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Unravelling growth trajectories from complicated otoliths – the case of Brazilian codling *Urophycis brasiliensis*

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Uncertainty regarding the age determination of the Brazilian codling *Urophycis brasiliensis* has hampered its stock assessment. Transverse sections of otoliths displayed up to seven (in males) and 12 (in females) alternate opaque and translucent bands that could not be conclusively validated as annuli, resulting in unrealistically high ages of first maturity (A_{50}) ($A_{50\text{male}} = 4{\cdot}5$ years and $A_{50\text{female}} = 6$ years). Therefore, growth was described by the von Bertalanffy (VB) model using an alternative approach that combined microstructure data (daily growth increments) and a fixed asymptotic total length (L_∞). This approach was supported by applying it to two other co-occurring species, the whitemouth croaker *Micropogonias furnieri* and the king weakfish *Macrodon atricauda*, for which daily and annual ring formation has previously been validated. The sensitivity to realistic errors associated with the choice of the L_∞ and the daily increment readings was shown to be low. The results show that *U. brasiliensis* has a fast growth rate ($K_{\text{male}} = 1{\cdot}19\ \text{year}^{-1}$, $K_{\text{female}} = 0{\cdot}71\ \text{year}^{-1}$) and early maturation ($A_{50\text{male}} = 1{\cdot}1–1{\cdot}5$ years, $A_{50\text{female}} = 1{\cdot}6–1{\cdot}8$ years); typical life-history traits for a sub-tropical coastal gadiform. This novel study offers an alternative approach for age and growth reconstruction for species with complex patterns of opaque and translucent bands provided that daily growth increments in the yearlings can be counted and L_∞ reliably estimated.

Key words: age validation; bayesian inference; life-history-traits; otolith microstructure.

INTRODUCTION

Age determination is one of the most important aspects in understanding fish population dynamics. It is however, subject to various sources of error (due to otolith structural features and subjectivity involved in age estimation), which may severely change the outcomes of stock assessments for species targeted by fisheries (Campana, 2001). For several species from around the world, annual periodicity of otolith bands has been erroneously assumed, resulting in inaccurate ageing (usually underestimation) and in optimistic estimates of growth and mortality rates. This has been contributing to serious overexploitation of some fish populations. For instance, off New Zealand, the orange

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roughy *Hoplostethus atlanticus* Collett 1889 was fished intensively based on a presumed longevity of 20–30 years (W. L. F. van den Broek, unpubl. data) instead of over 100 years (Smith *et al.,* 1995).

Overestimation of maximum ages may also occur. Recent tag-recapture studies showed that counts of alternate opaque and translucent bands, previously considered annuli (annual bands), may produce overestimates of age and underestimates of growth rates in gadiform species (Kacher & Amara, 2005; De Pontual *et al.,* 2006; Piñeiro *et al.,* 2007, 2008; Mellon-Duval *et al.,* 2010). Age estimation has also proved to be particularly elusive for the gadiform subfamily Phycidae, as growth checks (false annuli) were frequently observed in their otoliths, as in in *Urophycis chuss* (Walbaum 1792) (Dery, 1988) and *Urophycis tenuis* (Mitchill 1814) (Clay & Clay, 1991) in the North Atlantic Ocean, as well as *Urophycis cirrata* (Goode & Bean 1896) (Martins & Haimovici, 2000) and *Urophycis brasiliensis* (Kaup 1858) (Acuña, 2000) in the South Atlantic Ocean.

The Brazilian codling *U. brasilienis* is part of the mixed demersal catches of the industrial trawling and gillnet fisheries in south-east Brazil (Haimovici *et al.,* 1996). Its age determination in Uruguay (Acuña, 2000) and southern Brazil (Andrade *et al.,* 2004, 2005) was not validated due to the great difficulty in identifying their annuli. As a result, its growth trajectory and population parameters remain unknown.

Daily growth increments were observed for the first time almost five decades ago, when Pannella (1971) counted *c.* 360 micro-increments between otolith annuli, opening a new field for understanding early life stages, age, growth, recruitment, migration, mortality and stock structure of fish populations (Jones, 1992).

The present study combines reproductive information and daily growth increment counts to develop an alternative approach of estimating age and growth in *U. brasilienis*.

The assumed annuli led to unrealistic estimates of the age at first maturity (A_{50}) for both sexes. An alternative von Bertalanffy (VB) growth model was built using daily growth increments and a fixed value for the asymptotic length (L_∞) that was inferred from long-term sampling of the size structure of the population. The consistency of this approach was evaluated by comparing the resulting ages at first maturity with reported values from the literature for related species. The accuracy of using daily growth increments to calculate the VB growth parameters was tested by applying this methodology to other two co-occurring species; the whitemouth croacker *Micropogonias furnieri* (Dermarest 1823)*,* for which annual rings were validated by Haimovici & Umpierre (1996) and daily growth increments by Cavole & Haimovici (2015) and the king weakfish *Macrodon atricauda* (Günther 1880), for which annual rings were validated by Cardoso & Haimovici (2011) and daily growth increments by M. S. Almeida (unpubl. data). This approach could provide an alternative means to elucidate age and growth of fish with complex patterns of otolith band formation provided that the early growth of the species is known.

MATERIALS AND METHODS

DATA COLLECTION

The adults of *U. brasiliensis* (133–600 mm total length; L_T) were obtained from commercial bottom trawling and gillnets in Rio Grande, southern Brazil (30–34°S) between

June 2012 and July 2013. Small juveniles (46–231 mm) were collected in shallow waters (>10 m) by the R.V. *Atlântico Sul* in January 2013. Sex, L_T (mm), total mass (M, g), gonad mass (M_G, 0·1 g) were recorded and sagittal otoliths were collected from all sampled specimens.

The juveniles and adults of *M. furnieri* and *M. atricauda* were obtained from a long-term sampling programme that monitors coastal demersal fisheries on the southern Brazilian shelf (28–34° S). This sampling programme has been carried out by the Oceanography Institute of the University of Rio Grande since 1976 (Haimovici, 1987, 1998).

The present study includes: 14 044 measured and 845 aged *M. furnieri* adults and juveniles (Haimovici & Ignácio, 2005; Cavole & Haimovici, 2015); 14 493 measured and 797 aged *M. atricauda* adults and juveniles (Cardoso & Haimovici, 2011; M. S. Almeida, unpubl. data); 1331 measured and 493 aged *U. brasiliensis* adults and juveniles.

REPRODUCTIVE BIOLOGY

For the reproductive analysis, fresh or fixed (in 10% formalin) ovaries and oocytes were visually examined. Oocyte diameters and characteristics (presence of lipidic or proteic yolk vesicles, hydration) were recorded from samples examined with a binocular microscope at up to ×40 magnification. A scale of seven stages was used to characterize the ovaries of females (Haimovici & Cousin, 1989; West, 1990). Females in stages I (virginal or immature) and II (developing virginal) have a very thin and poorly irrigated gonad membrane; oocyte diameters are <0·15 mm, with no signs of vitellogenesis. In the ovaries of stages III (developing), IV (advanced development), V (running) and VI (partly spent), the ovary membrane is clearly vascularized and shows both oocytes with no sign of vitellogenesis and oocytes in vitellogenesis of up to 0·6 mm in diameter. Post-spawned ovaries in stage VII (recovering) are flabby, haemorrhagic and exhibit a thickened membrane, without mature oocytes. Males with threadlike transparent testes (stages I and II) were considered immature. Males with whitish enlarged testes that released sperm when cut and compressed (stages III, IV, V and VI) were considered to have reached sexual maturity. Spent testes (stage VII) were brownish with longitudinal grooves and no sperm. Stage III was considered the onset on maturation for both sexes.

The gonado-somatic index (I_G) was calculated as (Wootton, 1998): $I_G(\%) = 100 M_G M^{-1}$, where M_G is the gonad mass and M is the total fish mass. The monthly I_G averages were used to analyse the reproduction seasonality. Normality (Kolmogorov–Smirnov one-sample test), homogeneity of variance (Levene's test) and the differences between months were tested with one-way analysis of variance (ANOVA) and *post hoc* Tukey tests (Zar, 1984).

Length-based maturity ogives were estimated with data obtained throughout the year as seasonal reproduction was not observed. The total number (n_i) and the number of mature specimens (y_i) were calculated for males and females in 10 mm L_T size classes. θ_i denotes the probability of an individual of the *i*th age or *i*th length class being mature and y_i was assumed to follow a binomial distribution $B_{in}\ (n_i,\ \theta_i)$. Data were fitted by logistic regression, defined by a logit link function that transforms the parameter θ_i, restricts to the range [0, 1] in the binomial distribution in m defined between $(-\infty, +\infty)$. From this model, the length at first maturity (L_{50}) and the age of first maturity (A_{50}) were defined as (Kinas & Andrade, 2010; Cardoso & Haimovici, 2014): L_{50} (or A_{50}) $= -\beta_0 {\beta_1}^{-1}$.

The posterior distribution $p(\beta_0,\ \beta_1 |\ D)$, where $D = \{(y_i,\ n_i,\ x_i);\ i = 1,\ \ldots,\ k\}$, was obtained *via* the stochastic process Markov chain Monte-Carlo (MCMC). The posterior distributions of β_0 and β_1 were considered independent and a normal distribution with mean of 0 and a large variance (1000) was used as the *a priori* distribution. After 50 000 burn-in runs, every third value of the remaining 9000 was retained, resulting in a final sample of 3000 in the posterior distribution $p(\beta_0,\ \beta_1 | D)$ (Kinas & Andrade, 2010). The posterior distribution of the estimated A_{50} and L_{50} provides an easy and clear way to compare the results among males and females; no overlap indicates a statistically significant difference.

AGE AND GROWTH

ADULTS AND OTOLITH MACROSTRUCTURE

The macrostructure of 441 otoliths from specimens between 270–600 mm L_T were examined. Sagittal otoliths were transversally sectioned and the alternate opaque and translucent bands were counted. Sections of 0·2–0·3 mm width were obtained through the nucleus with a low speed rotary saw. The images of the otolith sections were taken using a stereoscopic microscope at ×10 objective power on a camera with 2048 × 1536 pixels. The distances between the otolith core and the end of the opaque bands, assumed *a priori* as annuli (annual bands), were measured with the free software ImageJ 1·47 (www.imagej.nih.gov). Fifty eight otoliths (13%) were discarded during the preparation and increment analysis due to the difficulty in discerning the miscellaneous annual rings.

JUVENILES AND OTOLITH MICROSTRUCTURE

The microstructure (assumed daily growth increments) of 52 otoliths from specimens measuring 46–231 mm L_T were examined. Sagittae were prepared and polished following the methods described by Cavole & Haimovici (2015).

Sections were examined using a transmitted light microscopy at x400 magnification (Olympus CX41; www.olympus-ims.com), suitable for examination of fast growing otoliths with microincrements larger than 2 μm in width (Campana & Jones, 1992). The microscope focus was frequently adjusted to correctly interpret the entire microincrement sequence. Daily growth increments were counted between the otolith core and the outer edge of the otolith along the ventral axis (Fig. 1). Numbers of daily growth increments (otolith microstructure) were compared between two readers. The mean coefficient of variation (C.V.) was used to evaluate the precision of age readings from macro and microstructure (Campana & Jones, 1992): $\text{C.V.}_{j} = 100[\sqrt{\Sigma^{R}{}_{i=1}}\ (x_{ij}-x_{j})^{2}\ (R-1)^{-1}]x_{j}{}^{-1}$, where C.V._{j} is the age precision estimate for the *j*th fish; x_{ij} is the age determination of the *j*th fish by the i^{th} reader; x_j is the mean age of *jth* fish and R is the number of readings.

MACROSTRUCTURE VALIDATION ATTEMPT

The periodicity of the formation of opaque and translucent bands on the edge of the otoliths was evaluated by counting monthly opaque and translucent edges. The marginal increment index (I_M) was calculated as: $I_M = (R - R_n)[R_n - (R_{n-1})]^{-1}$, where R is the distance from the nucleus to the edge, R_n is the distance from the nucleus to the end of the last opaque band and R_{n-1} is the distance from the nucleus to the end of the penultimate opaque band. One-way ANOVA and Tukey *post hoc* tests were used to compare mean I_M between months.

GROWTH MODEL FITTING USING VON BERTALANFFY GROWTH FUNCTION: ADULTS AND JUVENILES

The von Bertalanffy (VB) parameters t_0 and K (mean and credibility intervals of 95%) were both calculated using a Bayesian approach. The VB growth model was

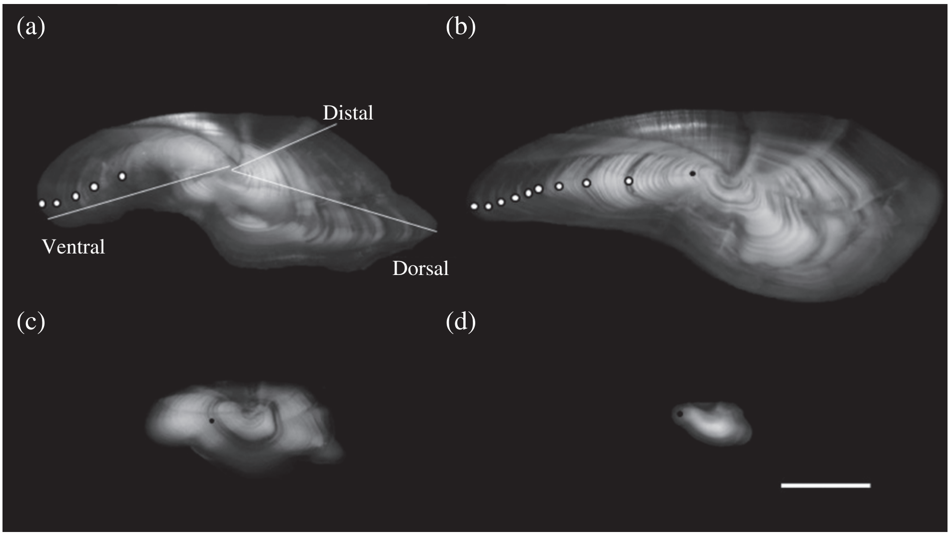

Fig. 1. Transverse sections of *Urophycis brasiliensis* sagittal otoliths from fish (a) 385 mm total length (L_T) with 5 bands and showing the ventral axis (◘); (b) 516 mm L_T and 9 bands; (c) 172 mm L_T showing the demersal check (●); (d) 46 mm L_T and a demersal check (●) forming on the edge. Scale bar 1 mm.

fitted using the micro-increments (assumed daily growth increments) and large opaque bands (assumed annual rings) and the observed length data: $L_t = L_\infty\ (1 - e^{-K(t - to)})$, where L_t is the total length (mm) at age t (years), L_∞ is the asymptotic length (mm), K is the growth coefficient representing how fast L_∞ is reached and t_0 is the theoretical age at which $L_t = 0$ (years or days).

An ultimate validation of the annual periodicity of large opaque bands was not achieved by the present or previous works for *U. brasiliensis*. To overcome this, an alternative approach was used to calculate its growth parameters combining daily growth increments and a fixed value of L_∞. This approach was tested by comparing the posterior distributions of the K parameter estimated separately using annuli or daily growth increments in other co-occurring species: *M. furnieri* and *M. atricauda*. *Micropogonias furnieri* lives up to 35 years (Cotrina & Lasta, 1986; Schwingel & Castello, 1990; Haimovici & Umpierre, 1996). Daily periodicity in juvenile otoliths of *M. furnieri* was experimentally validated by an oxytetracycline marking experiment (Cavole & Haimovici, 2015). *Macrodon atricauda* attains up to 7 years (Cardoso & Haimovici, 2011); daily growth increments have been validated by comparing the back-calculated lengths of juveniles with 250–350 micro-increments with the back-calculated length at age 1 year and comparing the juvenile birthdates with their known period of reproduction (M. S. Almeida, unpubl. data).

The posterior distributions and credibility intervals of the VB parameters t_0 and K were calculated for fixed values of L_∞. The choice of L_∞ was based on the length composition in commercial landings of a non-selective gear (*i.e*. trawling), the size classes by sex (males and females) and the L_{50} estimate. The L_∞ was the upper limit of the size class that contains 95% of the mature individuals for each sex and for each of the three species, *M. furnieri, M. atricauda, U. brasiliensis* (Fig. 2).

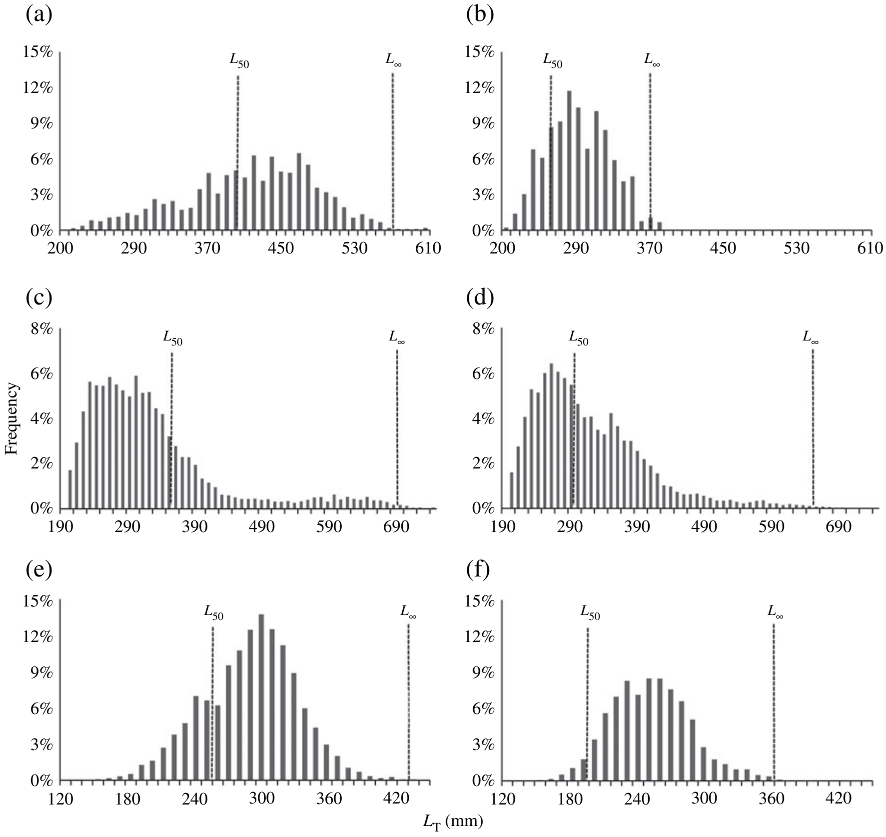

FIG. 2. Total length (L_T)-frequency distributions with estimates of mean length at first maturity (L_{50}) and mean asymptotic length (L_∞) estimated for (a) female ($n = 1033$) and (b) male *Urophycis brasiliensis* ($n = 298$), (c) female ($n = 6650$) and (d) male *Micropogonias furnieri* ($n = 7394$), (e) female ($n = 5488$) and (f) male *Macrodon atricauda* ($n = 9005$). The L_∞ was based on L_{50} and the length composition from a non-selective trawl fishery in southern Brazil.

The age–length data followed a log-normal distribution: $y_i = log\,N\,(\mu_i, \sigma^2)$, where y_i is the length distribution with an average expected length at an age class (or opaque band class, in the case of *U. brasiliensis*) i with variance σ^2. A logarithmic version of the VB equation was used for computational convenience: $\mu_i = \log\left(L_\infty\right) + \log\left(1^{-K\left(i-t_0\right)}\right)$.

The seed values of each parameter were constructed as uninformative priors with wide intervals. The probability of log K was considered to follow a normal distribution with mean = 0 and variance = 0·001 and restricted to the interval −5 and 5. The probability of t_0 was considered to follow a uniform distribution with minimum of −3 and maximum of zero. The probability of σ was considered to follow a uniform distribution with minimum of 0 and maximum of 5.

The posterior distribution was obtained *via* the stochastic process (MCMC) as it provides an easy and clear way to compare the results among the types of age data by analysing the overlap degrees between the density of the resulting parameter values.

After 10 000 burn-in runs, every second value of the remaining 20 000 was retained, resulting in a final sample of 10 500 in the posterior distribution (Kinas & Andrade, 2010). All statistics (growth and reproduction parameters) were run by R 2·12·0 (www.r-project.org). The MCMC was performed by OpenBUGS, using the libraries R2WinBUGS (Sturtz *et al.,* 2005) and BRugs (Thomas *et al.,* 2006).

The age of first maturity (A_{50}) was estimated for both sexes using the length of first maturity and the VB growth equation. The age corresponding to the length of first maturity was assumed to be the A_{50}.

To assess the sensitivity of the estimation of K to the accuracy of daily increment counts, the K was estimated considering the number of daily increments being 10, 30 and 50% higher and lower than those observed. Considering that the L_∞ values were, in a certain way, arbitrarily determined, the modelling was repeated for each species considering the L_∞ being 5 and 10% higher and lower than the ones chosen.

GROWTH RATES USING LAIRD-GOMPERTZ – JUVENILES

The Laird-Gompertz (LG) model was used to obtain specific growth rates for the *U. brasiliensis* juveniles. The LG growth model was fitted to the length and daily increment counts (Laird *et al.,* 1965; Ricker, 1979; Campana & Jones, 1992): $L_\mathrm{t} = L_\infty\ \mathrm{e}^{[-K\ \mathrm{e}^{(-Gx)}]}$, where L_t is length at age t expressed in days; L_∞ is the asymptotic length (mm); K is a dimensionless parameter, G is the instantaneous rate of growth at age x_0, x_0 is the inflection point of the curve and the age at which absolute growth rate begins to decline, x is the number of daily growth increments. Birthdates were estimated for each juvenile by subtracting the increment count from the date of capture.

RESULTS

REPRODUCTIVE SEASONALITY AND LENGTH AT FIRST MATURITY

Gonads of 384 females between 133 and 582 mm L_T *and* 123 males between 151 and 379 mm L_T were analysed. The presence of oocytes of different diameters and stages of vitellogenesis indicates multiple spawning events in *U. brasilienis* [Fig. 3(a)]. Monthly mean I_G were highly variable; lower values were recorded in January, March, April, June and July and higher values in February, May, August, October and November [Fig. 3(b)]. Monthly mean I_G did not differ significantly among months (ANOVA $F_{9,112} = 1{\cdot}84$, $P > 0{\cdot}05$). These results indicate that the species reproduces year-round in southern Brazil without any marked seasonality [Fig. 3(b)–(d)]. The mean length at first maturity (L_{50}) of females was estimated at 402·8 mm with a 95% credibility interval from 392·4 to 412·5 mm and at 296·8 mm for males with a 95% credibility interval from 275·4 to 318·1 mm [Fig. 4(a), (b)].

AGE ESTIMATED FROM THE MACROSTRUCTURE OF OTOLITHS

Otolith sections of 104 males measuring between 231 and 379 mm L_T and 279 females measuring between 227 and 600 mm L_T were examined (Table I). A large

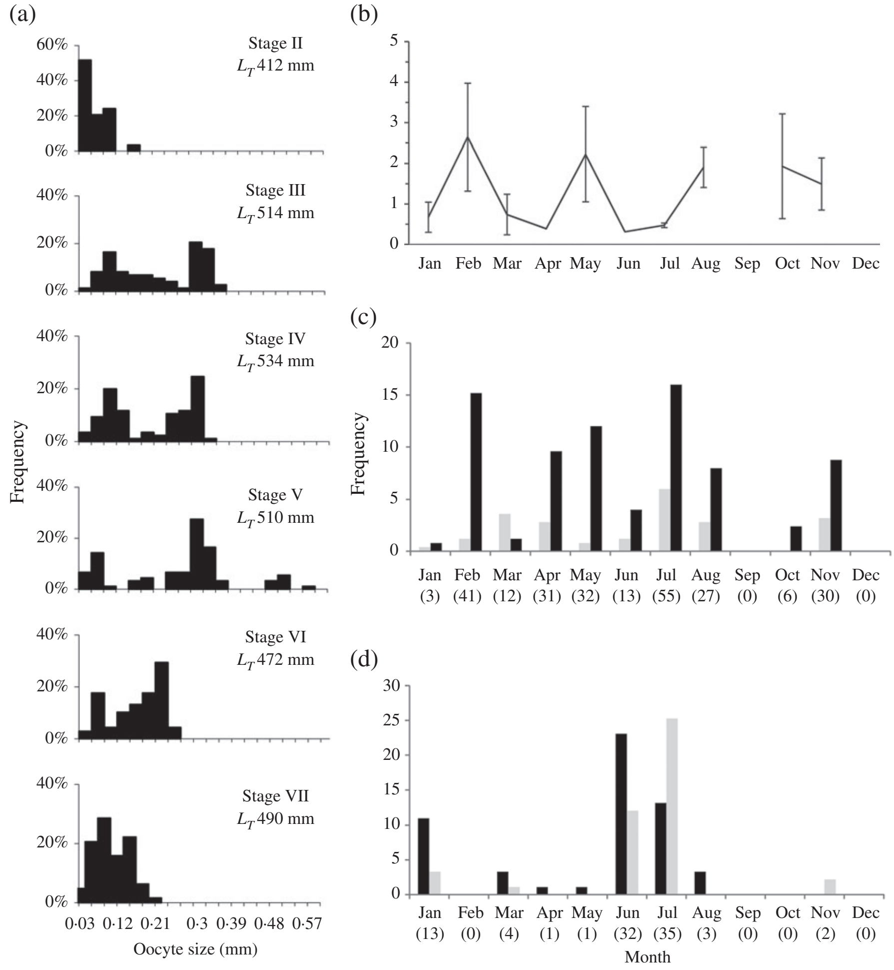

FIG. 3. Reproductive biology of Brazilian codling *Urophycis brasiliensis* showing: (a) size-frequency distribution of oocytes at maturity stages II–VII ($n = 6$ fish; L_T, total length); (b) mean (± 95% credibility interval) values of female gonado-somatic index (I_G) by month; (c) monthly relative frequency distribution of mature and immature females and (d) mature and immature males (sample size in parentheses on the x-axis). ■, Mature; □, Immature.

opaque region (core) was frequently interrupted by several thin translucent rings [Fig. 1(a), (b)]. The following alternate wider translucent and opaque bands were counted along the ventral axis of the otolith. The average back-calculated length of females ranged between 156 mm at the onset of the 1st band and 574 mm at the 12th band, while males ranged between 150 mm at the 1st band and 338 mm at the 7th band (Table I).

ANNULI VALIDATION ATTEMPT

The mean I_M for all ages combined showed similar values throughout the year, with no clear commencement period (*i.e.* a season of the year) for increment formation.

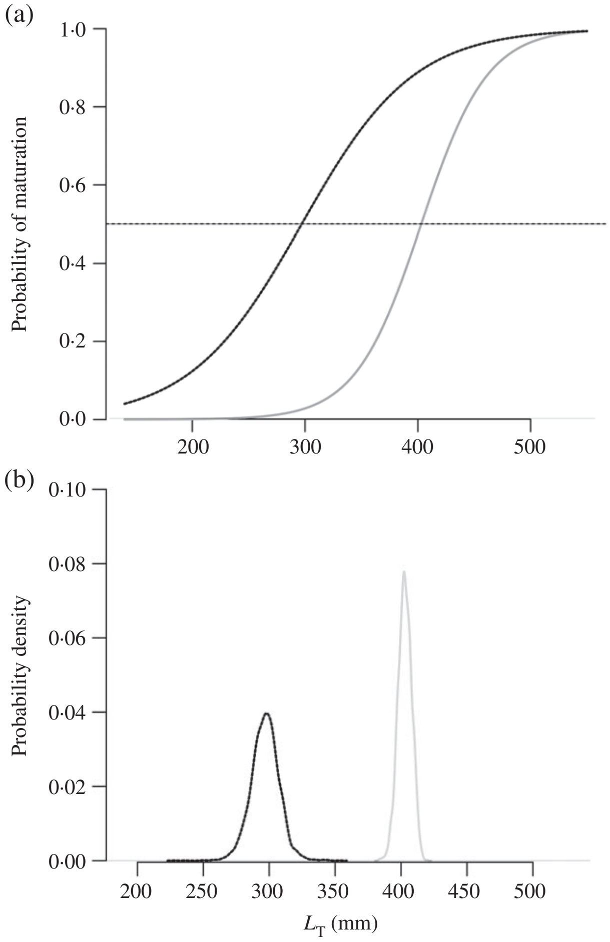

FIG. 4. (a) Length–maturity ogives and (b) posterior distribution of the estimated length at first maturity (L_{50}) for *Urophycis brasiliensis* fished in southern Brazil. ——, Female; ——, Males.

Monthly mean marginal increments (I_M) were 0·56 during spring, 0·60 during summer, 0·66 in autumn and 0·82 in winter [Fig. 5(a)]. Although I_M differed significantly between seasons (ANOVA $F_{3,380} = 10{\cdot}54$, $P < 0{\cdot}05$), Tukey *post hoc* tests showed that these differences were mainly driven by variation between spring and winter and between summer and winter. The monthly proportion of specimens with opaque edges was 73 to 100% from June to October while it ranged from 16 to 45% from November to May, initially suggesting an annual cycle in the type of edge formation [Fig. 5(b)]. August, however, was the only month in which 100% of samples had opaque edges and there were no months when 100% of samples had translucent edges, indicating no clear seasonal pattern. Furthermore, the C.V. using the macrostructure data was high, both between successive readings of one reader (13·8%) and between different readers (15·5%). These values were more than double those found in an extensive review of 117 publications (Campana, 2001) and show difficulties in reproducing the readings of the assumed annuli bands in *U. brasiliensis* otoliths.

TABLE I. Otolith-band–length keys for females and males of *Urophycis brasiliensis* in southern Brazil

	Females												Males						
		Opaque band												Opaque band					
Total Length (mm)	*n*	2	3	4	5	6	7	8	9	10	11	12	*n*	2	3	4	5	6	7
210–239	2	2	–	–	–	–	–	–	–	–	–	–	2	2	–	–	–	–	–
240–269	15	5	7	3	–	–	–	–	–	–	–	–	21	5	14	1	1	–	–
270–299	14	3	8	3	–	–	–	–	–	–	–	–	32	–	14	8	7	3	–
300–329	30	–	6	12	9	2	1	–	–	–	–	–	26	–	–	7	10	7	2
330–359	27	–	2	10	10	4	1	–	–	–	–	–	20	–	–	7	8	3	2
360–389	20	–	2	4	6	6	2	–	–	–	–	–	3	–	–	–	–	2	1
390–419	28	–	–	3	7	7	6	4	1	–	–	–	–	–	–	–	–	–	–
420–449	37	–	–	1	5	2	18	5	4	2	–	–	–	–	–	–	–	–	–
450–479	30	–	–	–	4	8	12	4	2	–	–	–	–	–	–	–	–	–	–
480–509	37	–	–	–	1	5	13	7	8	1	2	–	–	–	–	–	–	–	–
510–539	20	–	–	–	–	1	3	8	5	2	1	–	–	–	–	–	–	–	–
540–569	16	–	–	–	–	1		5	4	4	2	–	–	–	–	–	–	–	–
570–599	2	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	–	–	–
600–629	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–

n, The total number of individuals in each size class.

AGE DETERMINED FROM THE MICROSTRUCTURE OF OTOLITHS

Thin sections of otoliths from 52 juveniles showed a concentric pattern of growth increment zones from the first discernible micro-increment to the edge of the section [Fig. 6(a)]. These growth increment zones were assumed to be daily growth increments due to their well-marked appearance [Fig. 6(a), (b)]. The readings were from 50 to 285 micro-increments in specimens of 45 and 210 mm L_T, respectively [Fig. 6(d)]. The C.V. between readers was low (5·25%), showing a consistent pattern not previously achieved by the macrostructure readings in *U. brasiliensis*.

The central zone of the otolith sections was blurred. From the first discernible micro-increment, 36–65 increments appeared with a progressively wider pattern until the edge of a thin translucent band (TTB), visible in both macro and microstructure [Fig. 6(a), (b)]. Back-calculated mean length at the formation of the TTB in larger specimens was 47 mm, with no differences between sexes (ANOVA $F_{1,366} = 0{\cdot}084$, $P > 0{\cdot}05$) or size classes (ANOVA $F_{4,363} = 0{\cdot}957$, $P > 0{\cdot}05$). The TTB observed is similar in appearance and width to the settlement check, associated with the transition from the pelagic to demersal habitat (Arneri & Morales-Nin, 2000; Casas & Piñeiro, 2000). Coincidentally, the smallest specimen examined measured 46 mm L_T and showed 50 increments and a well-defined translucent zone forming at the edge of the otolith [Fig. 1(d)]. From the TTB onwards increments are regular with occasional variations in thickness, becoming narrower at the edge of sections.

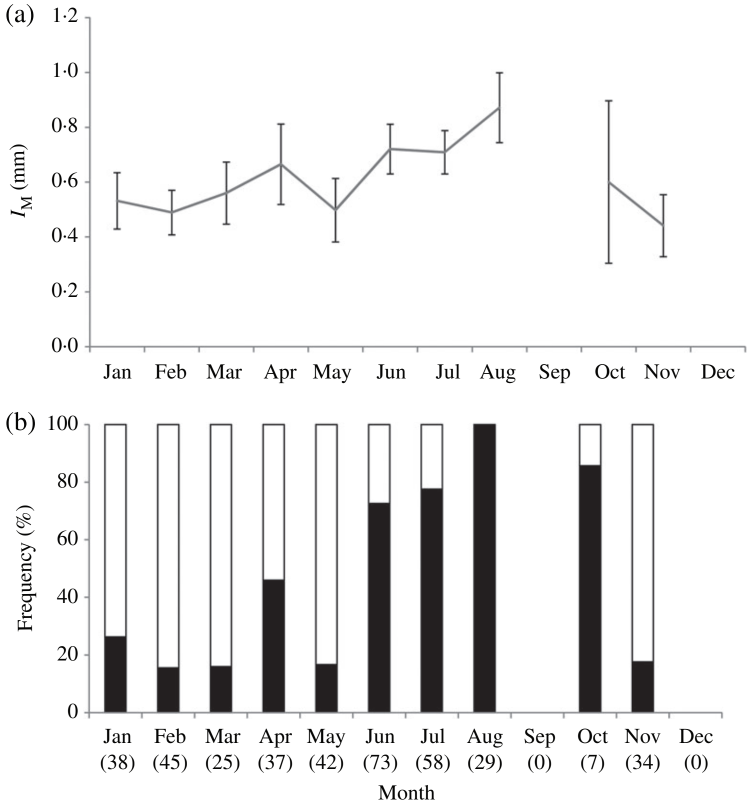

FIG. 5. (a) Monthly mean (±95% credibility interval) marginal increment (I_M) and (b) monthly frequency distribution of translucent (□) and opaque (■) edges observed in the otolith sections of *Urophycis brasiliensis* (sample size is given in parentheses).

ALTERNATIVE APPROACH: VON BERTALANFFY'S GROWTH PARAMETERS

The VB parameters were estimated considering the ring timescale (micro and macrostructure), each sex (male, female) and the life history of three different species: *U. brasiliensis, M. furnieri, M. atricauda* (Table II and Fig. 7).

For *U. brasiliensis*, the growth model fitted to the macrostructure data (opaque bands) [Fig. 7(a), (b)] showed an initial slow growth and predicted that 95% of L_∞ would be reached within 10·6 opaque bands by males and 16·3 opaque bands by females. If these opaque bands were considered annuli, the first maturity would be achieved in 4·5 years for males and 6·0 years for females. Conversely, the model derived from the microstructure data [Fig. 7(a), (b)] showed an initial rapid growth and predicted that 95% of L_∞ would be reached by males of 2·5 years and by females of 4·2 years. The estimated age at first sexual maturity (A_{50}) was between 1·1 and 1·5 years for males and between 1·6 and 1·8 years for females. The estimated K values were nearly five times higher for males and nearly four times higher for females [Fig. 7(a), (b) and Table II) using the microstructure data compared with the K values calculated with the macrostructure opaque bands [Fig. 8(a), (b)].

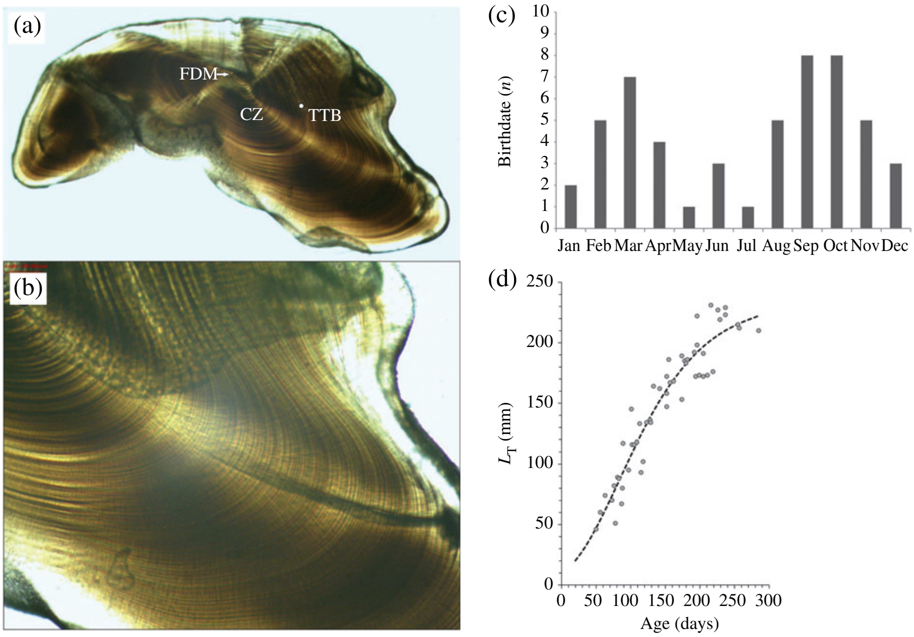

FIG. 6. (a) Otolith section from a juvenile of *Urophycis brasiliensis* (176 mm total length; L_T) (FDM, The first discernible micro-increment; CZ, central zone; TTB, the thin translucent band) and (b) bands showing daily growth increments. (c) Monthly frequency distribution of back-calculated birth date ($n = 52$ juveniles). (d) Gompertz L_T growth curve fitted to age data from 52 juveniles. Gompertz (mm).

For *M. furnieri*, the differences in the *K* parameter estimates between the two macrostructure and the microstructure models were 7% for females and 3% for males [Fig. 7(c), (d)] and there was total overlap of credibility intervals [Fig. 8(c), (d) and Table II). For *M. atricauda*, the differences of the *K* parameter estimates were 12% for females and 8% for males [Fig. 7(e), (f)] and there was partial overlap of the credibility intervals [Fig. 8(e), (f) and Table II). The lack of significant statistical difference between *K* calculated with different data sources (annual and daily rings) for each sex (male and female) for both species (*M. furnieri* and *M. atricauda*) was assumed to reflect good performance of this alternative approach and showed that the micro and macrostructure ageing information matched with each other.

The sensitivity analysis showed that the underestimation of the number of daily increments would lead to higher errors in the estimation of *K* than the overestimation (Fig. 8). The *K* credibility intervals with errors of less than 10% overlap partially with those considered without error for all three species (Fig. 8). The sensitivity test for possible errors associated with the choice of the L_∞ showed that overestimations or underestimations of up to 5% of the assumed value of L_∞ would not result in significant errors in the estimate of *K* for any of the three species (Fig. 9).

JUVENILE GROWTH

Length–age data of juvenile *U. brasiliensis* were fitted to the Laird-Gompertz model: L (mm) $= 235\mathrm{e}^{-3.26\ \mathrm{e}^{-0.014\ \text{days}}}$, ($r = 0{\cdot}90$, $n = 52$). The mean daily growth rate

TABLE II. Posterior mean estimates (with 95% probability intervals; I_{Cr}) of von Bertalanffy parameters t_0 and K estimated by Bayesian fit for female and male of *Micropogonias furnieri*, *Urophycis brasiliensis* and *Macrodon atricauda*

Species	Author	Sex	L_∞ (mm)	Otolith scale	Posterior mean K (I_{Cr})	Posterior mean t_0 (I_{Cr})
Micropogonias furnieri	Haimovici & Ignácio (2005)	Female	700	Microstructure[a]	0·29 (0·28–0·31)	−0·077 (− 0.11; −0·05)
				Macrostructure[b]	0·27 (0·27–0·28)	−0·033 (− 0·12; −0·001)
	Cavole & Haimovici (2015)	Male	650	Microstructure	0·32 (0·30–0·35)	−0·071 (− 0.10; −0·04)
				Macrostructure	0·31 (0·29–0·32)	−0·089 (− 0·28; −0·003)
Urophycis brasiliensis	This study	Female	580	Microstructure	0·71 (0·65–0·75)	−0·009 (− 0·03; −0·001)
				Macrostructure*	0·18 (0·17–0.20)	−0·441 (− 0·84; −0·10)
		Male	380	Microstructure	1·19 (1·11–1·26)	−0·006 (− 0·02; −0·001)
				Macrostructure*	0·24 (0·21–0·28)	−1·937 (− 2·86; −1·032)
Macrodon atricauda	Cardoso & Haimovici (2011)	Female	430	Microstructure	0·47 (0·41–0·53)	−0·022 (− 0·08; −0.01)
				Macrostructure	0·53 (0·50–0·55)	−0·052 (− 0·16; −0·002)
	M. S. Almeida (unpubl. data)	Male	360	Microstructure	0·58 (0·50–0·66)	−0·023 (− 0·09; −0·001)
				Macrostructure	0·63 (0·59–0·66)	−0·049 (− 0·17; −0·001)

[a] Microstructure was at daily scale for *Micropogonias furnieri*, *Macrodon atricauda* and *Urophycis brasiliensis*.

[b] Macrostructure was at annual scale for *M. furnieri* and *M. atricauda*, and (*) at opaque band scale for *Urophycis brasiliensis*.

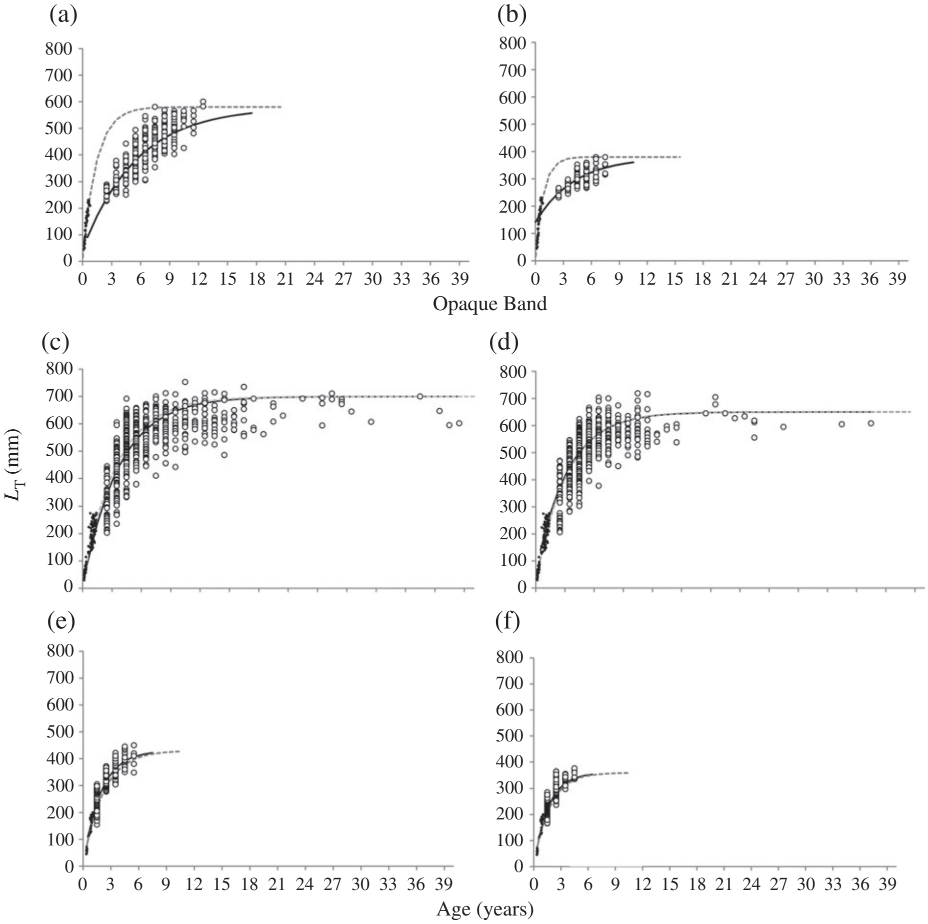

FIG. 7. Growth curves estimated from the microstructure (●, - - - - -) and the macrostructure (○, ——) and the von Bertalanffy growth coefficient K in adults (K_a) and juveniles (K_j) in: (a) female ($K_a = 0{\cdot}18$, $K_j = 0{\cdot}71$) and (b) male *Urophycis brasiliensis*($K_a = 0{\cdot}24$, $K_j = 1{\cdot}19$), (c) female ($K_a = 0{\cdot}27$, $K_j = 0{\cdot}29$) and (d) male *Micropogonias furnieri* ($K_a = 0{\cdot}31$, $K_j = 0{\cdot}32$), (e) female ($K_a = 0{\cdot}53$, $K_j = 0{\cdot}47$) and (f) male *Macrodon atricauda* ($K_a = 0{\cdot}63$, $K_j = 0{\cdot}58$), all captured on the southern Brazil continental shelf.

was 0·85 mm between 50 and 285 days of life, suggesting an approximately linear and fast growth for the *U. brasiliensis* juveniles [Fig. 6(d)]. The back-calculated birthdates were distributed throughout the year [Fig. 6(c)], matching the year-round spawning [Fig. 3(b), (c)].

DISCUSSION

Difficulty in the discrimination between annuli and false rings in Gadiformes is a common feature of their age estimation (Dery, 1988, Clay & Clay, 1991; Arneri &

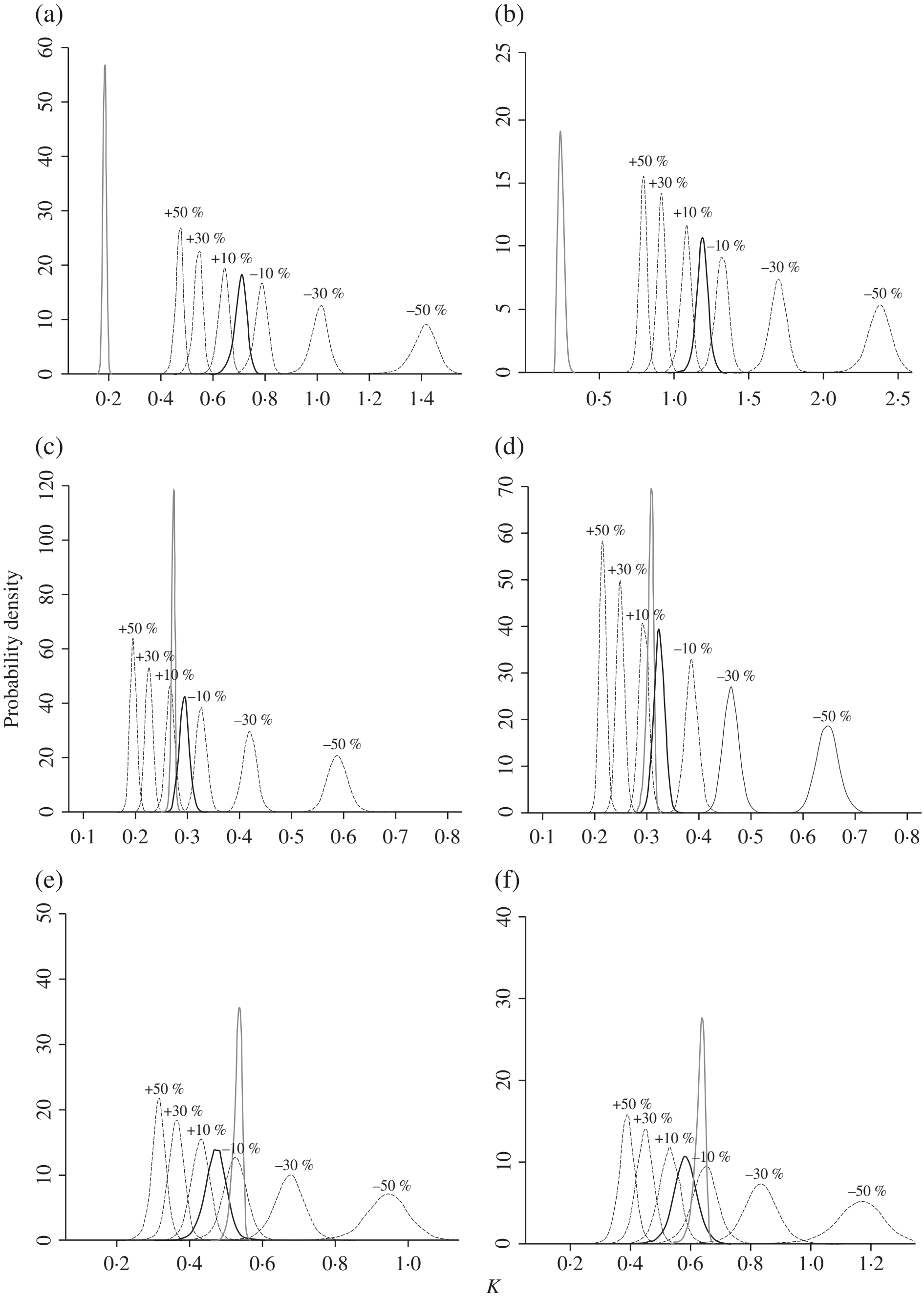

FIG. 8. Probability densities of growth coefficient K for the counts of daily rings (——) and opaque bands or annuli (——) in the otolith sections of three demersal species in southern Brazil: (a) female and (b) male *Urophycis brasiliensis*, (c) female and (d) male *Micropogonias furnieri* and (e) female and (f) male *Macrodon atricauda*. ------, The sensitivities of K estimates to errors of ±10, 30 and 50% in daily counting.

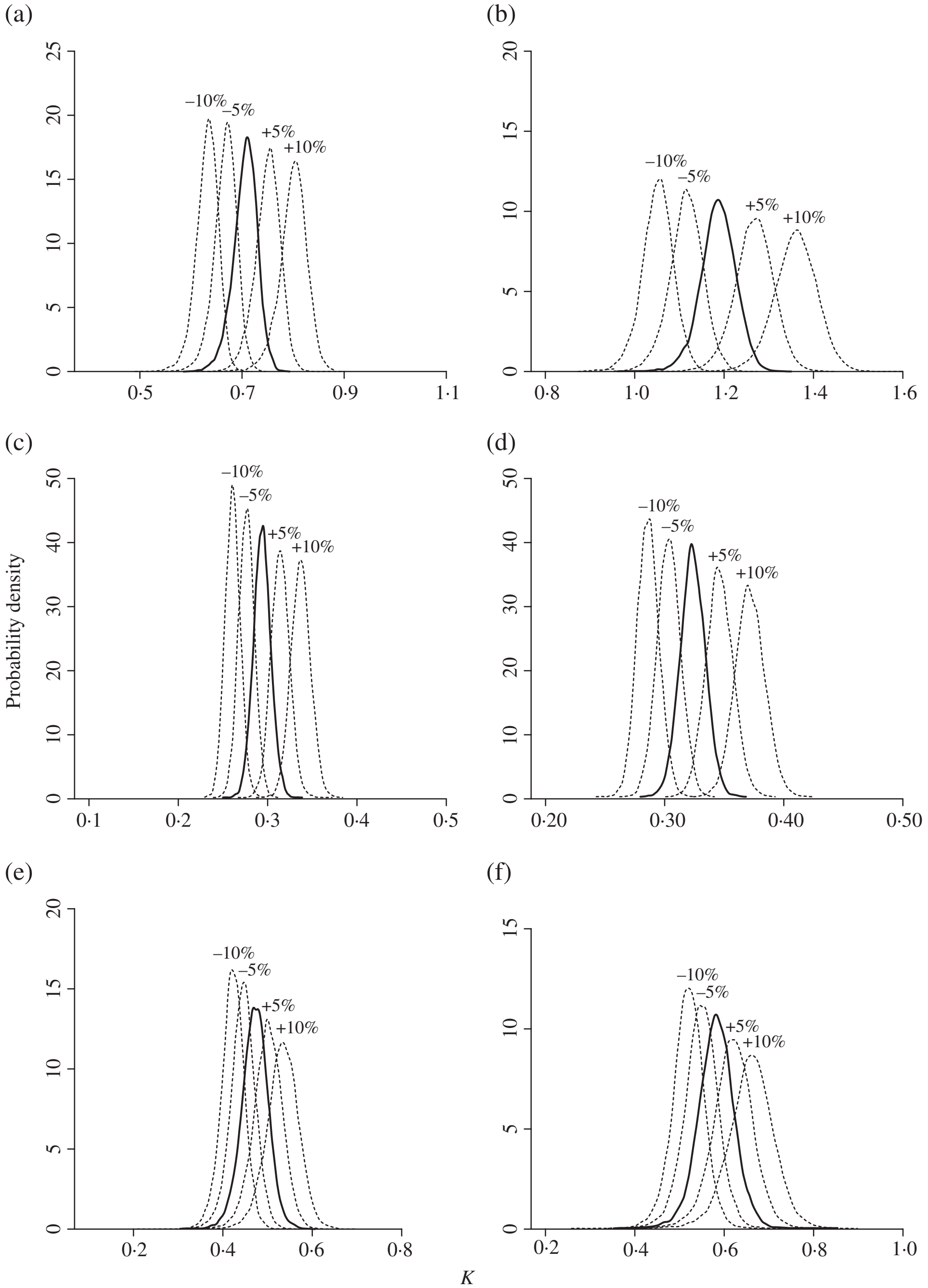

FIG. 9. Probability densities of the growth coefficient K calculated with fixed L_∞ for three demersal species in southern Brazil: (a) female and (b) male *Urophycis brasiliensis*, (c) female and (d) male *Micropogonias furnier* and (e) female and (f) male *Macrodon atricauda*. ------, The sensitivities of K estimations to errors of ±5 and 10% in assumption of the L_∞. ——, Fixed L_∞; ------, L_∞ with errors.

Morales-Nin, 2000) and has resulted in age overestimation and growth underestimation for several species in this order (Morales-Nin *et al.,* 1998; Kacher & Amara, 2005; De Pontual *et al.,* 2006; Piñeiro *et al.,* 2007, 2008; Mellon-Duval *et al.,* 2010). In *U. brasilienis* difficulty in discerning the annuli from false rings, hinders the ability to assess age with precision and accuracy. Although the edge type and marginal increment analyses had initially suggested an annual periodicity of the opaque bands, there were strong reasons to doubt this interpretation. Marginal-increment analysis is a difficult and questionable validation method that is widely overused (Campana, 2001) and has previously resulted in incorrect validation of annual periodicity in many species, especially for long-lived fishes (Campana, 1984; Campana *et al.,* 1990; Hyndes *et al.,* 1992). Based on these previous findings, we did not expect to have a robust result from this specific analysis. In addition, the number of opaque bands that would correspond to the length at first maturity in *U. brasiliensis* was very high: 4·5 for males and 6·0 for females, when compared with congeneric species (Table III). On the other hand, the microstructure interpretation suggested a fast-initial growth of the yearlings and an early age of first maturation, $A_{50\text{male}}$ (1·1–1·5 years) and $A_{50\text{female}}$ (1·6–1·8 years), as also found in other Phycidae (O'Brien *et al.,* 1993) (Table III).

The microstructure information (daily growth increments) and a feasible estimation of the asymptotic length (L_∞) were used to model the growth of *U. brasiliensis* across its entire life history. This model was validated by testing it on two other well-known species in the same region. The lack of correspondence between growth estimated from daily growth increments and adult opaque bands of *U. brasiliensis* contrasts with the strong correspondence between the VB curves of *M. atricauda* and *M. furnieri,* for which daily and annual increment deposition were both validated (Fig. 7). This supports the assumption that *U. brasiliensis* present several checks and probable false annuli.

The growth of juveniles inferred by the microstructure analysis showed a consistent pattern (Fig. 6), but the daily periodicity has not been directly validated. Indirect validation following the increment numbers of representative samples over known periods (Geffen, 1992) was also not possible for *U. brasiliensis* due to the lack of seasonality in the reproduction and the low abundance of juveniles in the landings. The deposition pattern observed is, however, like the one assumed as representing a daily formation by other authors (Fahay & Able, 1989; Lang *et al.,* 1996; Able & Fahay, 1998).

The estimated growth rate for *U. brasiliensis* juveniles (0·85 mm day^{-1}, 46–231 mm L_T) in southern Brazilian waters was lower than the rate for *U. tenuis* juveniles (1·01 mm day^{-1}, 28–187 mm L_T) on the coast of New England, U.S.A. (Lang *et al.,* 1996). This difference was expected, since *U. tenuis* attains larger sizes than *U. brasiliensis*. These rates are also within the range observed for other Gadiformes, as some species of hake (*e.g.* 0·71–1·11 day^{-1}; Woodbury *et al.,* 1995; Kacher & Amara, 2005). The back-calculated length of the TTB for *U. brasiliensis* (47 mm) was close to the back-calculated length of settlement for *U. chuss* (35–40 mm) (Able & Fahay, 1998), with both species reaching maximum lengths around 600 mm. Despite the unknown origin of these marks, the TTB observed in all the present samples ranged between 1 and 2 months, a period commonly associated with the transition between the pelagic and demersal phases of the life cycle.

The presence of maturing females was observed in samples from all seasons and indicate that *U. brasiliensis* spawns throughout the year in the region [Fig. 3(a)–(c)]. The lack of seasonality in reproduction is not typical of subtropical marine fish from

TABLE III. Size (L50) and age (A50) at first maturity, size and age ranges of the samples and number of individuals (n) for each fish species of the genus Urophycis

Species	Area	Study year	Sex	L_{50} (cm)	Size-range L (cm)	A_{50} (years)	Age-range (years)	n
Urophycis tenuis[a]	Gulf of Maine-Georges Bank	1987–1989	Male	32·7	20·3–52·0	1·4	1·0–7·0	346
Urophycis tenuis[a]	Gulf of Maine-Georges Bank	1987–1990	Female	35·1	13·6–68·7	1·4	1·0–18·0	455
Urophycis chuss[a]	Gulf of Maine-Northern Georges Bank	1985–1989	Male	22·2	16·8–30·7	1·4	1·0–12·0	595
Urophycis chuss[a]	Gulf of Maine-Northern Georges Bank	1985–1990	Female	26·9	21·0–36·0	1·8	1·0–12·0	667
Urophycis chuss[a]	Southern Georges Bank-Middle Atlantic	1985–1991	Male	23·8	17·8–33·2	1·7	1·0–12·0	753
Urophycis chuss[a]	Southern Georges Bank-Middle Atlantic	1985–1992	Female	25·1	19·3–34·1	1·8	1·0–10·0	1020
Urophycis brasilienis[b]	Southern Brazil	2012–2013	Male	29·7	15·1–37·9	1·2	–	123
Urophycis brasilienis[b]	Southern Brazil	2012–2013	Female	40·2	13·3–58·2	1·6	–	384

[a] O'Brien *et al.* (1993).

[b] This study.

southern Brazil. In this region, most bony fishes of commercial interest spawn multiple times over several months between spring and autumn, like *Umbrina canosai* Berg 1895 (Haimovici & Cousin, 1989), *M. furnieri* (Haimovici & Ignácio, 2005), *Trichiurus lepturus* L. 1758 (Martins & Haimovici, 1997), *M. atricauda* (Cardoso & Haimovici, 2014), *Paralichthys orbignyanus* (Valenciennes 1839) (Silveira *et al.,* 1995) and the congeneric *Urophycis mystacea* Miranda Ribeiro 1903 found in the upper slope (Haimovici *et al.,* 2008).

The lack of a reproductive seasonality in *U. brasiliensis* may have contributed to the inconsistent pattern of opaque and translucent band deposition in their otoliths. Energy expenditure during reproduction and migration slows the growth of fish and these events have been previously associated with the appearance of several checks in the otolith. For example, Harris (1985) validated the origin of many fine rings in the juveniles of Australian bass *Macquaria novemaculeata* (Steindachner 1866), which he termed 'migration checks' once they were formed during upstream recruitment migration from breeding grounds. The protracted spawning season of *U. brasiliensis* may have contributed to the appearance of several checks in their otoliths, particularly after the second year of life [Fig. 1(b)].

To deal with uncertainties in the age estimates of adult *U. brasiliensis* based on counts of alternate opaque and translucent bands, an alternative approach based on the daily growth increments was used. The strong correspondence between the VB K parameter calculated with validated ages at daily and annual scales for two co-occurring species (*M. furnieri* and *M. atricauda*) support this approach based on the microstructure interpretation and a fixed L_∞. The usefulness of this methodology however, requires accurate age estimates (daily growth increments) and an educated guess of the $L_{\infty.}$ The sensitivity analysis showed that for reliable estimations of the K growth parameter, the model does not support errors higher than 10% in the readings of daily increments and errors higher than 5% on the L_∞ assumption. This approach has the potential to elucidate the growth trajectories in those species with frequent false annuli and checks and can also serve as an age validation process for those species where microstructure and macrostructure information are currently available.

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