



Age validation and growth of the small-tooth flounder *Pseudorhombus jenynsii* from estuaries and coastal waters in south-western Australia

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Abstract

The small-tooth flounder *Pseudorhombus jenynsii* (Paralichthyidae) is a common, yet relatively unstudied, flatfish occurring in estuaries and coastal waters around Australia. This study determined the age and growth of *P. jenynsii* using 1,228 specimens collected between 2004 and 2013 as bycatch by seine netting in estuaries and trawling in coastal waters in south-western Australia. Opaque zones in 1,043 sectioned otoliths were validated as forming annually by otolith edge analysis, with the first opaque zone becoming delineated after the first spring when fish are ~ 12 months old. Female *P. jenynsii* ranged in total length from 79 to 406 mm and males from 96 to 354 mm. The maximum observed age for females and males was 5 and 4 years, respectively. While the von Bertalanffy growth functions (VBGF) fitted to the lengths at age differed significantly between the sexes, this difference in the length at age was < 5% between the ages of 1 and 3 years (where most of the data lay). The VBGF parameters for both sexes combined are L_{∞} : 381 mm, k : 0.53 year⁻¹, t_0 : -0.15 years. The large variation in size-at-age of *P. jenynsii* is indicative of a presumed extended 5–6 months spring and summer spawning period. The presence of small (< 200 mm) and young (< 2 years old) *P. jenynsii* in estuaries and shallow coastal waters confirms the use of these environments as nursery habitats.

Keywords Paralichthyidae · Otoliths · Nursery · Temperate

Introduction

Globally, estuaries and inshore marine waters, particularly coastal embayments, are important environments for many fish species, especially during their juvenile phase of life (Blaber and Blaber 1980; Claridge et al. 1986; Potter et al. 1990; Maes et al. 2005). The characteristics of these environments such as their shallow depths, diverse habitat types (seagrass, mangroves, reefs) and greater productivity, make these waters attractive to juvenile fishes, affording them protection against larger piscivores (Kennish 1990; Potter and

Hyndes 1999) and promoting faster growth (Able and Fahay 2010; Veale et al. 2016). Of those fishes that use estuaries and inshore coastal waters, flatfishes (flounders, halibuts, soles) make a significant contribution to the ecology of the fish communities in these environments (Young and Potter 2003; França et al. 2011; Vieser et al. 2018), so much so that for some estuaries these species are used as indicators of the health of the system (e.g. Amara et al. 2009) or of environmental change (e.g. Martinho et al. 2010). In addition, the importance of these habitats to flatfishes, and indeed other groups of fishes, is the fact that the fisheries for their adults, which depend on the recruitment from nursery habitats, contribute over 1–2 million tonnes to world fisheries production (Nelson et al. 2016; Cheung and Oyinlola 2018).

The small-tooth flounder *Pseudorhombus jenynsii* (Bleeker 1985) is medium-sized flatfish, attaining a maximum total length of 550 mm, which is found across northern Australia extending southwards on both sides of the continent to the south-western and south-eastern corners (Hutchins and Swainston 1986; Gomon et al. 2008). This species is typically associated with sandy and muddy substrates in water depths from only a few metres up to 70 m (Gomon

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et al. 2008). In south-western Australia, this species is a consistent member of both estuarine and marine inshore fish communities (Ayvazian and Hyndes 1995; Valesini et al. 1997; Hoeksema et al. 2009; Potter et al. 2016) and, as such, has been characterised as a “marine-estuarine-opportunist”, thus regularly entering estuaries, but also using coastal waters as alternative nursery areas (Potter et al. 2015). This species is only taken in small numbers by recreational line fishers (Ryan et al. 2019) and is a bycatch species taken by commercial scallop and prawn trawlers (P. Coulson, personal observation).

The genus *Pseudorhombus* contains ~20 species, which are largely restricted to the Indo-Pacific region and contributes to the family Paralichthyidae which contains a further 13 genera and ~90 species (Gomon et al. 2008; Nelson et al. 2016). There has been no published information on the age and growth of any species in this genus apart from a preliminary study on *P. jenynsii* from estuaries in New South Wales for which non-validated ages of up to 4 years were estimated from counts of opaque zones in sectioned otoliths (McKinley et al. 2012). Some aspects of the reproductive biology of the congener *Pseudorhombus arsius* in Indian coastal waters have been studied (Ramanathan and Natarajan 1979; Menezes 1980). Previous age and growth studies of other paralichthyids, largely those in the genus *Paralichthys*, demonstrate that there is a wide range in the maximum size and age attained by these species. They also typically display sexually dimorphic growth, with females attaining a larger size at age in comparison to the males (e.g. Fischer and Thompson 2004; Amezcua et al. 2006; Barnes et al. 2015).

Despite the regular occurrence of *P. jenynsii* in estuarine and coastal fish community surveys in south-western Australia, there have been no biological studies undertaken to understand the age and growth characteristics of this species. Thus, the specific aims of this study were to (1) validate whether growth (opaque) zones in sectioned otoliths are formed annually and can thus be used for age determination purposes, (2) determine the ages of fish in estuarine, coastal and offshore waters, and (3) investigate whether, like other paralichthyids, females and males exhibit divergent growth.

Materials and methods

Sampling localities and methods. Samples of *Pseudorhombus jenynsii* were collected from the Swan-Canning (31°53'S, 115°59'E) and Peel-Harvey (32°36'S, 115°38'E) estuaries, coastal waters of Cockburn Sound (32°10'S, 115°43'E) and Comet Bay (32°29'S, 115°43'E) and from offshore waters to the north of Rottnest Island (31°58'S, 115°33'E) between 2004 and 2013 (Fig. 1). It should be noted that these five sites are all in close proximity, ~50 km, to one another. *Pseudorhombus jenynsii* in the

Swan-Canning and Peel-Harvey estuaries were caught by researchers using 21.5 m-, 40.5 m- or 102.5 m-long seine nets (Table 1) that had 3 mm, 9 mm or 16 mm mesh in the bunt, respectively, and swept an area of approximately 116 m², 274 m² or 1,600 m², respectively (Kanandjembo et al. 2001; Potter et al. 2016; Coulson et al. 2017). Samples from Comet Bay and Rottnest Island were caught as bycatch by commercial scallop and prawn fishers using otter trawl nets, which were 1 m high, ~15 m wide and had 51 mm mesh in the wings and 45 mm mesh in the cod end (Marshall et al. 2007). Those *P. jenynsii* collected from Cockburn Sound were caught as bycatch during blue swimmer crab *Portunus armatus* recruitment surveys conducted by the Western Australian Department of Primary Industries and Regional Development between April and October 2008 using a trawl net with the same dimensions as those given above.

The total length (TL) and total weight (TW) of each *P. jenynsii* specimen were recorded to the nearest 1 mm and 0.1 g, respectively. The sex of the majority of fish > 75 mm was determined macroscopically. Analysis of covariance (ANCOVA), employing TW as the dependent variable and TL as the independent variable and sex as the fixed factor, was employed to determine if the relationships between TW and TL were significantly different between sexes (Coulson et al. 2005, 2010). Length and age frequency distributions for each sex were constructed to investigate whether there were any differences in the size and age composition of *P. jenynsii* collected from the five localities and or differences between sexes in the same locality.

Ageing and validation. The sagittal otoliths were removed, dried and stored in labelled seed envelopes. In those months between February and May in Comet Bay, when large numbers of *P. jenynsii* < 150 mm were caught, the otoliths of only a subsample of individuals below this length were removed for ageing purposes. In addition, some of those *P. jenynsii* > 250 mm (i.e. the minimum legal length) were retained and sold by the fisher, and thus only the lengths were recorded for these individuals ($n = 19$). Thus, of the 1230 fish measured in this study, the otoliths of only 1,024 *P. jenynsii* were prepared for ageing purposes.

One otolith from each pair was mounted in epoxy resin and cut transversely through the primordium into ~250 µm sections using an Isomet Buehler low-speed saw with a diamond-etched blade. The sections were mounted onto glass microscope slides using DePX mounting adhesive and a coverslip placed over the sections. Each otolith was photographed at 40X magnification using transmitted light and an Olympus DP70 camera mounted on an Olympus BX51 compound microscope. All sectioned otolith images were analysed using the software Leica Application Suite (LAS v. 3.1), enabling individual opaque zones to be marked and counted (Fig. 2).

Fig. 1 Map of the south-western coast of Australia and inset showing the estuaries and embayments in which *Pseudorhombus jenynsii* was sampled

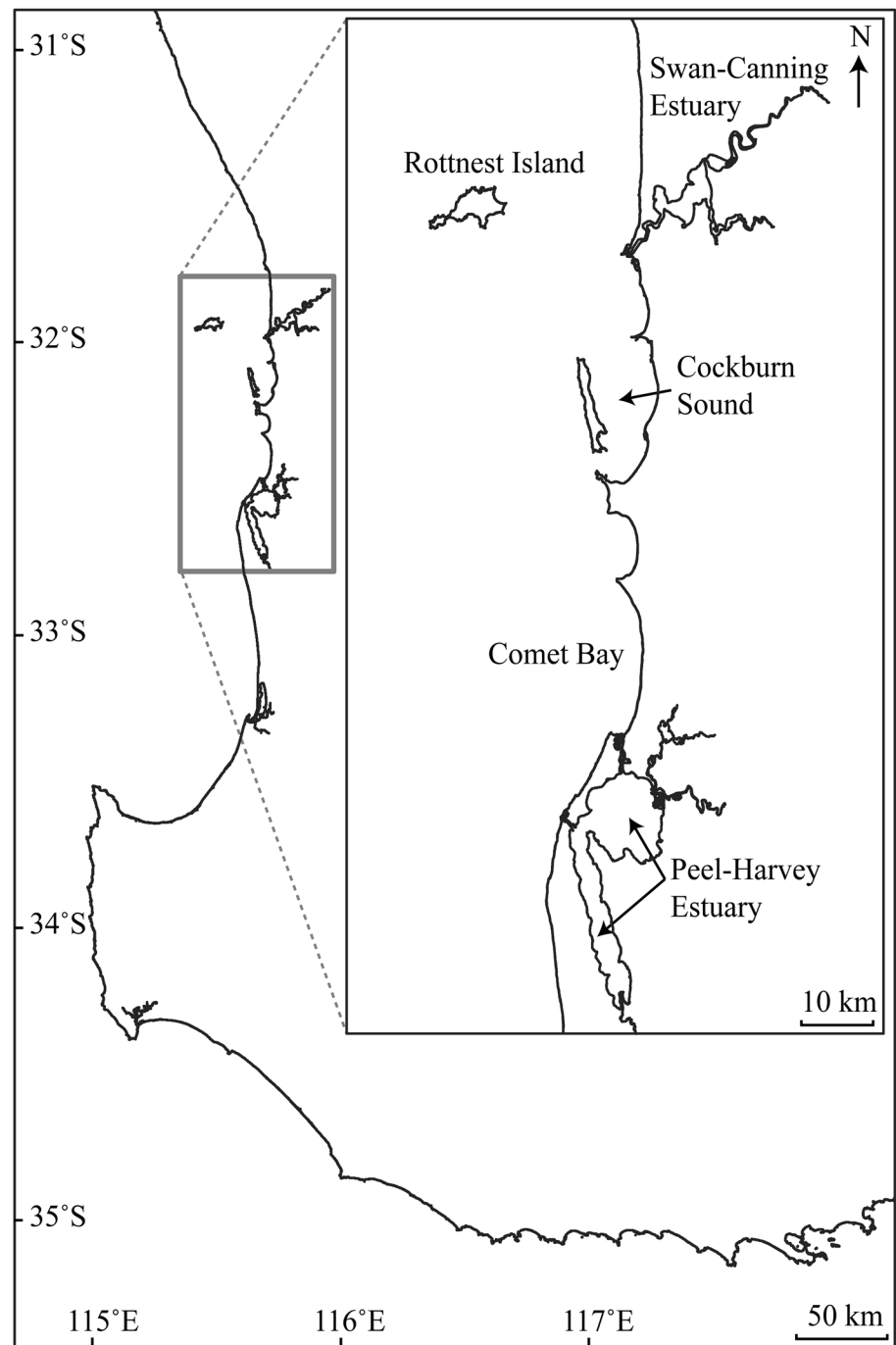
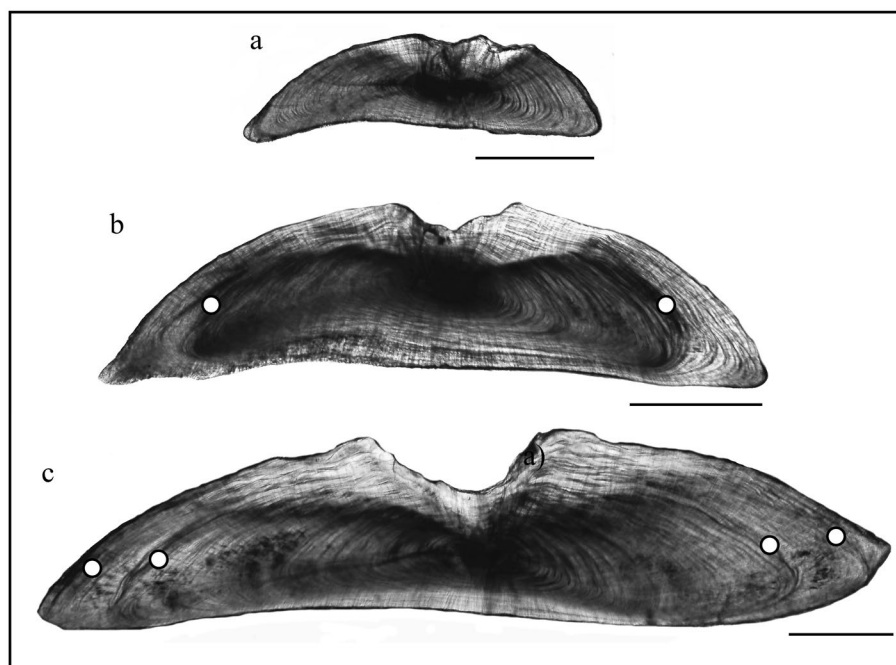


Table 1 The localities, sampling dates, collection methods and water depths (m) where *Pseudorhombus jenynsii* were collected in south-western Australia

Localities	Sampling dates	Method	Depth	<i>n</i>
Swan-Canning Estuary	November 2004–April 2006	21.5, 40.5 m seine nets	< 5	70
Peel-Harvey Estuary	November 2005–April 2010	21.5, 102.5 m seine nets	< 5	48
Cockburn Sound	April, June–August, and October 2008	Research trawl	10–20	153
Comet Bay	November 2009–May 2010	Commercial trawl	10–20	908
Rottneest Island	February 2013	Commercial trawl	30–40	49

n = sample size

Fig. 2 The sectioned otoliths of *Pseudorhombus jenynsii* with (a) zero, (b) one and (c) two opaque zones (denoted by white circles), respectively. All scale bars = 500 μ m



The margin of each sectioned otolith was categorised as either narrow translucent (i.e. < 50% width of preceding translucent zone), wide translucent (i.e. > 50% width of preceding translucent zone) or opaque (Wakefield et al. 2010). The proportions of each category of the otolith margin were pooled for each calendar month and used to determine the timing of opaque and translucent zone deposition in otoliths.

The number of opaque zones in each sectioned otolith were counted once by the first author (PGC), and then the otoliths of a subsample of 200 fish, across the full age range, were re-read by the same reader. The level of precision between repeat counts was assessed by calculating the coefficient of variation (CV),

$$CV_j = 100\% \times \frac{\sqrt{\sum_{i=1}^R (X_{ij} - X_j)^2 / (R - 1)}}{X_j},$$

where, for the j th fish, CV_j is the age precision estimate; X_{ij} is the i th age determination; X_j is the mean age estimate; and R is the number of times each fish is aged (Chang 1982; Campana 2001).

Growth. Each *P. jenynsii* specimen was assigned an age, based on the number of opaque zones in its otolith, the time of formation of those zones, its date of capture and an assigned birth date of October 1st (approximated to be the start of the spawning period) and the time of year when the single or outermost of those zones become delineated. The birth date was chosen as spring–summer and is the typical spawning period of many fish species in the south-west region of Australia (e.g. Hyndes and

Potter 1996, 1997; Hyndes et al. 1996; Coulson et al. 2017). Von Bertalanffy growth functions (VBGF) were fitted to the TLs at the age of female and male of *P. jenynsii*. The von Bertalanffy growth equation has the form: $L_t = L_\infty (1 - \exp(-k(t - t_0)))$, where L_t is the total length (mm) at age t (years), L_∞ is the asymptotic total length (mm), k is the growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which fish would have zero length (von Bertalanffy 1938). VBGFs were fitted to the length at age of fish using a non-linear least squares model in R (R Core Team 2013). Those small (< 100 mm) individuals whose sex could not be determined macroscopically were alternately, and randomly, assigned to the datasets for females and males.

A likelihood-ratio test (Cerrato 1990) was used to compare the VBGFs of females and males. The test statistic was determined as twice the difference between the log-likelihoods obtained by fitting a common growth curve to the TLs at age for both sexes collectively and by fitting separate growth curves to the TLs at age for each sex. The hypothesis that the growth of the two groups could be appropriately represented by a single growth curve was rejected at the $\alpha = 0.05$ level of significance if the above test statistic exceeded $\chi_a^2(q)$, where q is the difference between the numbers of parameters in the two approaches, i.e. 3 (Cerrato 1990). The log-likelihood, λ , for each curve, ignoring constants, was calculated as $\lambda = (-n/2)\ln(ss/n)$, where n is the sample size, ss refers to the sum of the squared residuals between the observed and expected TLs at age and \ln represents the natural logarithm.

Results

Description of growth zones in otoliths and validation of the ageing method. The otoliths of small (55–89 mm) *Pseudorhombus jenynsii* caught in January and February possessed a discrete opaque nucleus surrounded by a narrow translucent zone. In subsequent austral autumn months, the translucent zone surrounding the nucleus in the otoliths of fish ranging from 98 to 178 mm in March and 84 to 211 mm in May increased in width. By austral spring (October and November), the otoliths of fish of this cohort, which ranged in size from 132 to 221 mm, possessed a wide translucent zone that was surrounded by the first opaque zone, which was broad and diffuse. As the proposed birth date for *P. jenynsii* is October 1, the very small individuals caught in the initial January and February samples were ~3 and 4 months old, respectively, while those caught between the following March and May were ~5–7 months old and those caught in October and November were ~12 and 13 months old, respectively. Therefore, the first opaque zone becomes delineated in the otoliths of *P. jenynsii* during the first spring of life when fish are ~10–11 months old.

The majority (i.e. $\geq 70\%$) of otoliths with no opaque zones of *P. jenynsii* collected between January and March possessed a narrow translucent (NT) margin, while the remainder possessed a wide translucent (WT) margin (Fig. 3). In April and May, the otoliths of all *P. jenynsii* with no opaque zones possessed a WT margin, with such otoliths also being observed, but in lower frequencies, up until December. The proportion of *P. jenynsii* otoliths with ≥ 1 opaque zone, with either NT, WT or opaque margins, followed a similar trend. Thus, the otoliths with NT margins were observed between October and March, and while otoliths with WT were also present in some of these months, they were most prevalent between February and June (Fig. 3). The margins of otoliths with ≥ 1 opaque zones with opaque margins were observed in August, October and November. Thus, a single opaque zone is typically deposited during the cooler winter (June–August) and spring (September–November) months and a translucent zone deposited during the warmer summer (December–February) and autumn (March–May) months. As such, the counts of opaque zones can be used to accurately age this species. The resultant CV of 1.6% demonstrates an acceptable level of reproducibility of the counts of the number of opaque zones in the otoliths of *P. jenynsii*, falling below the reference level of 5% for correspondence recommended by Campana (2001).

Length and age composition and length–weight relationship. Overall in the sample, female *P. jenynsii* ranged in length from 79 to 406 mm, while males ranged from 96

to 354 mm, and unsexed ranged from 55 to 328 mm. Males were more abundant in those length classes between 125 and 300 mm, with females being more abundant in the largest size classes, i.e. ≥ 300 mm (Fig. 4a). While the ages of female and male *P. jenynsii* ranged from 0 to 5 years and 0 to 4 years, respectively, those individuals in the 0+ and 1+ age class were the most abundant, comprising 42% and 40% in females and 40% and 47% in males collected (Fig. 4b). The 2+ age classes constituted 13% and 10% of all females and males, respectively. There was no evidence to suggest that females or males were more abundant in any of the three youngest age classes, for which there were the greatest sample sizes. Females and males were both found in the 3+ and 4+ age classes, while a single female constituted the 5+ age class (Fig. 4b).

In the Swan-Canning Estuary, the majority of *P. jenynsii* ranged in length from 50 to 150 mm, with some larger individuals present, including the largest fish (406 mm) recorded in this study. In this estuary, most individuals were in the 0+ and 1+ age classes, with a few 2-, 3- and 4-year-olds present (Fig. 5). In the Peel-Harvey Estuary, there were two length cohorts present, one ranging from 50 to 200 mm and another from 225 to 325 mm. The former group consisted solely of 0+ fish, while the larger group comprised 2+, 3+ and 4+ fish. The length structures of *P. jenynsii* in Cockburn Sound and Comet Bay were almost identical, with a modal length class of 125–149 mm, which was slightly larger than that for the estuaries, i.e. 75–100 mm (Fig. 5). The ages of *P. jenynsii* from the two coastal embayments, like those from the estuaries, were dominated by individuals in the 0+ age class. Comet Bay possessed a greater proportion of individuals in the 1+, 2+ and 3+ age classes than Cockburn Sound (Fig. 5). Unlike the two estuaries and two coastal embayments, there were no *P. jenynsii* in the 0+ or 1+ age classes in samples from the deeper, offshore waters near Rottnest Island. In these waters, individuals were larger, with lengths ranging from 256 to 389 mm, and were between 2 and 4 years old (Fig. 5).

Monthly samples of *P. jenynsii* collected from Comet Bay and Cockburn Sound show distinct cohorts of fish throughout most of the year. In January, the 1+ cohort dominated the sample and formed a distinct modal length range between 175 and 224 mm, which increased to between 225 and 274 mm in February and 250 and 299 mm in March (Fig. 6). However, in March, the 0+ cohort was first observed and formed a strong modal length range between 100 and 174 mm. The modal length range of the 0+ cohort increased to 125–199 mm in April and remained largely at this length range in May and June–August. In October, the length range of the 1+ cohort, was still 125–199 mm, but increased to 150–224 mm in November and December (Fig. 6).

ANCOVA showed that the relationships between TW and TL did not differ significantly between female and

Fig. 3 Monthly percentage contribution of three classifications describing the outer margin of the sectioned otoliths of *Pseudorhombus jenynsii* with different numbers of opaque zones. Dark grey bars, opaque margin; white bars, thin translucent margin (50% of the width of the preceding translucent zone); grey bars, wide translucent margin (50% of the width of the preceding translucent zone). Sample sizes are given above each month. On the x-axis on this figure, closed rectangles refer to austral summer (December–February) and winter (June–August) months and the open rectangles to autumn (March–May) and spring (September–November) months

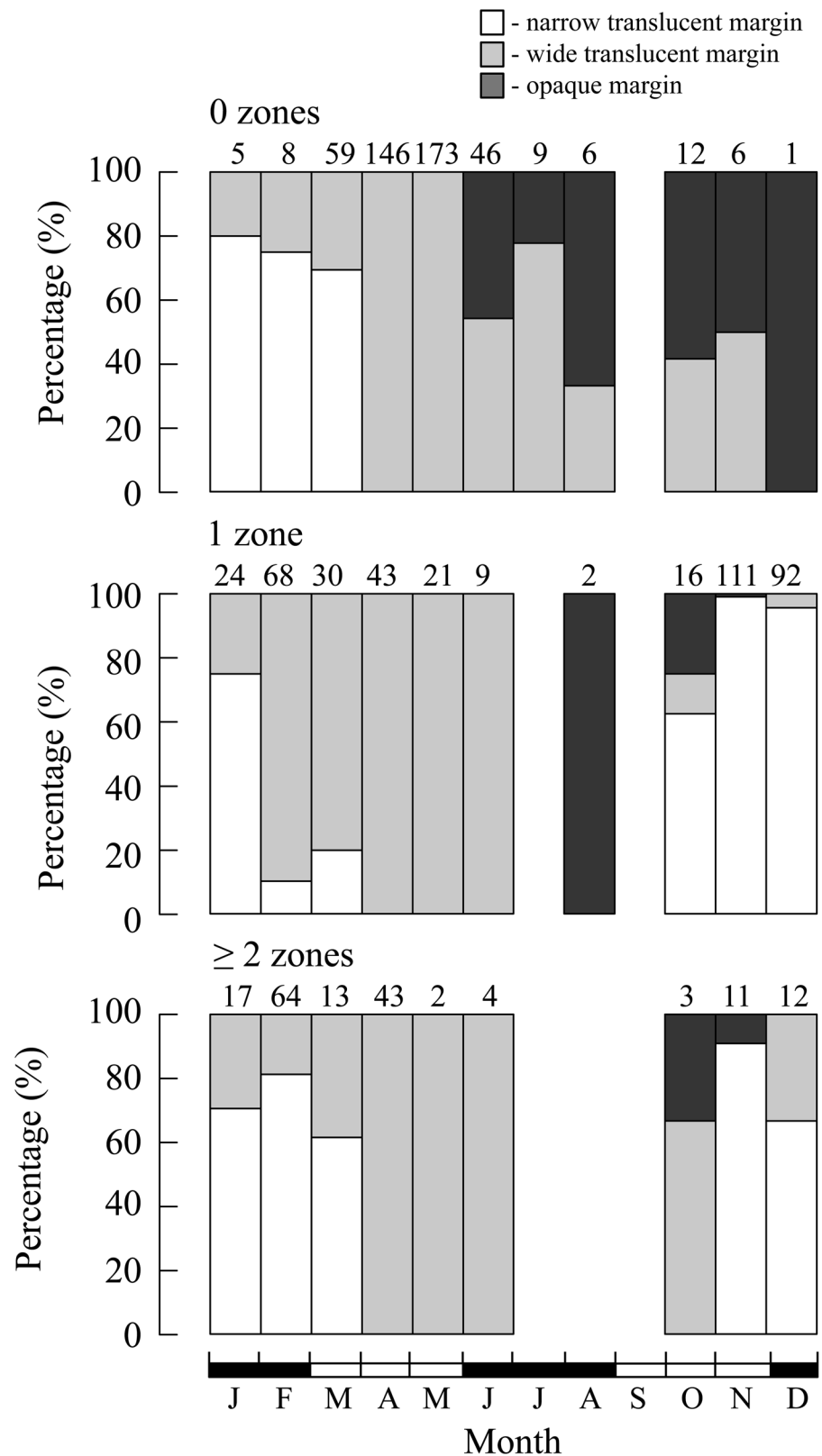


Fig. 4 (a) Length and (b) age frequency distributions for unsexed individuals, female and male *Pseudorhombus jenynsii* caught in estuaries, coastal embayments and offshore waters in south-western Australia. n = sample size

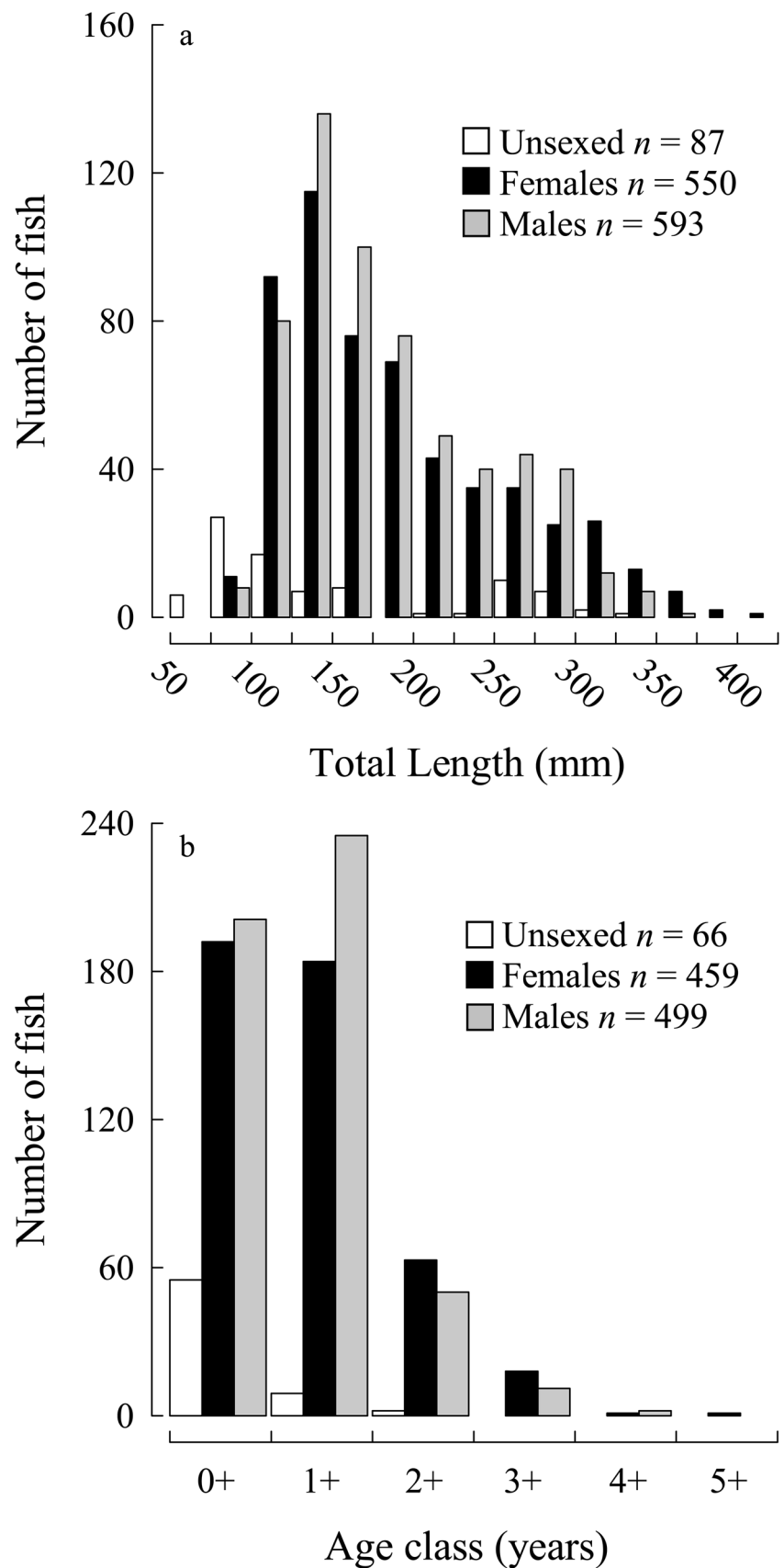


Fig. 5 Length–age frequency distributions for *Pseudorhombus jenynsii* caught from each of the five sampling localities in south-western Australia

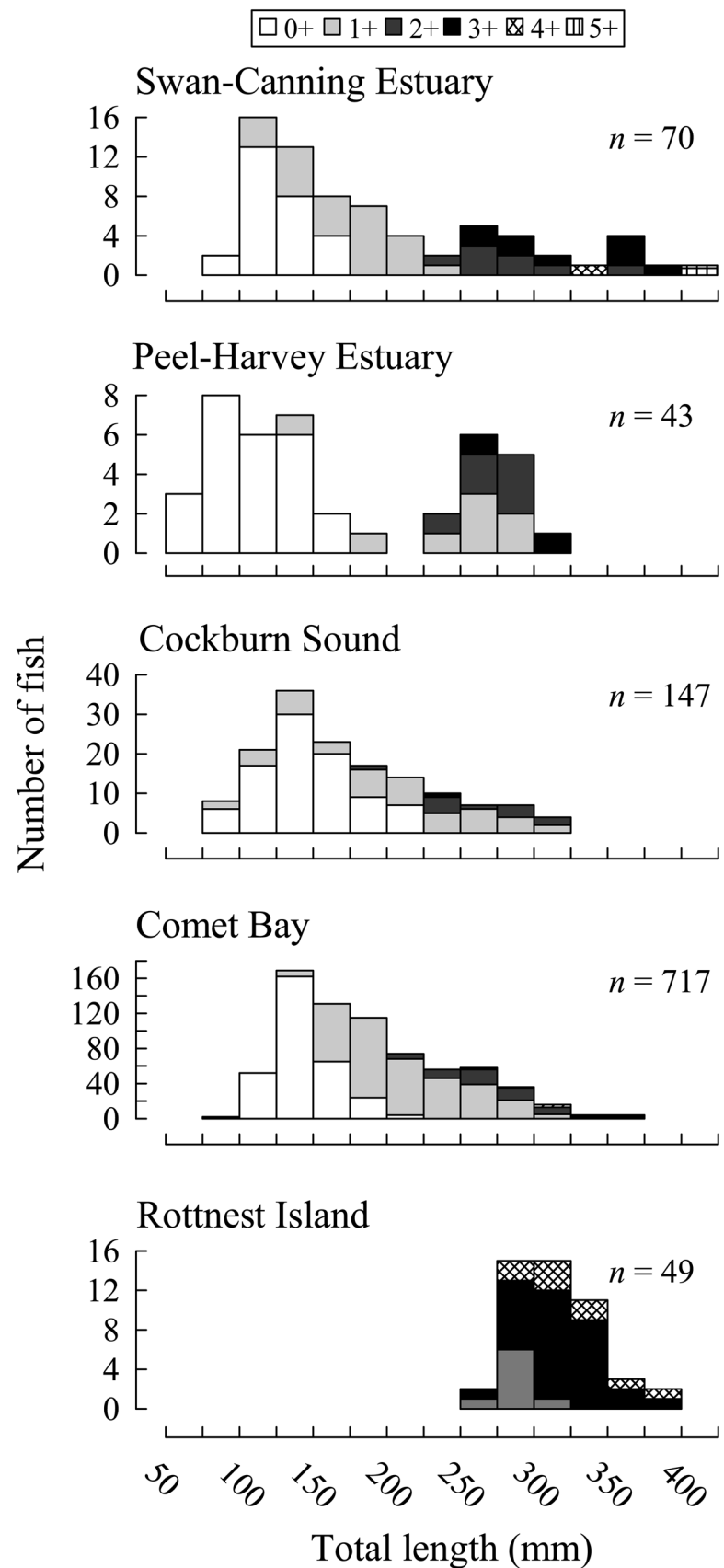


Fig. 6 Monthly age-length frequency distributions of *Pseudorhombus jenynsii* from Comet Bay and Cockburn Sound combined. Note that as the number of specimens caught between June and August were very small, they have been combined

male *P. jenynsii* ($P > 0.05$). The linear relationship between the natural logarithms of TW and TL for *P. jenynsii* is: $\ln TW = 3.01(\ln TL) - 11.56$ ($r^2 = 0.98$, $P < 0.001$, $n = 1201$).

Growth. Although the likelihood ratio test demonstrated that the VBGFs for the two sexes were significantly different ($P = 0.04$), this difference was very small. In addition, the percentage difference between the lengths at age, as determined from the two separate VBGFs, was always $< 5\%$ at those ages between 0 and 3 years where most of the data occurred (Fig. 7). As these differences were small and growth curves will almost inevitably tend to differ significantly when based on large sample sizes (Cerrato, 1990), the differences were assumed, as in comparable cases (Coulson et al. 2005, 2019), to be of little or no biological significance. Thus, the lengths at age for females and males were combined to derive a single growth curve for this species (Table 2; Fig. 7). Although the von Bertalanffy growth curve intersected the length at age data, the low r^2 value of 0.71 (Table 2) reflects the considerable variation in the length at age of female and male *P. jenynsii*.

Discussion

Ageing. The changes in the monthly percentage contributions of the different edge types on sectioned otoliths of *Pseudorhombus jenynsii*, irrespective of the number of opaque zones in those otoliths, demonstrate that a single opaque zone is formed annually in the otoliths of this species. It was thus valid to use the number of growth zones in sectioned otoliths to age this species. In the otoliths of *P. jenynsii*, the newly formed opaque zone becomes delineated from the edge from October to March (i.e. from spring through summer to early autumn). It is during this time that the temperature of the shallow waters in estuaries and along the coast is particularly warm (see Veale et al. 2015, 2016), thus promoting increased somatic (body) growth of *P. jenynsii*, which is translated into the commencement of the growth of the translucent zone in their otoliths. This is consistent with the otolith growth, as indicated by trends in marginal increment analysis, of other fish species in estuaries and coastal waters in this region (e.g. Hyndes and Potter 1997; Veale et al. 2015; Coulson et al. 2017). This also coincides with the monthly edge-type frequencies for the section otoliths from *Rhombosolea tapirina* in another temperate Australian estuary (Earl et al. 2014) and the monthly changes in the occurrences of opaque bands on the outer margin of the

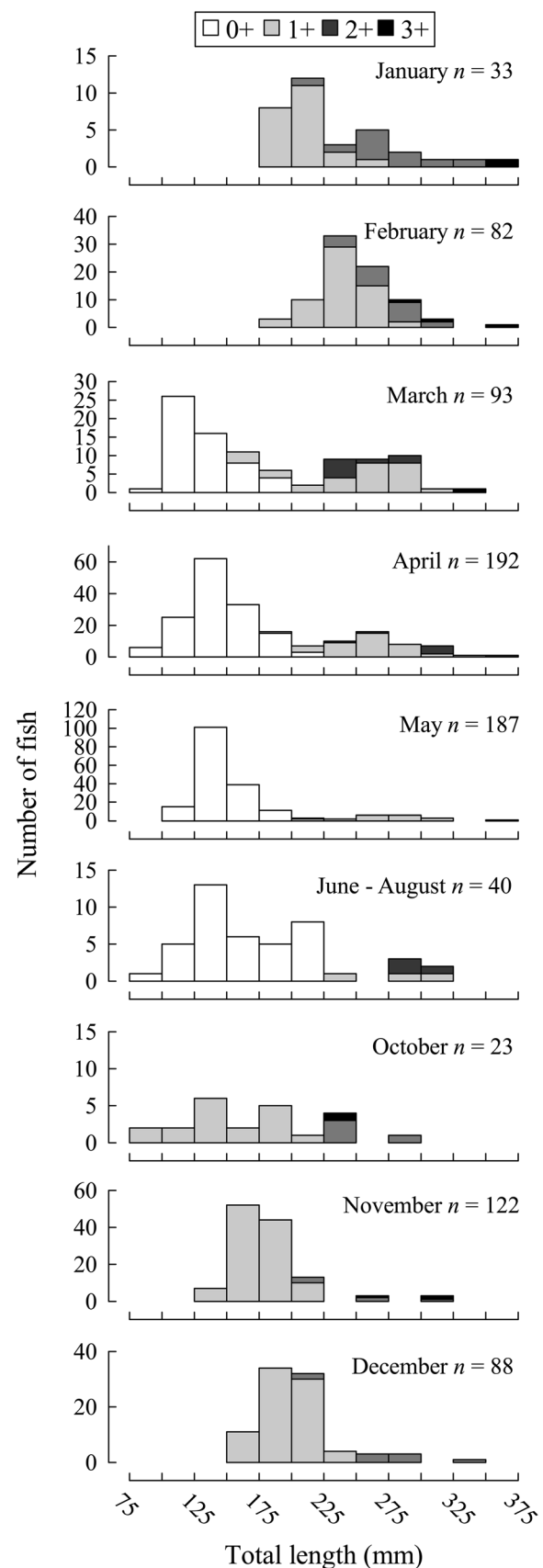


Fig. 7 von Bertalanffy growth curve (solid black line), and its 95% confidence limits (dotted black lines), fitted to the total length at age of female (grey circles) and male (white circles) *Pseudorhombus jenynsii*. For comparative purposes, the von Bertalanffy growth curves for females (solid grey line) and males (dashed grey line) are also shown. n = sample sizes

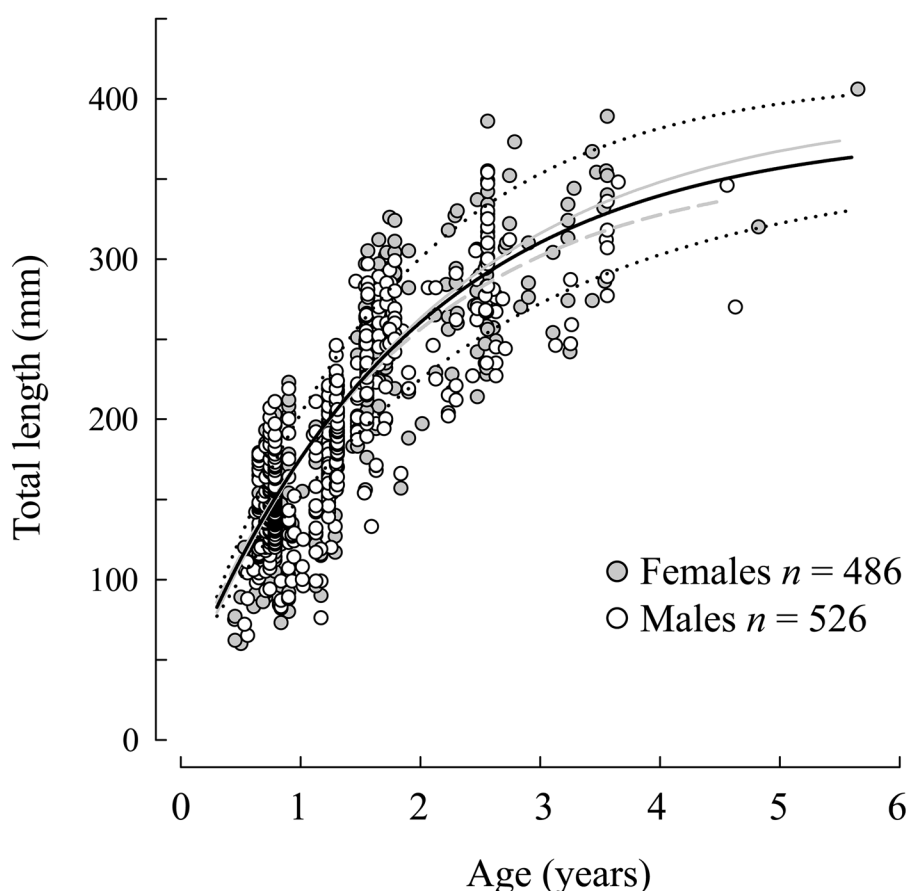


Table 2 The von Bertalanffy growth curve parameters L_{∞} , k and t_0 , and their upper and lower 95% confidence limits, for *Pseudorhombus jenynsii* derived from the total lengths at age of females and males combined and also determined for females and males separately

		L_{∞}	k	t_0	r^2	n
Sexes combined	Estimate	381	0.53	- 0.15	0.71	1012
	Upper	415	0.62	- 0.09		
	Lower	357	0.44	- 0.25		
Females	Estimate	396	0.51	- 0.13	0.73	486
	Upper	447	0.63	- 0.04		
	Lower	361	0.39	- 0.26		
Males	Estimate	362	0.57	- 0.17	0.70	526
	Upper	411	0.70	- 0.07		
	Lower	332	0.42	- 0.30		

r^2 = coefficient of determination

n = sample size

otoliths of *Paralichthys olivaceus* in temperate waters off Japan (Yoneda et al. 2007).

The temperate waters from which *P. jenynsii* were collected for this study are at the southern extent of the distribution for this species in Western Australia, with most of the geographical range of this species extending through subtropical and tropical waters of Northern Australia (Hutchins and Swainston 1986; Gomon et al. 2008). Comprehensive age and growth studies of tropical flatfishes

based on ages derived from counts of growth zones in otoliths, and which cover the entire life cycle of a species, are scarce, and can be attributed, in part, to the difficulty in reading their otoliths (Fowler 2009). In addition, some authors have attempted to use length frequency data to estimate growth (e.g. Martinez-Munoz and Ortega-Salas 2010; Gilanshahi et al. 2012). Although the analysis of trends in monthly length frequency data using ELEFAN and MULTIFAN is a valuable approach for determining

growth in fishes, this method should be restricted to fast-growing, short-lived species, in which discrete length modes for individual age groups can be easily identified (e.g. Morales-Nin and Aldebert 1997; Bellido et al. 2000; Campana 2001).

The short life span of *P. jenynsii* determined in the current study, noting that our sample number of larger fish was small, appears to be a characteristic of subtropical/tropical flatfishes, such as *Cyclopsetta querna*, *Citharichthys arenaceus*, and *Citharichthys spilopterus* (Joyeux et al. 1995; Amezcua et al. 2006). Moreover, while there are exceptions (e.g. Reichert 1998; Sutton et al. 2010; Earl et al. 2014), most large-bodied temperate flatfishes have a life span exceeding 10 years, with some species such as the Atlantic halibut *Hippoglossus hippoglossus* attaining a maximum age of 50 years (Armsworthy and Campana 2010). Furthermore, *Colistium nudipinnis* and *Colistium guntheri* from a temperate estuary, which attain a similar size (i.e. 400–500 mm) to that of *P. jenynsii*, attain maximum ages of 16 and 21 years, respectively (Stevens et al. 2005). Even small temperate flatfish species, such as *Arnoglossus laterna* and *Lepidorhombus boschii*, have been found to live for up to 13 years (Gibson and Ezzi 1980; Cengiz et al. 2013). The maximum age of 5 years recorded in this study might reflect the fact that *P. jenynsii* is a tropical species, which inhabits temperate waters.

Growth. A comparison of the VBGFs derived from the lengths at age of female and male *P. jenynsii* demonstrated that, although there was a significant difference, with females attaining a larger size at age than males, the difference was small. This lack of difference between the growth of female and male *P. jenynsii* is also seen in other small (< 500 mm) and short-lived (< 5 years) flatfishes such as *C. querna*, *Bothus podas* and *R. tapirina* (Amezcua et al. 2006; Morato et al. 2007; Earl et al. 2014). Despite a few exceptions, i.e. *Paralichthys lethostigma* whose females attain maximum lengths and ages of 764 and 414 mm and 8 and 4 years (Fischer and Thompson 2004), it appears that flatfish species that attain larger sizes and greater maximum ages exhibit sexually dimorphic growth. For example, the females of *P. olivaceus*, *Paralichthys californicus* and *H. hippoglossus*, which all grow to a significantly larger size than the males, all attain maximum sizes > 800 mm and maximum ages > 20 years (Jákupsstovu and Haug 1988; Atsuchi et al. 2004; Barnes et al. 2015). In these large, long-lived species, earlier maturation and a reduction in the surplus energy acquisition, due to reduced feeding, above a certain size in males are understood to contribute to sexually dimorphic growth (Rijnsdorp and Ibelings 1989). In addition, males receive a depreciating benefit from reproductive investment with increasing size, in comparison to females (Mollet 2010; Rijnsdorp et al. 2015). Thus, as *P. jenynsii* and *C. querna*, *B. podas* and *R. tapirina* only grow to a small size and live for

a limited number of years, there is little future benefit to the males of these species in reducing growth.

The length at age of individuals of *P. jenynsii* was highly variable, with the 0+ and 1+ cohorts ranging in length from 60 to 223 mm and 76 to 326 mm, respectively. This large variability in size-at-age is also observed in other flatfishes including *Limanda ferruginea*, *B. podas*, *P. olivaceus* and *P. lethostigma* (Dwyer et al. 2003; Atsuchi et al. 2004; Morato et al. 2007; Yoneda et al. 2007). Although information on the time and duration of spawning of *P. jenynsii* is not conclusive, it does suggest that spawning occurs over an extended period from over the warmer months (P. Coulson, unpublished data). This is also consistent with several other estuarine and inshore fish species in south-western Australia that spawn for an extended period during this time of year (e.g. Hyndes and Potter 1997; Hesp and Potter 2003; Veale et al. 2015; Coulson et al. 2017). The extended spawning period of *P. jenynsii* could potentially result in an age difference of up to five months for individuals in the same cohort. In addition, individuals spawned at different times during the spawning period will experience very different conditions at the beginning of their lives, which will have a compounding effect of their later growth. For example, individuals “born” at the beginning of the spawning period will experience the entire summer and autumn, thus experiencing the warmest water temperatures promoting rapid growth prior to their first winter. In contrast, those “born” towards the end of the spawning period will only experience one or two months of warmer water before entering their first winter.

Use of estuaries and nearshore marine waters by *Pseudorhombus jenynsii*. The length–age frequencies for *P. jenynsii* from the Swan-Canning and Peel-Harvey Estuaries demonstrate that this species utilises these environments primarily during the first two years of life, when they range in size typically from ~ 50 to 250 mm. The young age and small size confirm that this species uses estuaries primarily as a nursery area, similar to other flatfish species (Norcross et al. 1995; Cabral et al. 2007; Nãñez-James et al. 2009). *Pseudorhombus jenynsii*, however, are typically found in their lower reaches of estuaries in south-western Australia (Loneragan et al. 1989; Young and Potter 2003), where environmental conditions for much of the year are marine in nature. The length and age data for *P. jenynsii* from this study confirms the assignment of this species to the marine estuarine-opportunist (MEO) guild, defined by species that regularly enter estuaries, particularly as juveniles, but also use coastal marine waters as alternative nursery areas (Potter et al. 2015).

The presence of large numbers of small, young *P. jenynsii* in Comet Bay and Cockburn Sound indicates that this species also utilises marine embayments as nursery areas. This concurs with the presence of numerous *P. jenynsii* in marine embayments elsewhere in Australia (Weng 1990;

Travers and Potter 2002) as well as with the use of embayments as nurseries by flatfish in other regions (e.g. Trimoreau et al. 2013; Hurst 2016). Marine embayments are recognised as nursery habitats for many marine fish species as their characteristics, i.e. shallow water and greater food and habitat resources, offer very similar benefits to juveniles as do the attributes of estuaries (Lenanton 1982; Bennett 1989; Lugendo et al. 2005). Thus, as *P. jenynsii* is a marine species, its use of estuaries in south-western Australia is opportunistic, rather than dependent, as suggested by its assignment to the MEO guild by Potter et al. (2015).

Conclusions. This study has demonstrated that the growth (opaque) zones in otoliths of *P. jenynsii* are formed annually and can be used for ageing this species. The relatively small maximum size and low maximum age of *P. jenynsii* negate any future benefit to males in reducing their growth, as is seen in other larger and long-lived flatfish species that display sexually dimorphic growth patterns. The size and age structures of *P. jenynsii* in estuaries, coastal embayments and offshore waters confirm the use of the first two as juvenile nursery areas with evidence of offshore movement with increasing size and age. Future studies on the reproductive biology of this species would help elucidate whether the offshore movement is also related to spawning.

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