- Götz A, Cowley PC. 2013. Cape stumpnose (*Rhabdosargus holubi*). In: Mann BQ (ed.), *Southern African marine linefish status reports. Special Publication No. 9*. Durban: Oceanographic Research Institute. pp 268–269.
- Griffiths MH, Wilke C, Penney AJ, Melo Y. 2002. Life history of white stumpnose *Rhabdosargus globiceps* (Pisces: Sparidae) off South Africa. *South African Journal of Marine Science* 24: 281–300.
- Harrison TD. 2005. Ichthyofauna of South African estuaries in relation to the zoogeography of the region. *Smithiana* 6: 2–27.
- Heemstra PC, Heemstra E. 2004. *Coastal fishes of southern Africa*. Grahamstown: NISC [National Inquiry Services Centre] and SAIAB [South African Institute for Aquatic Biodiversity].
- Hughes JM, Stewart J, Kendall BW, Gray CA. 2008. Growth and reproductive biology of tarwhine *Rhabdosargus sarba* (Sparidae) in eastern Australia. *Marine and Freshwater Research* 59: 1111–1123.
- James NC, Cowley PD, Whitfield AK. 2007b. Abundance, recruitment and residency of two sparids in an intermittently open estuary in South Africa. *African Journal of Marine Science* 29: 527–538.
- James NC, Cowley PD, Whitfield AK, Lamberth SJ. 2007a. Fish communities in temporarily open/closed estuaries from the warm- and cool-temperate regions of South Africa: a review. *Reviews in Fish Biology and Fisheries* 17: 565–580.
- Kallianiotis A, Torre M, Argyri A. 2005. Age, growth, mortality, reproduction and feeding habits of the striped seabream, *Lithognathus mormyrus* (Pisces: Sparidae), in the coastal waters of the Thracian Sea, Greece. *Scientia Marina* 69: 391–404.
- Kimura DK. 1980. Likelihood methods for the von Bertalanffy growth curve. *Fishery Bulletin* 77: 765–776.
- Knight W. 1968. Asymptotic growth: an example of nonsense disguised as mathematics. *Journal of the Fisheries Research Board of Canada* 25: 1303–1307.
- Liu RK, Walford RL. 1966. Increased growth and life-span with lowered ambient temperature in the annual fish, *Cynolebias adloffii*. *Nature* 212: 1277–1278.
- Mann BQ. 1992. Aspects of the biology of two inshore sparid fishes (*Diplodus sargus capensis* and *Diplodus cervinus hottentotus*) off the south east coast of South Africa. MSc thesis, Rhodes University, South Africa.
- Marais JFK, Baird D. 1980. Seasonal abundance, distribution and catch per unit effort of fishes in the Swartkops estuary. *South African Journal of Zoology* 15: 66–71.
- Pajuelo [JG], Lorenzo [LM]. 2001. Biology of the annular seabream, *Diplodus annularis* (Sparidae), in coastal waters of the Canary Islands. *Journal of Applied Ichthyology* 17: 121–125.
- Pauly D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil / Conseil Permanent International pour l'Exploration de la Mer* 39: 175–192.
- Potts WM, Cowley PD. 2005. Validation of the periodicity of opaque zone formation in the otoliths of four temperate reef fish from South Africa. *African Journal of Marine Science* 27: 659–669.
- Pradervand P, Baird D. 2002. Assessment of the recreational linefishery in selected Eastern Cape estuaries: trends in catches and effort. *African Journal of Marine Science* 24: 87–101.
- Radebe PV, Mann BQ, Beckley LE, Govender A. 2002. Age and growth of *Rhabdosargus sarba* (Pisces: Sparidae), from KwaZulu-Natal, South Africa. *Fisheries Research* 58: 193–201.
- Richardson TJ. 2010. The taxonomy, life-history and population dynamics of blacktail, *Diplodus capensis* (Perciformes: Sparidae), in southern Angola. MSc thesis, Rhodes University, South Africa.
- Richardson TJ, Potts WM, Sauer WHH. 2011. The reproductive style of *Diplodus capensis* (Sparidae) in southern Angola: rudimentary hermaphroditism or partial protandry? *African Journal of Marine Science* 33: 321–326.
- Sadovy YJ. 1996. Reproduction of reef fishery species. In: Polunin NVC, Roberts CM (eds), *Reef fisheries*. London: Chapman and Hall. pp 15–59.
- Sadovy YJ. 2001. The threat to fishing highly fecund fishes. *Journal of Fish Biology* 59: 90–108.
- Secor DH, Dean JM, Laban EH. 1991. Otolith removal and preparation for microstructural examination: a user's manual. Technical Report No. 1. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina.
- Smale MJ, Punt AE. 1991. Age and growth of the red steenbras *Petrus rupestris* (Pisces: Sparidae) on the south-east coast of South Africa. *South African Journal of Marine Science* 10: 131–139.
- van der Walt BA, Beckley LE. 1997. Age and growth of *Sarpa salpa* (Pisces: Sparidae) off the east coast of South Africa. *Fisheries Research* 31: 241–248.
- Wallace JH. 1975. The estuarine fishes of the east coast of South Africa: III. Reproduction. *Investigational Report No. 41*. Durban: Oceanographic Research Institute.
- Whitfield AK. 1998. Biology and ecology of fishes in southern African estuaries. *Ichthyological Monographs of the JLB Smith Institute of Ichthyology* 2.
- Winkler A, Santos CV, Potts WM. 2014. Diagnosing the sexual pattern of *Diplodus cervinus hottentotus* (Pisces: Sparidae) from southern Angola. *African Journal of Marine Science* 36: 505–512.