

Biological characteristics of three co-occurring species of armorhead from different genera vary markedly from previous results for the Pentacerotidae

P. G. COULSON*, N. G. HALL AND I. C. POTTER

Centre for Fish and Fisheries Research, School of Veterinary and Life Sciences, Murdoch University, 90 South Street, Murdoch, WA 6150, Australia

(Received 2 November 2015, Accepted 28 April 2016)

Biological characteristics of *Pentaceropsis recurvirostris*, *Paristiopertus gallipavo* and *Parazanclostius hutchinsi* were determined from commercial gillnet samples from temperate south-western Australian coastal waters. Growth zones in otoliths, with more than a few such zones, were readily detectable only after the otoliths had been sectioned. Visual analyses and modelling of the trends in marginal increments on sectioned otoliths demonstrate that these opaque zones are formed annually. Maximum ages of 55, 36 and 49 years, derived for *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, respectively, reflect relatively low mortalities. These longevitys greatly exceed those estimated, using otoliths, for *Pentaceros wheeleri* and *Pentaceros richardsoni*, which belong to the other pentacerotid subfamily. These differences may be due to the counts of 'daily' growth zones in sectioned otoliths of *P. wheeleri* not representing the complete age range of that species and the zones detected in whole otoliths of *P. richardsoni* not constituting the complete range of annually-formed zones. *Pentaceropsis recurvirostris*, *P. gallipavo* and *P. hutchinsi* recruited into the fishery in the sampling area as 2–3 year-old fishes. *Pentaceropsis recurvirostris* and *P. hutchinsi* exhibited little or no subsequent growth throughout the remainder of their protracted life, whereas, *P. gallipavo* continued to grow for *c.* 5 years and then underwent little further growth. Spawning of *P. recurvirostris* and *P. hutchinsi* peaked in the austral winter and autumn, respectively, but in the austral spring and summer with *P. gallipavo*, which is more typical of temperate species. Although the females of *P. gallipavo* and *P. hutchinsi* were mature, this did not apply to a few *P. recurvirostris*, some of which were >20 years old, implying that any given female of this species does not always spawn every year. Ovarian mass greatly exceeded testis mass, indicative of pair spawning, which is consistent with field observations. In contrast to *P. recurvirostris* and *P. hutchinsi*, the sex ratio was heavily biased towards males and the spawning period longer in *P. gallipavo*, suggesting that selection pressures for spawning success were greater for this latter species.

© 2016 The Fisheries Society of the British Isles

Key words: age validation; growth; longevity; maturity; natural mortality; spawning period.

INTRODUCTION

The Pentacerotidae (armorheads or boarfishes) are distributed in the Indo-Pacific Ocean and south-western Atlantic Ocean, where they are represented by 13 species allocated to seven genera and two subfamilies (Kim, 2012; Eschmeyer & Fricke, 2016). Seven species of pentacerotids are found along the southern Australian coast (Gomon *et al.*,

*Author to whom correspondence should be addressed. Tel.: +61 89360 2695; email: p.coulson@murdoch.edu.au

2008), among which the longsnout boarfish *Pentaceropsis recurvirostris* (Richardson 1845), the yellowspotted boarfish *Paristiopterus gallipavo* Whitley 1944 and the short boarfish *Parazanclistius hutchinsi* Hardy 1983 are the most abundant in south-western Australia, where the current study was undertaken.

The Pentacerotidae came into fishery prominence in the 1960s, when large, nocturnal aggregations of the pelagic armorhead *Pentaceros wheeleri* (Hardy 1983), previously assigned to *Pseudopentaceros*, were discovered over seamounts of the southern Emperor-northern Hawaiian Ridge (SE-NHR) by fishers of the Soviet Union. These seamounts are located at the transition zone between sub-Arctic and sub-tropical water masses in the central North Pacific Ocean (Borets, 1980; Boehlert & Sasaki, 1988; Somerton & Kikkawa, 1992). This led to the establishment of a trawl fishery for *P. wheeleri* by the Soviet Union in 1967 and 2 years later by the Japanese (Sasaki, 1986; Kiyota *et al.*, 2016). The intensity of fishing was so great that it led to a dramatic decline of this species on the Northwest and Southeast Hancock Seamounts, the south-eastern limits of the SE-NHR, and thus, in August 1986, to the introduction of a 6-year fishing moratorium in U.S. waters (Somerton & Kikkawa, 1992), which was subsequently extended to November 2010 (Anon., 2010). As the stock was still classified as overfished in the most recent assessment in 2015, the moratorium remains in effect (Anon., 2015).

In the southern hemisphere, the southern boarfish *Pentaceros richardsoni* Smith 1844, which, like *P. wheeleri*, was previously assigned to the genus *Pseudopentaceros*, is targeted sporadically over seamounts of the south-east Atlantic Ocean and south-west Indian Ocean (López-Abellán *et al.*, 2008). This species was, however, either the most or second most numerous species taken by Soviet Union fishing vessels during exploratory trawls over certain south-western Indian Ocean Ridge seamounts between 1972 and 1992 (Romanov, 2003). Although *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* are taken incidentally by the commercial gillnet fishery on the southern coast of Western Australia and thus make only a small contribution to that fishery (Braccini *et al.*, 2013), they are considered excellent table fish and command a high market price (Anon., 2008; Gomon *et al.*, 2008). *Paristiopterus gallipavo* is also taken by trawl fishing further east in the Great Australian Bight (Koopman *et al.*, 2008) and *P. recurvirostris* is taken incidentally off the south-eastern Australian coast by trawling and off Tasmania by commercial and recreational gillnetting (Anon., 2008; Lyle *et al.*, 2014).

Although the Pentacerotidae, which contains several and often abundant species, has a relatively wide distribution and contributes to certain fisheries, published details of the biological characteristics of this family are restricted to those for *P. wheeleri* and, to a lesser extent, *P. richardsoni*. This reflects the commercial importance of *P. wheeleri* and potential importance of *P. richardsoni*. In the central North Pacific Ocean, *P. wheeleri* spawns around seamounts in winter and its somatic growth occurs entirely or mainly during the resultant larval and juvenile pelagic phases (Humphreys, 2000; Yanagimoto & Humphreys, 2005). Recruitment to the adult demersal (seamount) habitat thus occurs at the size at which maturity is attained and after the majority of individuals have essentially ceased somatic growth, a combination of life-history traits rare among exclusively marine teleosts (Humphreys, 2000).

On the basis of what were regarded as daily growth increments and annually-formed 'check marks' in whole otoliths, Uchiyama & Sampaga (1990) considered that the individuals of *P. wheeleri* on the Southeast Hancock Seamounts (29° 47' N; 179° 04' E) in summer were mainly 1.5 years-old and, to a lesser extent, 2.5 years-old, but were up to

8 years-old in waters around the north-western Hawaiian Islands. Following sectioning of the otoliths of *P. wheeleri*, which provided greater resolution of the growth increments, Humphreys (2000) concluded that this species is recruited on to the Southeast Hancock Seamounts when they are 2 to 2+ years-old and thus, on average, older than estimated by Uchiyama & Sampaga (1990). During attempts to use growth zones to age the adults of *P. wheeleri*, it was recognized that such zones become very closely spaced towards the periphery of their otoliths and thus difficult to count (R. Humphreys pers. comm. in Somerton & Kikkawa, 1992). After estimating mortality from the declining abundance of two strong year classes, which were clearly identified in modal progressions of an index of fatness, Somerton & Kikkawa (1992) considered that *P. wheeleri* has a maximum age of 4–5 years.

Although López-Abellán *et al.* (2008) recognized that there were ‘important differences’ between the counts of ‘growth rings’ obtained using the otoliths of *P. richardsoni*, prior to and after sectioning, they discarded the sectioned otoliths owing to their ‘poor readability’. They thus employed backcalculation and the growth zones in whole otoliths to determine the growth of *P. richardsoni* from the individuals they sampled, which were large, ranging in length from 460 to 725 mm. The maximum age of this species was estimated to be 14 years (López-Abellán *et al.*, 2008). Although several studies have used the zones in scales or otoliths to age armorhead species (Uchiyama & Sampaga, 1990; Humphreys, 2000; López-Abellán *et al.*, 2008), none has used approaches, such as marginal increment trends and appropriate statistical analyses, to validate that the zones on those hard structures are typically formed annually throughout the full range of counts for those zones.

The present study has determined the length and age compositions, sex ratios, longevity, growth and spawning periods of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, and thus provides the first biological data for any species in these three genera of pentacerotid. The fishes were aged using the number of growth zones in sectioned otoliths, having first established that individual growth zones were invariably difficult to distinguish in whole otoliths when there were more than a few of those zones. The trends exhibited by marginal increments on sectioned otoliths with different numbers of opaque zones were statistically analysed to validate that a single growth zone is typically laid down annually in the otoliths of the above three boarfish species. The data on ageing, growth and reproduction for *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* were then collated and compared with those for *P. wheeleri* and *P. richardsoni*, thus representing four of the seven genera of the Pentacerotidae. This substantially expands the knowledge of the biological characteristics of this relatively neglected family and the extent of any variations in those characteristics, recognising that the first three species are placed in the same subfamily (Histiopterinae) and thus phylogenetically distinct from the latter two species, which belong to the Pentacerotinae, the other subfamily of pentacerotid (Kim, 2012).

MATERIALS AND METHODS

SAMPLES

Randomly collected samples of 761 *P. recurvirostris*, 523 *P. gallipavo* and 176 *P. hutchinsi* were provided as frozen filleted fish by a commercial fish processor at intervals between December 2006 and November 2012. The fishes had been caught by commercial fishers using demersal

gillnets (mesh range = 165–178 mm) at depths of 30–120 m in marine waters in the vicinity of Esperance at 33° 45' S; 121° 55' E on the south coast of Western Australia. *Pentaceropsis recurvirostris*, *P. gallipavo* and *P. hutchinsi* were caught over flat substrata in water depths of 30–120 m and often near reefs. These three species were represented in commercial catches taken in 11, 12 and 10 of the 12 calendar months of the year, respectively. A small *P. hutchinsi*, with a total length (L_T) of 84 mm, which could not be sexed and was caught by trawling during research along the south coast of Western Australia in 2007, was provided by the Western Australian Museum and used when calculating von Bertalanffy growth equations for both sexes of that species.

Gonads were provided with 614 of the *P. recurvirostris*, 428 of the *P. gallipavo* and 152 of the *P. hutchinsi*, among which the majority, i.e. 83, 86 and 65%, respectively, were fully intact. The L_T of each fish was measured to the nearest 1 mm and the mass of each intact gonad (M_G) recorded to the nearest 0.01 g.

AGE DETERMINATION, GROWTH AND NATURAL MORTALITY

The sagittal otoliths of each *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* were removed, cleaned, dried and stored in envelopes. The procedures for preparing and examining sectioned otoliths for ageing were described in detail in Coulson *et al.* (2009, 2010, 2012). In brief, one sagittal otolith from each fish was embedded in clear epoxy resin and cut transversely through its primordium into c. 0.3 mm sections employing a low-speed saw (www.buehler.com/equipment/sectioningequipment/precision-diamond-wafering-saws/isomet-low-speed-saw). Unenhanced digital images of each sectioned otolith were taken, using an Olympus DP70 12 megapixel camera mounted on an Olympus BX51 compound microscope (www.olympus.com) and employing transmitted light. The use of Leica Application Suite Version 3.6.0 (www.leica-microsystems.com/products/microscope-software/software-for-materials-sciences/details/product/leica-application-suite) enabled the opaque zones to be marked and readily counted and the distances required for marginal increment analysis to be measured with confidence. The otoliths of each species were examined in random order without knowledge of either when the sample was obtained or of the size of the fish. Counts of opaque zones and all measurements were made on the dorsal side of the otolith section, along the edge closest to the sulcus. All distances were measured to the nearest 0.01 mm along the same axis, perpendicular to the opaque zones.

Analyses of the trends exhibited throughout the year by the mean monthly marginal increments on sectioned otoliths, i.e. the distance between the outer edge of the single or outermost opaque zone and the otolith periphery, were used to validate that a single opaque zone is typically formed annually in the otoliths of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*. The marginal increment, i.e. the distance between the outer edge of the single or outermost opaque zone and the otolith periphery, was expressed as a proportion of the distance between the primordium and the outer edge of the single opaque zone, when one such zone was present, or as a proportion of the distance between the outer edges of the two outermost opaque zones when two or more such zones were present. The approach described by Okamura & Semba (2009) was applied to determine the periodicity of occurrence of otoliths of each species with marginal increments falling within the lower 30 percentile of values for each category of zone counts. For this, binomial models linked with von Mises circular distributions were fitted assuming (1) no cycle, (2) an annual cycle or (3) a biannual cycle. The models were then compared using the Akaike information criterion (AIC), where the model with the smallest value was selected as best representing the data (Burnham & Anderson, 2002).

The number of opaque zones in each sectioned otolith of each species was counted by the same person on three occasions, separated by intervals of at least 3 months. The third count was always the same as one of the first two counts and thus the count recorded. The level of precision between the three counts was assessed by calculating the c.v. (y):

$$y_j = 100 \left[\sqrt{(X_{ij} - X_j)^2 (R - 1) - 1} \right] X_j^{-1}$$
 where, for the j th fish, y_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). The resultant c.v. of 0.9, 0.3 and 0.3% for *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, respectively, demonstrate that the three

repeat counts on each otolith of each species showed a high degree of agreement, falling well below the reference level of 5% for correspondence recommended by Campana (2001). The number of opaque zones in each otolith in a random sub-sample of 100 otoliths of each species, which essentially encompasses the range of numbers recorded by the first reader, was counted independently by a second reader. The level of consistency between the counts of the second reader and the final counts recorded were assessed using the c.v. as described above. The resultant c.v. of 3.4 for *P. recurvirostris*, 4.8 for *P. gallipavo* and 2.3% for *P. hutchinsi* show an acceptable level of agreement between the counts of the two readers.

Each *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* was assigned an age, based on the number of opaque zones in sectioned otoliths and taking into account the date of capture of the fish, the 'average' birth date (approximate mid-point of the spawning period) of 1 July, 1 November and 1 May, respectively, and the time of year when the outermost opaque zone typically becomes delineated in the otoliths of those species. Growth was described by fitting von Bertalanffy growth curves to the L_T at age of the females and males of each species. The von Bertalanffy growth equation is $L_t = L_\infty \{1 - \exp[-k(t - t_0)]\}$, where L_t is the L_T (mm) at age t (years), L_∞ is the asymptotic length (mm) predicted by the equation, k is the growth coefficient (year^{-1}) and t_0 is the hypothetical age (years) at which fish would have zero length.

A likelihood-ratio test was used to compare the von Bertalanffy growth curves of the females and males of each species. The test statistic was determined as twice the difference between the log-likelihoods obtained by fitting separate growth curves to the L_T at age for each sex and by fitting a common growth curve to the L_T at age for females and males collectively (Cerrato, 1990). The hypothesis that the growth of the two groups could appropriately be represented by a single growth curve was rejected at the $\alpha = 0.05$ level of significance if the above test statistic exceeded $\chi^2(q)$, 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 $\lambda = (n/2) \ln(sn^{-1})$, where n is sample size, s refers to the sum of the squared residuals between the observed and expected lengths at age.

The natural mortality (M) of each sex of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* was determined using both the equation for fish in Hoenig (1983), i.e. $M = \exp(1.44) t_{\max}^{-0.984}$, and the refitted version of this equation calculated by Then *et al.* (2015), i.e. $M = 4.899 t_{\max}^{-0.916}$, in which t_{\max} is the maximum age of the respective sex of each species. Frequencies at age for each sex of each of these three lightly fished species were combined into 2 year intervals. Total mortality ($Z \text{ year}^{-1}$) was estimated as 50% of the biennial mortality, which was calculated from the resulting catch curve (Chapman & Robson, 1960) and employed the frequencies for the 2 yearly age classes following that at which the age frequency peaked (Smith *et al.*, 2012). Note that, as the frequencies for female *P. hutchinsi* exhibited peaks at both 8–9 and 22–23 years, the mortality estimate for this species was based on fish with ages >23 years.

MATURATION AND SPAWNING

The pair of gonads of each *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* was identified as either ovaries or testes and, when intact, weighed to the nearest 0.01 g. On the basis of their macroscopic characteristics, each ovary was allocated to one of the following five maturity stages adapted from the criteria used by Laevastu (1965). I/II, immature/resting; III, developing; IV, maturing; V/VI, prespawning/spawning; VII, spent. Ovaries at stages III–VII in each year were considered likely to become mature (stages III–V) or to have matured (VI–VII) during that year and thus, for convenience, are referred to as mature. The prevalence of the females of each species with gonads at each developmental stage in each month was determined. It was not possible to identify macroscopically the different stages in the development of the particularly small testes of these three species as the structure and colour of these gonads were lost during freezing.

The mean mass of the intact gonads of each *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* in each calendar month was plotted to elucidate the trends exhibited by this variable during the year. Note that it was not possible to calculate a gonado-somatic index, based on the mass of the whole fish, as each fish was provided as a filleted frame together with its gonads.

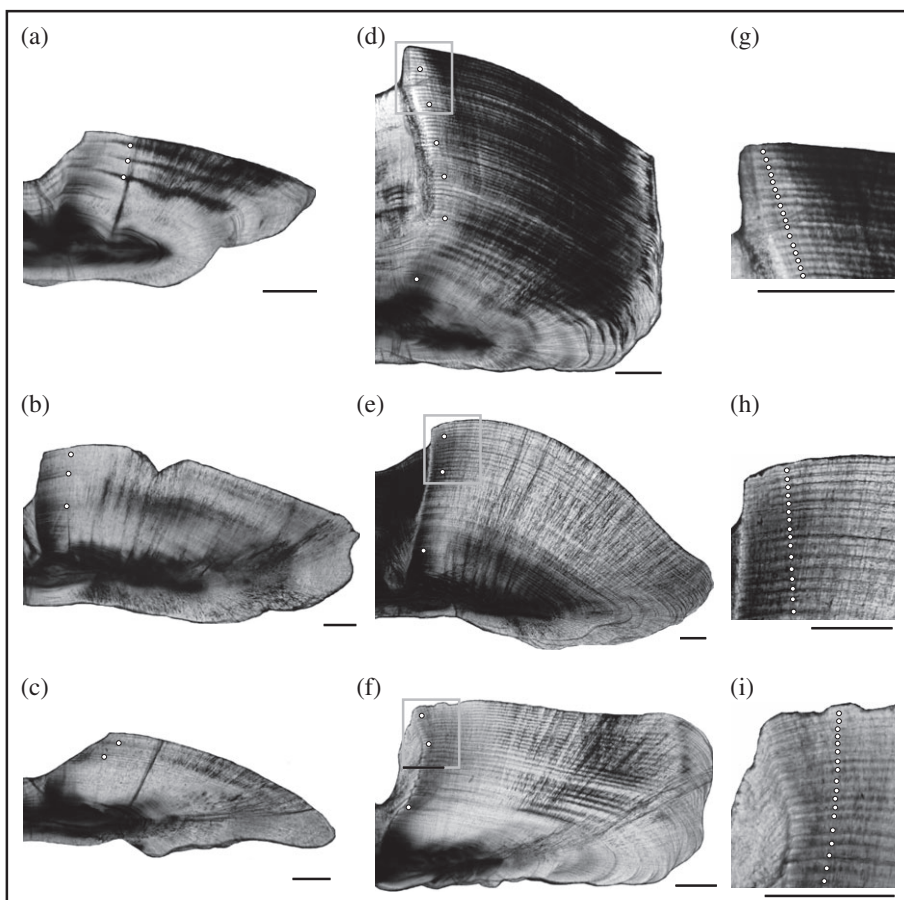


FIG. 1. The dorsal side of sectioned otoliths of (a), (d) and (g) *Pentaceropsis recurvirostris*, (b), (e) and (h) *Parisiapterus gallipavo* and (c), (f) and (i) *Parazanclostius hutchinsi* viewed using transmitted light. White dots identify each opaque zone in (a)–(c), the first and every tenth opaque zone in (d)–(f) and every opaque zone in the outer region of otoliths with larger numbers of growth zones (g)–(i). Note that (g)–(i) are high magnifications of the outer regions of (d)–(f) shown in boxes. Scale bars = 0.5 mm.

RESULTS

MARGINAL INCREMENT ANALYSES

Alternating opaque and translucent zones were clearly visible in sectioned otoliths of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* when viewed under transmitted light (Fig. 1). The mean monthly marginal increments on otoliths of *P. recurvirostris* with two to nine opaque zones rose progressively from 0.35 in February to a maximum of 0.75 in May and subsequently declined from 0.71 in July to 0.34 in November (Fig. 2). Although the mean monthly marginal increments on the otoliths of the species with 10–19 and ≥ 20 opaque zones followed essentially the same trend, they reached their maxima slightly later, *i.e.* between July and September, before declining to low levels in December. The mean monthly marginal increments on otoliths of *P. gallipavo* with

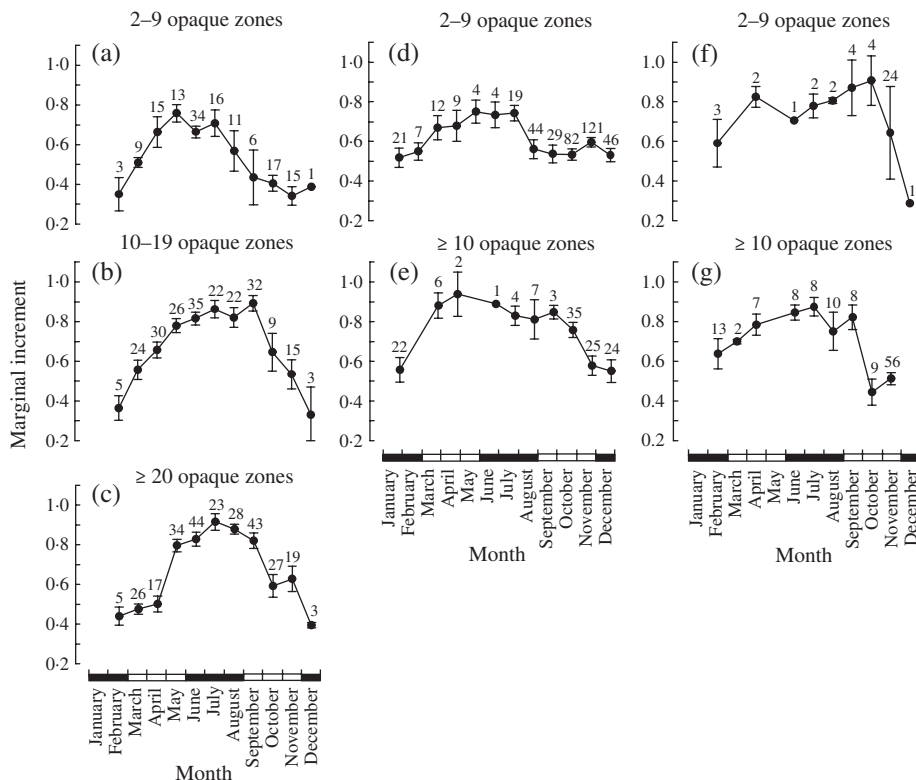


FIG. 2. Mean \pm S.E. monthly marginal increments on sectioned sagittal otoliths of (a)–(c) *Pentaceropterus recurvirostris*, (d), (e) *Paristiopertus gallipavo* and (f), (g) *Parazanclostius hutchinsi* with different numbers of opaque zones. Sample sizes are given above each mean. On the x-axis closed rectangles refer to summer and winter months and the open rectangles to autumn and spring months.

two to nine opaque zones followed a similar pattern to that of otoliths of *P. recurvirostris* with two to nine opaque zones, thus likewise peaking in May to July and then decreasing (Fig. 2). The mean marginal increments on the otoliths of *P. gallipavo* with ≥ 10 opaque zones rose conspicuously in March and declined markedly in November. Although the monthly sample sizes for *P. hutchinsi* were smaller than those for the other two species, the mean marginal increments of *P. hutchinsi* could still be seen to follow the same seasonal pattern (Fig. 2).

The progressive increase and then single pronounced decline, undergone during the year, by the mean monthly marginal increments on sectioned otoliths of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* with different numbers of opaque zones, imply that, irrespective of the number of opaque zones, a single opaque zone is typically formed annually in the otoliths of each of these species. This conclusion is substantiated by the results of circular distribution models (Okamura & Semba, 2009) and the concomitant AIC values (Table I). Thus, for all three species, the AIC was less for an annual cycle than no cycle or a biannual cycle for each of the two or three groups into which the otoliths had been pooled according to the number of their opaque zones (Table I). Furthermore, the difference between the lowest AIC and each of the other two AICs

TABLE I. Akaike information criterion values, for otoliths of *Pentaceropsis recurvirostris*, *Paristiopterus gallipavo* and *Parazanclistius hutchinsi* with marginal increments falling within the lower 30 percentile of values for each category of zone counts, determined by binomial circular distribution models fitted assuming no cycle, an annual cycle and a biannual cycle. Values in bold text are the smallest, for which the associated models were selected as best representing the data

		2–9 zones	10–19 zones	≥20 zones
<i>P. recurvirostris</i>	No cycle	191.8	252.2	405.7
	Annual cycle	151.0	206.0	310.2
	Biannual cycle	189.1	247.5	360.4
<i>P. gallipavo</i>		2–9 zones	≥10 zones	
	No cycle	491.3	162.1	
	Annual cycle	478.7	146.9	
<i>P. hutchinsi</i>	Biannual cycle	491.3	150.6	
		2–9 zones	≥10 zones	
	No cycle	59.8	157.6	
	Annual cycle	55.6	134.0	
	Biannual cycle	58.0	147.6	

for each group of otoliths was >2, the number required to identify definitively the best model in terms of the Kullback–Leibler distance (Burnham & Anderson, 2002). The number of opaque zones in sectioned otoliths can thus be used to age the individuals of each of the three boarfish species, after taking into account the age at which the first opaque zone becomes delineated.

DESCRIPTION OF GROWTH ZONES IN OTOLITHS

In sectioned otoliths from *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* examined under transmitted light, the central core is opaque throughout much of its width, but becomes translucent in some outer areas [Fig. 1(a)–(f)]. The first two or three opaque zones were detectable [Fig. 1(a)–(f)], with the definition of subsequent zones becoming more clearly defined [Fig. 1(g)–(i)].

The otoliths of the two smallest *P. recurvirostris* (366 and 368 mm L_T), caught in late winter and mid-spring, respectively, possessed a central opaque core and two opaque zones. The second opaque zone was separated from the edge of the otolith by a narrow translucent zone. This implies that the outermost opaque zone on the otoliths of *P. recurvirostris* had only recently become delineated from the otolith edge, which is consistent with the mean monthly marginal increment for the otoliths with two to nine opaque zones for this species declining between mid-winter and late spring (Fig. 2). As *P. recurvirostris* has been assigned a birthdate of 1 July (mid-winter), on the basis that this date represented the mid-point of the spawning period of this species, these two individuals were c. 25 and 27 months old, respectively.

The translucent zone surrounding the distinct central opaque core of the otoliths of the three smallest *P. gallipavo*, caught in early spring and mid-summer and measuring between 322 and 352 mm L_T , was surrounded by a translucent region bounded by an opaque zone. As this latter translucent zone was narrow, particularly in the otoliths of individuals from early spring, it is assumed to have recently become delineated from

the otolith edge. Since the birth date for *P. gallipavo* is 1 November (mid-spring), these three individuals were c. 11–14 months old.

The entire cross section of the otolith of the small (84 mm L_T) *P. hutchinsi*, which was caught in late spring, was opaque, and thus did not possess the translucent margin, which has typically just started to become delineated in the otoliths of older individuals at this time of year (see Fig. 2). The sectioned otolith of the next smallest *P. hutchinsi*, which was 240 mm L_T and also caught in late spring, possessed five opaque zones, the last of which was delineated from the edge of the otolith by a very narrow translucent zone. As the birth date for *P. hutchinsi* is 1 May (late autumn), the 84 mm individual was c. 6 months old and the 240 mm fish c. 5.5 years old, noting that some younger fish were longer than 240 mm.

LENGTH AND AGE COMPOSITIONS AND MORTALITY

The *P. recurvirostris* caught by commercial gillnetting ranged in L_T from 323 to 645 mm and in age from 2 to 55 years for females and from 350 to 553 mm and 2 to 43 years for males [Fig. 3(a), (b)]. The corresponding L_T and age ranges for *P. gallipavo* were 322–684 mm and 1–27 years for females and 348–700 mm and 2–36 years for males [Fig. 3(c), (d)], while, for *P. hutchinsi*, they were 253–378 mm and 2–49 years for females and 240–351 mm and 5–48 years for males [Fig. 3(e), (f)]. In addition, a *P. gallipavo*, which could not be sexed because its gonads were not provided with its filleted carcass, measured 737 mm [Fig. 4(e)]. The maximum L_T of 645, 737 and 378 mm, recorded during the present study for *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, exceed the 600, 500 and 340 mm given by Gomon *et al.* (2008) for these species, noting that Hutchins & Swainston (1986) recorded a far greater maximum L_T of 740 mm for *P. gallipavo*. There are no previous estimates of the ages of the individuals of any of these three species.

Although males outnumbered the females of *P. recurvirostris* in each of the three L_T classes between 350–374 and 400–424 mm, the reverse was the case with the subsequent eight 25 mm length classes between 425–449 mm and 550–574 mm and only females were present in the two L_T classes comprising the largest fish [Fig. 3(a)]. Females predominated in each age class of *P. recurvirostris*, producing an overall sex ratio of one female to 0.5 males ($\chi^2 = 71.8$, $P < 0.001$). Males outnumbered females in each L_T class of *P. gallipavo* for which sample size exceeded 10 [Fig. 3(c)], and likewise dominated each age class [Fig. 3(d)]. The sex ratio of *P. gallipavo* was one female to 1.4 males ($\chi^2 = 12.1$, $P < 0.001$). Females were the most numerous sex in each L_T class of *P. hutchinsi* between 250–274 and 325–349 mm, which represented the vast majority of the individuals of this species [Fig. 3(e)], and were numerically the dominant sex in each age class of this species [Fig. 3(f)]. The sex ratio for *P. hutchinsi* was one female to 0.5 males ($\chi^2 = 20.6$, $P < 0.001$).

Estimates of M , derived for females and males of *P. recurvirostris* and *P. hutchinsi* using the Hoenig_{NLS} model, as fitted by Then *et al.* (2015), were all $\leq 0.16 \text{ year}^{-1}$, and 0.24 and 0.18 year^{-1} for females and males of *P. gallipavo* (Table II). The estimate, derived using this modified equation, was greater for each sex of each species than that obtained using the Hoenig (1983) equation (Table II). The catch curve estimates for Z for each sex of each species correspond closely to those derived using the Then *et al.* (2015) equation and were thus likewise greater for *P. gallipavo* than for the other two species (Table II).

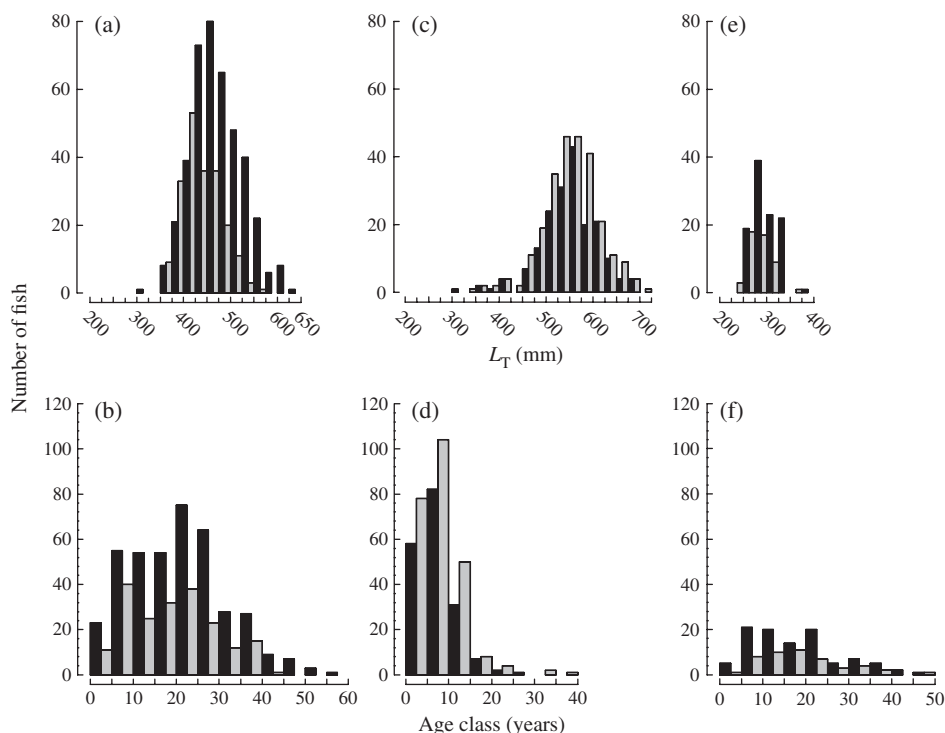


FIG. 3. (a), (c), (e) Total length (L_T) and (b), (d), (f) age-frequency distributions for female (■) and male (□) (a), (b) *Pentaceropsis recurvirostris*, (c), (d) *Paristiopterus gallipavo* and (e), (f) *Parazanclistius hutchinsi* [(a) females $n = 412$, males $n = 202$; (b) females $n = 400$, males $n = 197$; (c) females $n = 185$, males $n = 256$; (d) females $n = 181$, males $n = 247$; (e) females $n = 104$, males $n = 48$; (f) females $n = 99$, males $n = 47$].

GROWTH

The von Bertalanffy growth curve provided visually a good fit to the L_T at age of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* over the age ranges sampled [Fig. 4(a)–(g)]. The commercial gillnet samples did not contain, however, individuals of *P. recurvirostris* <323 mm, of *P. gallipavo* <322 mm and of *P. hutchinsi* <240 mm. The L_T of *P. recurvirostris* and *P. hutchinsi* exhibited little and no increase, respectively, across the wide age ranges represented in the samples of those species caught during this study, noting that the number of small and younger fish was low.

The von Bertalanffy growth curves for the females and males of *P. recurvirostris* were significantly different ($\chi^2 = 121.9$, d.f. = 3, $P < 0.001$) (Table III). The expected L_T at age of both sexes increased, to a small extent, during the first few years of the age range sampled, which commences at 2 years of age, and then rose only slightly over the last 40–50 years of life [Fig. 4(a), (b)]. Thus, for example, the expected L_T of females increased, on average, from 401 mm at 2 years of age to 471 mm at 15 years and then only rose further to 504 mm at 55 years of age. A comparison of the von Bertalanffy curves for the two sexes of *P. recurvirostris* demonstrated that the expected L_T at age were greater for females than males at the same age within the age range of the samples. Thus, for example, at ages 10 and 40 years, the expected L_T of females exceeded those

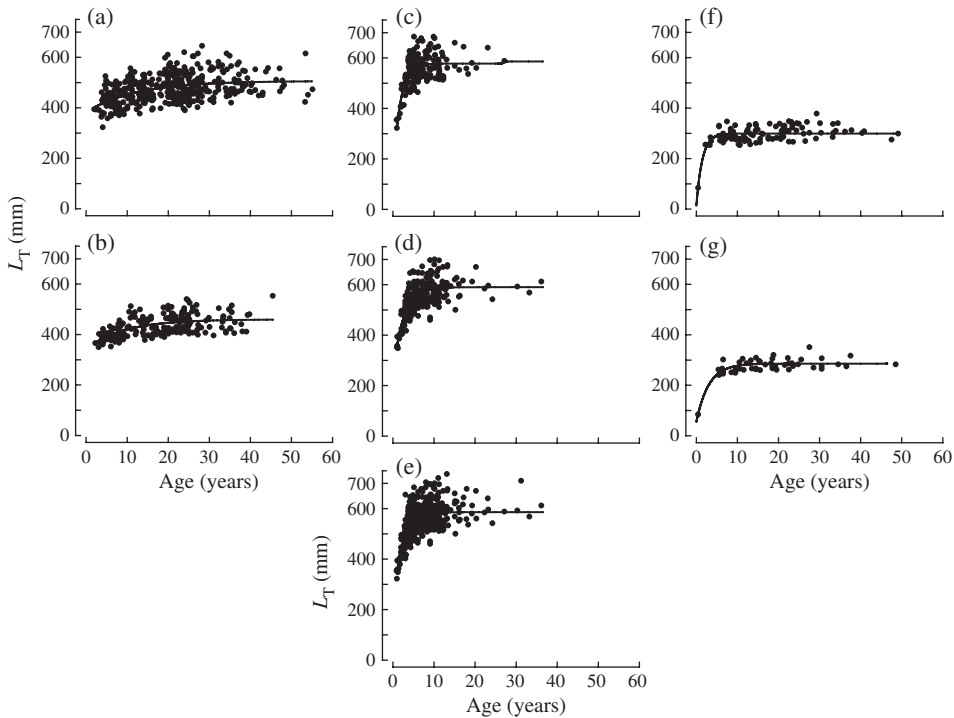


FIG. 4. von Bertalanffy growth curves fitted to the L_T at age of (a) females ($n=400$) and (b) males ($n=197$) of *Pentaceropsis recurvirostris* and of (c) females ($n=181$), (d) males ($n=247$) and (e) all individuals ($n=510$) of *Paristiopertus gallipavo* and of (f) females ($n=99$) and (g) males ($n=47$) of *Parazanclistius hutchinsi*.

of males by 32 and 43 mm. The absence of small, young fish and a relatively small increase in L_T over the age range sampled is reflected in low values for the growth coefficients and highly negative estimates for t_0 (Table III).

Although the L_T of all females and males of *P. gallipavo* exceeded 300 mm, the L_T at age of both sexes clearly increased early in life [Fig. 4(c), (d)]. While female and male growth curves were significantly different ($\chi^2 = 12.4$, d.f. = 3, $P < 0.05$), the difference in the expected L_T of the two sexes at each age between 1 and 27 years (the maximum age of females), as determined from von Bertalanffy growth equations, was always $\leq 3\%$. As these differences are small and growth curves will almost inevitably tend to differ significantly, when based on large sample sizes as with *P. gallipavo*, the differences are assumed, as in comparable cases (Coulson *et al.*, 2009, 2010), to be of little or no biological significance. Thus, the L_T at age for females and males, and those of *P. gallipavo* that could not be sexed, were combined to derive a third and composite growth curve for *P. gallipavo* [Fig. 4(e)]. This curve emphasizes that *P. gallipavo* grows rapidly until c. 7 years of age, after which the L_T at age levels off markedly through to the age of the oldest *P. gallipavo*, i.e. 36 years [Fig. 4(e)]. This is reflected in the moderately high k value of 0.47 year^{-1} and the estimate derived from the von Bertalanffy growth equation that, by 7 years of age, *P. gallipavo* had attained a L_T of 571 mm and thus 98% of its asymptotic L_T of 585 mm [Fig. 4(e) and Table III]. Despite the lack of small *P. gallipavo*, the t_0 of -0.94 years is not excessively negative for a relatively

TABLE II. Estimates of natural mortality (M) obtained by substituting the maximum age (year) into the Hoenig (1983) equation for fish and the refitted version (Hoenig_{nl}) of this equation calculated by Then *et al.* (2015) for females and males of *Pentaceropsis recurvirostris*, *Paristiopterus gallipavo*, *Parazanclostius hutchinsi* and of other commercially and recreationally-fished species from the south coast of Western Australia. Values for total mortality (Z), calculated using catch curve analysis (Chapman & Robson, 1960), are provided for the three pentacerotid species, which are not heavily exploited

Species	Sex	Maximum age (years)	Hoenig (1983) $M \text{ year}^{-1}$	Then <i>et al.</i> (2015) $M \text{ year}^{-1}$	$Z \text{ year}^{-1}$
<i>P. recurvirostris</i>	Female	55	0.08	0.12	0.12
	Males	43	0.10	0.16	0.14
<i>P. gallipavo</i>	Female	27	0.16	0.24	0.24
	Males	36	0.12	0.18	0.21
<i>P. hutchinsi</i>	Female	49	0.09	0.14	0.11
	Males	48	0.09	0.14	0.10
<i>Othos dentex</i> ^a	Female	37	0.12	0.18	
	Males	31	0.14	0.21	
<i>Polyprion oxygeneios</i> ^b	Female	35	0.13	0.19	
	Males	52	0.09	0.13	
<i>Scorpius aequipinnis</i> ^c	Female	68	0.07	0.10	
	Males	59	0.08	0.12	
<i>Achoerodus gouldii</i> ^d	Combined	70	0.06	0.10	
<i>Bodianus frenchii</i> ^e	Combined	78	0.06	0.09	
<i>Nemadactylus valenciennesi</i> ^f	Combined	21	0.21	0.30	

^aFrench *et al.* (2014).

^bWakefield *et al.* (2010).

^cCoulson *et al.* (2012).

^dCoulson *et al.* (2009).

^eCossington *et al.* (2010).

^fCoulson *et al.* (2010).

long-lived species and thus the von Bertalanffy growth curve provides a reasonable description of growth, rather than just a description of the L_T at age of this species.

The von Bertalanffy growth equations for the females and males of *P. hutchinsi*, following the inclusion, for both sexes, of the L_T at age of a single unsexed individual of 84 mm, caught independently in a trawl, were significantly different ($\chi^2 = 65.8$, d.f. = 3, $P < 0.001$). The L_∞ of 302 mm for females was greater than the 286 mm for males. Females attained L_T of 290 mm at 5 years and 299 mm at 10 years, which represent 91 and 99% of their asymptotic length, a trend paralleled by the data for males (Table III). This demonstrates that *P. hutchinsi* undergoes negligible growth over the age range of individuals in the samples, and thus for the majority of its life.

OVARIAN DEVELOPMENT AND ESTIMATION OF SPAWNING PERIODS

The mean monthly ovarian mass of female *P. recurvirostris* remained low (≤ 25 g) between February and June and then rose to a sharp peak of 82 g in July and then

TABLE III. The von Bertalanffy growth parameters: L_{∞} , asymptotic total length (mm), k , growth coefficient (year^{-1}) and t_0 , the hypothetical age (years) at which fish would have zero length, and their upper and lower 95% C.I., for females and males of *Pentaceropsis recurvirostris*, females and males and all individuals of *Paristiopertus gallipavo* and females and males of *Parazanclictus hutchinsi*

		L_{∞}	k	t_0	r^2	n
<i>P. recurvirostris</i>						
Females	Estimate	506	0.08	-16.78	0.21	400
	Upper	523	0.13	-5.62		
	Lower	489	0.04	-27.95		
Males	Estimate	459	0.11	-12.19	0.32	197
	Upper	474	0.17	-3.01		
	Lower	445	0.04	-21.97		
<i>P. gallipavo</i>						
Females	Estimate	578	0.60	-0.38	0.44	181
	Upper	588	0.76	0.19		
	Lower	567	0.45	-0.95		
Males	Estimate	590	0.41	-1.28	0.46	247
	Upper	601	0.52	-0.34		
	Lower	579	0.31	-2.22		
All individuals	Estimate	585	0.47	-0.94	0.44	510
	Upper	593	0.55	-0.41		
	Lower	578	0.39	-1.46		
<i>P. hutchinsi</i>						
Females	Estimate	302	0.46	-0.33	0.43	99
	Upper	306	0.62	0.35		
	Lower	296	0.30	-1.02		
Males	Estimate	286	0.32	-0.68	0.68	47
	Upper	293	0.44	0.16		
	Lower	278	0.22	-0.99		

n , the number of fish.

declined from 57 g in August to low levels (<20 g) between September and December [Fig. 5(a)]. The trend exhibited by the mean monthly ovarian mass of *P. gallipavo* differed from that of *P. recurvirostris*, with values declining from 58 g in January to low levels of 4–11 g in April to June and then increasing to 105 g in September and remaining between 68 and 91 g in October to December [Fig. 5(b)]. The mean monthly ovarian mass for female *P. hutchinsi* increased sharply from 5 g in February to ≥ 11 g in March, April and June, and then declined progressively to <6 g in July to December [Fig. 5(c)].

The masses of the testes of the males of *P. recurvirostris* and *P. gallipavo* were very low, even when those of the ovaries of females were elevated [Fig. 5(d), (e)]. Yet, the trends exhibited throughout the year by the mean monthly masses of the testes of these two species broadly parallel those exhibited by their ovaries. No male *P. hutchinsi* were caught during the period when ovarian mass was elevated [Fig. 5(f)].

Females of *P. recurvirostris* with stage II (immature/resting) ovaries were caught in all 11 calendar months for which samples of this species were obtained (Fig. 6). It is highly noteworthy, however, that (1) the number of females with stage II ovaries

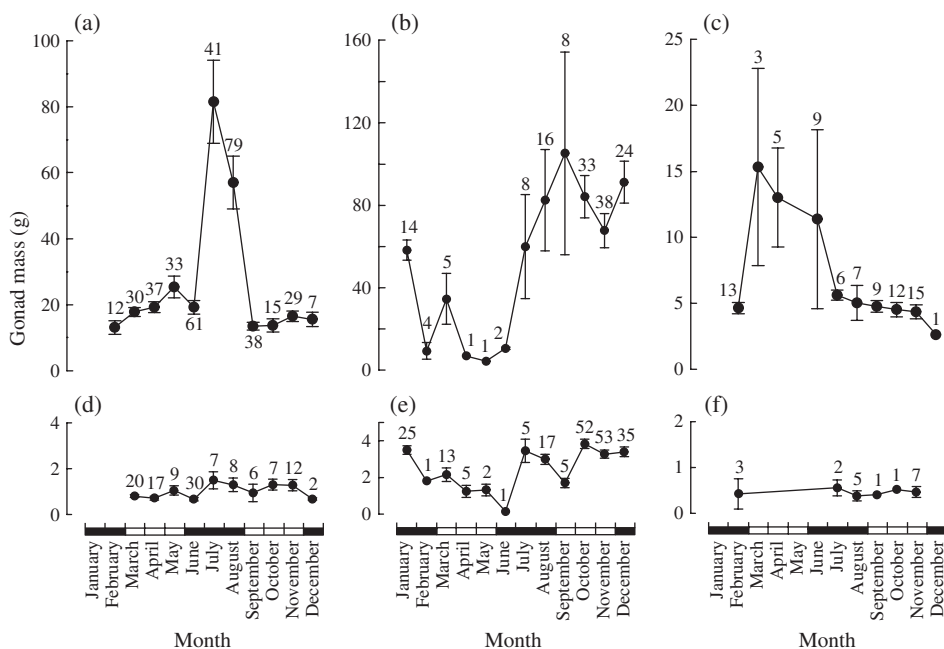


FIG. 5. Mean \pm S.E. monthly gonad mass for (a) female and (d) male *Pentaceropsis recurvirostris*, (b) female and (e) male *Paristiopterus gallipavo* and (c) female and (f) male *Parazanclistius hutchinsi*. Sample sizes are given above each mean. On the x-axis closed rectangles refer to summer and winter months and the open rectangles to autumn and spring months.

declined to relatively low levels between June and November, (2) females with stage III and IV ovaries were present only in May and June and (3) females with ovaries at stages $>II$ were dominated in June to August by *P. recurvirostris* with ovaries at stages V/VI and VII and contained exclusively those with stage VII ovaries in September to November (Fig. 6). These trends imply that most, but not all, female *P. recurvirostris* caught in a given year had become mature or were potentially destined to become mature in that year. The number of female *P. recurvirostris* with stage II ovaries during the spawning period, *i.e.* destined to remain immature during that period, ranged in L_T from 323 to 606 mm and produced a pronounced mode at 425–449 mm, compared with 358–645 mm and a well-defined mode at 450–474 mm for females with stage III–VII ovaries, *i.e.* mature or destined to become mature during that period (Fig. 7). The ages of immature and mature females during the spawning period ranged in age from 2 to 42 and 2 to 55 years, and in neither category produced a well-defined mode (Fig. 7). During that period, the mean L_T of 448 mm for immature females was significantly less than the corresponding value of 475 mm for mature females ($\chi^2 = 9.947$, d.f. = 1, $P < 0.01$), whereas the mean age of 19.9 years for immature fish was not significantly less than the 21.4 years mature females ($\chi^2 = 0.201$, d.f. = 1, $P > 0.05$).

Female *P. gallipavo* with stage II (immature/resting) ovaries were caught in most months between February and September, whereas those with stage III (developing) ovaries were restricted to June to August and the single female with a stage IV (maturing) ovary was caught in the latter month (Fig. 6). Fish with stage V–VI

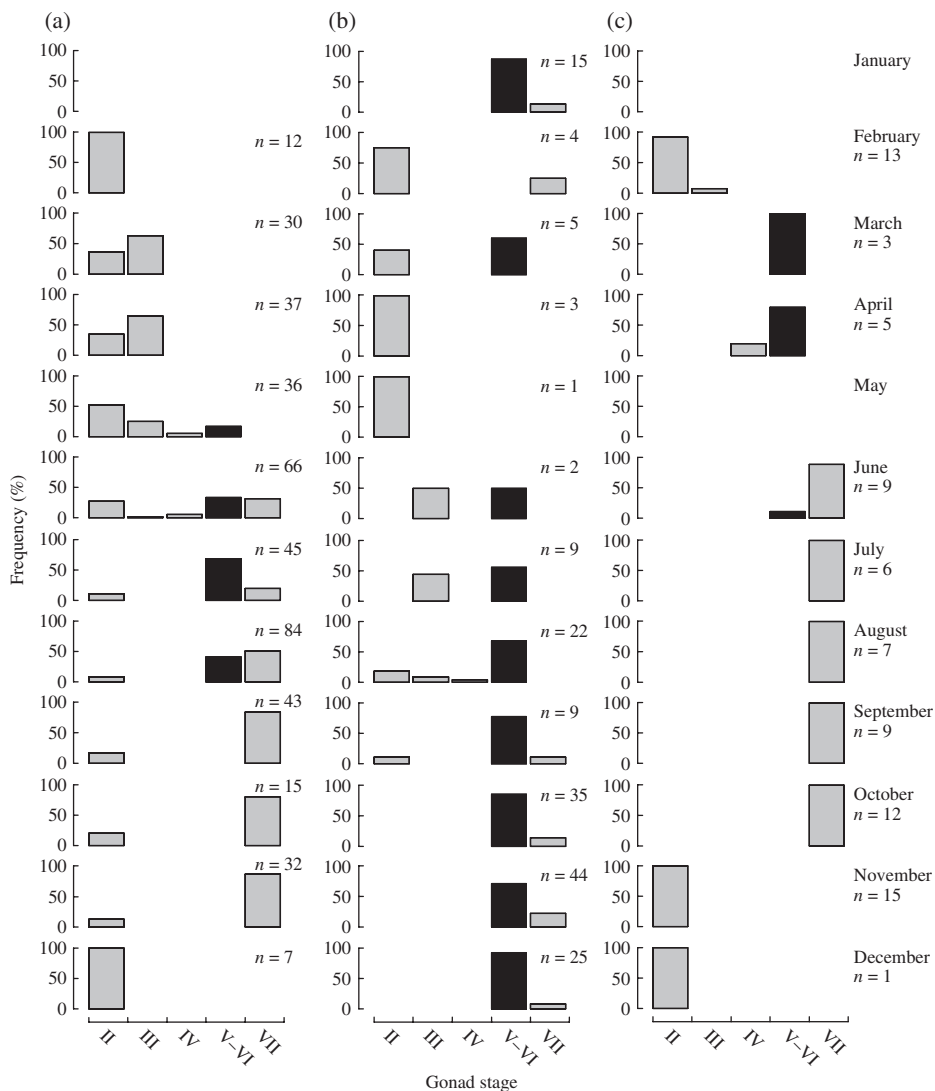


FIG. 6. Monthly percentage frequency of occurrence of sequential stages in ovarian development of (a) *Pentaceropsis recurvirostris*, (b) *Paristiopterus gallipavo* and (c) *Parazanclistius hutchinsi*. Histograms for stages V-VI are highlighted in black. n = sample size.

(prespawning/spawning) ovaries were caught in most months, dominating the substantial numbers of females obtained between August and January. Females of *P. gallipavo* with stage VII (spent) ovaries were found in each month between September and February. The absence of females with ovaries at stages II–IV in October to January, when all ovaries were at the prespawning/spawning or spent stages, implies that, in any month in a given year, at least the vast majority of female *P. gallipavo* were either mature or potentially destined to become mature.

The ovaries of *P. hutchinsi* in November, December and February were almost exclusively at stage II (immature/resting), whereas no females with ovaries at this stage were

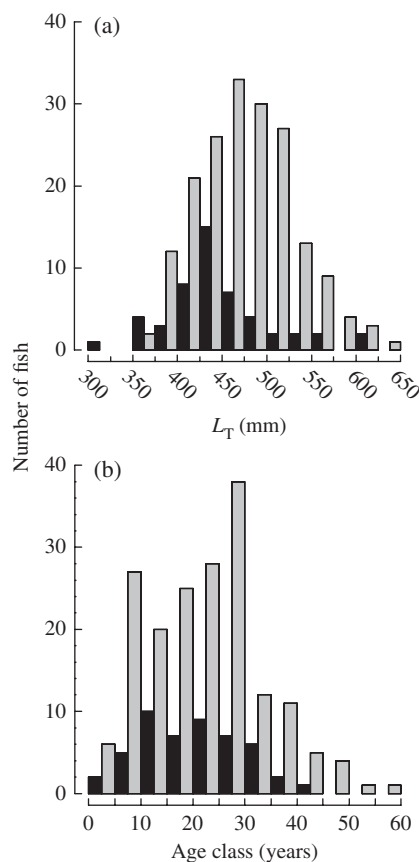


FIG. 7. (a) Total length (L_T ; immature $n = 50$, mature $n = 181$) and (b) age-frequency distributions for immature (immature $n = 49$, mature $n = 179$) (stage II, ■) and mature (stages III–VII, □) females of *Pentaceropsis recurvirostris* during their spawning period of May to August.

caught between March and October (Fig. 6). A single female with stage III (developing) and another with stage VI (maturing) ovaries were found in February and April, respectively. Females with stage V–VI (prespawning/spawning) ovaries were caught between March and June and those with VII (spent) ovaries between June and October. The above sequential trends in the prevalence of the different stages in ovarian development strongly suggest that, in any month in a given year, at least the vast majority of female *P. hutchinsi* were either mature or potentially destined to become mature.

As female *P. recurvirostris* with ovarian stages V–VI were caught exclusively in May to August and the mean monthly masses of ovaries were elevated in July and August, this species spawns between late autumn and late winter (Fig. 8). In the case of *P. gallipavo*, the dominance of females with ovaries at stages V–VI between July and January and elevated mean monthly ovarian masses during that period provide strong evidence that this species spawns between mid-winter and mid-summer and, on the basis of a single female with such ovaries in June, probably commences in early winter (Fig. 8). Although the data are not as comprehensive for *P. hutchinsi*, the similar close correspondence between the months when females with ovarian stages V–VI were

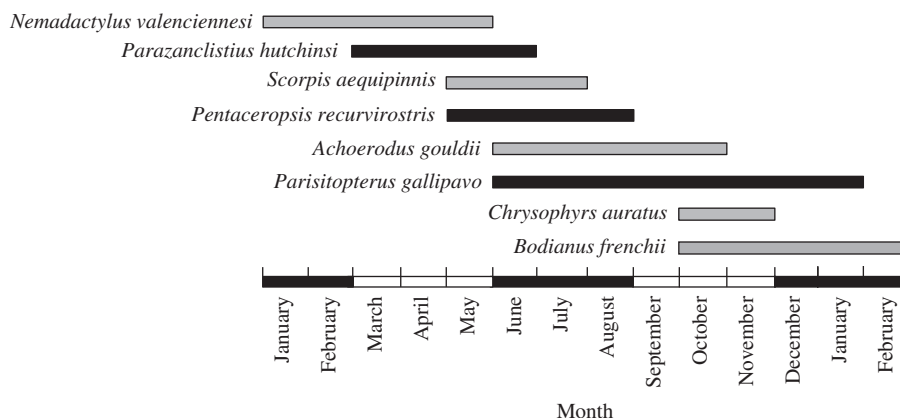


FIG. 8. Spawning periods (■, this study; □, other studies) of commercially and recreationally important demersal fish species on the southern coast of Western Australia. On the x-axis closed rectangles refer to summer and winter months and the open rectangles to autumn and spring months.

present and ovarian mass was elevated implies that this species spawns from early autumn to early winter (Fig. 8). As 1 July, 1 November and 1 May represent the approximate mid-point of the spawning period for *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, these dates were chosen as the birth dates for those species.

DISCUSSION

AGEING VALIDATION AND MAXIMUM AGES

The results of preliminary studies demonstrated that the otoliths of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* required sectioning to reveal all of their growth zones. Furthermore, analyses of the trends exhibited by the marginal increments, coupled with results from modelling using circular distributions (Okamura & Semba, 2009), validated that the growth (opaque) zones, detected in sectioned otoliths of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, are typically formed annually. This is the first time that the growth zones of any species of the Pentacerotidae have been validated as forming annually. The ability to use the trends exhibited by the marginal increments throughout the year was made possible through an ability to obtain samples of each species from either all or the vast majority of the calendar months in the year. Such data were not available for the studies of *P. wheeleri* and *P. richardsoni*, the other two species of pentacerotid that have been the subject of ageing studies using growth zones in otoliths (Uchiyama & Sampaga, 1990; Humphreys, 2000; López-Abellán *et al.*, 2008).

The maximum ages of 36 years for *P. gallipavo*, and particularly of 55 years for *P. recurvirostris* and 49 years for *P. hutchinsi*, far exceed the maximum ages estimated for *P. wheeleri* and *P. richardsoni*. On the basis of counts of 'check marks' in whole otoliths of *P. wheeleri* from the Hancock seamounts in the North Pacific Ocean, Uchiyama & Sampaga (1990) concluded that this population comprised mainly 1- and some 2-year-old individuals. Following sectioning of the otoliths of this species from

the same region, however, Humphreys (2000) concluded that the counts were underestimates and that the population consisted entirely of *P. wheeleri* in their third year of life. Humphreys (2000) attributed the lower values recorded by Uchiyama & Sampaga (1990) for *P. wheeleri* to the limitations posed for detecting the growth zones in whole rather than sectioned otoliths, as a result of their greater thickness, opacity and curvature. On the basis of two strong year classes, which were clearly identifiable in modal progressions of an index of fatness, Somerton & Kikkawa (1992) concluded that *P. wheeleri* has a maximum age of 4–5 years. Furthermore, Uchiyama & Sampaga (1990) identified, under reflected light, up to eight pairs of alternating bright (opaque) and dark (translucent) concentric bands in the whole otolith of a *P. wheeleri* from another region, suggesting that some individuals of this species live for up to 8 years.

Although López-Abellán *et al.* (2008) sectioned the otoliths of *P. richardsoni* from seamounts in the south-western Indian Ocean, they discarded these sections due to their 'poor readability'. These workers thus used counts of 'check marks' in whole otoliths and used these counts to estimate the ages of the individuals of this species. The far greater ability to detect opaque zones in the sectioned otoliths than whole otoliths of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, using the approaches adopted in the present study, raises the strong possibility that the maximum age of 14 years recorded by López-Abellán *et al.* (2008) for *P. richardsoni* underestimates substantially the longevity of this species. In this context it is noteworthy that those authors noted that the results of the reading of sectioned otoliths 'shows some important differences when compared with whole otolith readings'. It would seem unlikely that the large differences between the estimates of maximum ages of *P. wheeleri* and *P. richardsoni* and those of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* are due to phylogenetic differences, reflected in their assignment to different subfamilies. Since accurate estimates of the maximum ages of fish species are crucial for developing management decisions, there is a need to establish whether the far lower maximum ages recorded *P. wheeleri* and *P. richardsoni*, than for *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, represent serious underestimates of ages of the individuals of those species. This view is consistent with the recommendation recently made in a review of the biology and fishery for *P. wheeleri* (Kiyota *et al.*, 2016).

The above comparisons, together with the results of other studies (Beamish, 1979; Bedford, 1983; Hyndes *et al.*, 1992; Peres & Haimovici, 2004; Coulson *et al.*, 2009), reiterate the importance of determining whether the otoliths of a species require sectioning to produce reliable counts of their growth zones before using whole otoliths for ageing. This is particularly the case with pentacerotid species, whose otoliths are thick and within which, when substantial numbers of such zones are present, the peripheral growth zones become very closely apposed.

AGE AT MATURITY AND GROWTH

The absence of immature females of *P. gallipavo* and *P. hutchinsi* in the samples of these two species collected during their spawning periods precluded the possibility of estimating the length and age by which 50% (L_{T50} and A_{50}) of the females of these two pentacerotids attain maturity. The ages of fishes caught during the spawning period demonstrate that many individuals of these species are mature by the very young ages of 2–3 years, *i.e.* the age at which they start entering the fishery. This corresponds

closely to the situation recorded by Humphreys (2000) for the fishery for *P. wheeleri* on the seamounts in the central North Pacific Ocean. Furthermore, although some female *P. recurvirostris* with immature gonads were caught during the spawning period of this species, a few of these were >20 years old and thus likely to have spawned previously at an earlier age; it was not possible to use these to derive estimates of the L_{T50} and A_{50} for the females of *P. recurvirostris*.

As no small individuals of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* were caught during the present study, the growth curves reflected the L_T at age across the age range of each species in the samples. Although selectivity, associated with the restricted range in mesh size of the gillnets (165–178 mm) used by the commercial fishers, could potentially have contributed to the absence of small *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* in the samples from fish processors, the collection of only adults from the spawning areas of these species is consistent with the results of detailed studies of *P. wheeleri* in the North Pacific Ocean. The juveniles of *P. wheeleri* are pelagic, often distributed over large distances from their natal areas, and they only return to those seamounts and become demersal when they are 2 years old and reach adulthood (Humphreys, 2000; Yanagimoto & Humphreys, 2005). Furthermore, as the shapes of the three species are similar and virtually all *P. hutchinsi* were shorter than the sampled individuals of *P. recurvirostris* and *P. gallipavo*, selectivity of fishing gear would be unlikely to account for the absence of small individuals of those first two species.

Although it was originally thought that the somatic growth of *P. wheeleri* was confined entirely to the larval and juvenile pelagic phases in the life cycle (Humphreys, 2000), a subsequent study indicated that some of its individuals may grow slightly after they have become recruited to the seamounts (Yanagimoto & Humphreys, 2005). The plots of lengths at age and growth curves of *P. hutchinsi* demonstrate that, after entering the areas where they spawn and remain for their very protracted adult phase, this species exhibits negligible somatic growth during the whole of that very extensive period and the same is largely true of *P. recurvirostris*, but with a slight increase occurring initially. Although, *P. gallipavo* exhibits conspicuous growth during the first 8 years of adult life, it then follows the trend of the other two pentacerotid species by subsequently undergoing negligible growth. Somatic growth thus largely ceases in *P. recurvirostris* and *P. hutchinsi* after maturity has been attained at a very young age and consequently neither of these long-lived species increase in L_T over a very protracted period of their lives; the same is true, but to a lesser extent, for *P. gallipavo*. This parallels the situation recorded for the females of the Banded Morwong *Cheilodactylus spectabilis* Hutton 1872 in the shallow (<25 m) coastal waters of Tasmania (Ewing *et al.*, 2007).

A recent study has demonstrated that, as with *P. recurvirostris* and *P. hutchinsi*, two *Sebastes* species off the eastern coast of Canada are similarly long-lived (40–50 years) and exhibit a near cessation of growth after the attainment of sexual maturation (Campana *et al.*, 2016). These *Sebastes* species, however, grow at a slower rate and mature at a far older age (10–15 years). Furthermore, in contrast to *P. recurvirostris* and *P. hutchinsi* and also *C. spectabilis*, these *Sebastes* species live in deep waters, as do some other slow growing, long-lived and late maturing species, which makes them particularly susceptible to overfishing and slow to recover from depletion (Clarke *et al.*, 2003; Campana *et al.*, 2016).

MORTALITY AND COMPARISONS WITH OTHER SPECIES

The high maximum ages of the females and males of *P. recurvirostris* and *P. hutchinsi* reflect levels of natural mortality (M) of between 0.12 and 0.16 year⁻¹ and thus less than the value of 0.20 year⁻¹ regarded by Patrick *et al.* (2010) as low. Furthermore, the same applies to the males of *P. gallipavo*, *i.e.* 0.18 year⁻¹, and that of its females, *i.e.* 0.24 year⁻¹, only slightly exceeds 0.20. These estimates, which were obtained using the Hoenig_{NLS} equation, as fitted by Then *et al.* (2015), were appreciably greater than those derived employing the equation for fishes of Hoenig (1983). Although estimates using the latter equation have frequently been considered to represent the natural mortality of many species (Newman, 2002; Fischer *et al.*, 2005; Grandcourt *et al.*, 2006), Then *et al.* (2015) demonstrated, through cross validation, that their refitted version of this equation provides more accurate estimates of the natural mortalities than have been published. As these three pentacerotid species are collectively taken in only small amounts by the commercial gillnet fishery on the south coast of Western Australia (Braccini *et al.*, 2013) and are presumably lightly fished, their natural mortality would be expected to be similar to their total mortality. This assumption is confirmed by the similarity between the value derived for total mortality (Z) by catch curve analysis for each sex of each species and the corresponding value estimated for natural mortality using the Then *et al.* (2015) equation (Table II).

The substantial maximum ages of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* recorded in this study parallel those reported for five other demersal fish species that are abundant in inshore waters of the southern coast of Western Australian and which represent four different families (Table II). These maximum ages were 78 and 70 years for the protogynous hermaphroditic foxfish *Bodianus frenchii* (Klunzinger 1879) and western blue groper *Achoerodus gouldii* (Richardson 1843) (Labridae), 68 years for the sea sweep *Scorpius aequipinnis* Richardson 1848 (Kypnosidae), 52 years for the hapuku *Polyprion oxygeneios* (Schneider & Forster 1801) (Polyprionidae) and 37 years for the harlequin fish *Othos dentex* (Cuvier 1828) (Serranidae) (Coulson *et al.*, 2009, 2012; Cossington *et al.*, 2010; Wakefield *et al.*, 2010; French *et al.*, 2014). The estimates of natural mortality (M), calculated for these five species using the Hoenig_{NLS} equation (Then *et al.*, 2015), were likewise low, ranging from 0.09 year⁻¹ for *B. frenchii* to 0.21 year⁻¹ for the males of the gonochoristic anthiine *O. dentex* (Table II). It is possible that such longevities are related to the cool temperatures on the south-western coastal waters of Australia, the highest coastal latitude that these species occupy in this region, which would be consistent with predictions from the metabolic theory of ecology (Weber *et al.*, 2015). The considerable longevity of these species increases the susceptibility of these stocks to over-exploitation (Patrick *et al.*, 2010), as is the case with some deep-sea fish species that are long-lived, slow growing and late maturing (Clarke *et al.*, 2003). Although the three pentacerotid species are long-lived, they are reasonably fast growing early in life and become mature at younger ages than the other above species, characteristics that would presumably act, to a certain extent, as a buffer against such deleterious effects.

HABITAT AND SPAWNING CHARACTERISTICS

The samples of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* were collected by gill-netting in water depths of 30–120 m and within 200 m of the coast. The first of these species has frequently been observed in 3–10 m during scuba diving (P. G. Coulson,

pers. obs.) with most of these observations being in and around reefs. There is thus no doubt that, while these species also occur in rather deeper waters (Gomon *et al.*, 2008), their habitat as adults clearly differs from the seamounts and greater depths typically occupied by adult *P. wheeleri* and *P. richardsoni* (Humphreys, 2000; López-Abellán *et al.*, 2008). The numerous maturing and mature individuals of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* caught during this study demonstrate that these species spawn in the relatively shallow waters in which they were gillnetted.

The trends exhibited in sequential monthly samples, by the mean ovarian mass and prevalences of the different stages in ovarian development, demonstrated that the spawning periods of *P. hutchinsi* (early autumn to early winter) and *P. recurvirostris* (late autumn to late winter) overlap in south-western Australian coastal waters (Fig. 7). Thus, gonadal recrudescence and subsequently spawning of the above two southern hemisphere species commences when water temperatures and day length are declining [see Coulson *et al.* (2012) for local water temperatures and day length]. The trends exhibited by *P. hutchinsi* and *P. recurvirostris*, which essentially parallel those exhibited by *A. gouldii* and *S. aequipinnis* on the same coast (Coulson *et al.*, 2009, 2012), are more typical of tropical than temperate species (Lam, 1983).

In marked contrast to the above two pentaceratid species, the spawning of *P. gallipavo* in south-western Australia and of *P. richardsoni* elsewhere in the southern hemisphere (López-Abellán *et al.*, 2008) peaks between late winter and mid-summer and thus as water temperatures are increasing. Although this is typical of temperate species, to which category *P. gallipavo* belongs, and also of numerous other species in temperate south-western Australia, *e.g.* *Glaucosoma hebraicum* Richardson 1845, *Epinephelides armatus* (Castelnau 1875) and *O. dentex* (Hesp *et al.*, 2002; Moore *et al.*, 2007; French *et al.*, 2014), it is not usually the case with tropical species such as *P. richardsoni* (Lam, 1983). The trends exhibited by the mean monthly masses and prevalence of ovaries at different stages of maturation also demonstrate that *P. gallipavo* spawns over a far more protracted period than *P. recurvirostris* and *P. hutchinsi*.

On the basis of a detailed histological study of the ovaries of *P. wheeleri*, Yanagimoto & Humphreys (2005) concluded that this species spawns more than once in the period that it spends on the seamounts. As *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* had been frozen for some time before receipt, their gonads were not suitable for histological studies. Macroscopic staging of the gonads, however, demonstrated that the assemblages of *P. gallipavo* and *P. hutchinsi* were exclusively or mainly dominated by mature and spent fishes during and immediately after their spawning periods. This provides strong circumstantial evidence that, as each of these pentacerotids can live for many years, they are iteroparous. During the months comprising the spawning period of *P. recurvirostris*, a small number of females possessed ovaries at stage II (immature) and none at stages III and IV, and would thus potentially not have been destined to become mature during the current spawning period. As some of these immature *P. recurvirostris* were >20 years old, a small proportion of the adult females of this species fail in each year to develop mature ovaries and spawn during the annual spawning period.

The vast difference, at the time of peak of spawning, between the large ovarian mass of the females and minute mass of the testes of the males of *P. recurvirostris* (80 times) is a characteristic of species, such as certain serranids, which are known to spawn in pairs (Sadovy, 1996; Marino *et al.*, 2001; Moore *et al.*, 2007). It is thus relevant that scuba divers and spear fishers, have often observed *P. recurvirostris* in pairs. Although

there are no recorded observations of the behaviour of *P. gallipavo* and *P. hutchinsi*, the gonads of the two sexes of these two species likewise differ markedly in size.

It was striking that the proportion of males was far greater for *P. gallipavo* (1 female: 1.4 male) than *P. recurvirostris* and *P. hutchinsi* (both one female: 0.5 male). The greater proportion of males than females in *P. gallipavo* and the reverse situation with *P. recurvirostris* and *P. hutchinsi* suggests that there may have been stronger selection pressures for optimizing the effectiveness of the role of the males of *P. gallipavo* in spawning (Kvarnemo & Ahnesjö, 1996; Kokko & Monaghan, 2001). Furthermore, the far longer spawning period of *P. gallipavo* than the other two species would be likely to increase the potential for successful breeding within a spawning period (Kvarnemo & Merilaita, 2006). Spawning success may also be more crucial for *P. gallipavo* as the natural mortality of this species, albeit still low, is greater than that of *P. recurvirostris* and *P. hutchinsi*.

Extensive sampling has shown that the life cycle of *P. wheeleri* comprises an initial pelagic phase, during which the juveniles become widely distributed by ocean currents, from the seamounts where they were spawned, into the central and eastern regions of the sub-Arctic North Pacific Ocean, thousands of kilometres from their natal areas. After 2 or more years, they are recruited back onto the seamounts where they become demersal in depths of 300–400 m (Boehlert & Sasaki, 1988; Humphreys *et al.*, 1989; Mundy & Moser, 1997). The waters off the southern coast of Western Australia have been sampled at intervals by trawling, spear fishing and the use of rotenone. Yet, the records of the specimens kept by the Western Australian, Victorian and Australian Museums, include only one *P. gallipavo* with a $L_T < 212$ mm, one *P. hutchinsi* with a $L_T < 188$ mm and no *P. recurvirostris* < 102 mm L_T (G. Moore, S. Morrison, M. Gomon, D. Bray & A. Hay, pers. comm.). Moreover, the only pentacerotid observed during hundreds of hours of diving along the southern coast of Western Australia was *P. recurvirostris* and all of those individuals were adults (P. G. Coulson, pers. obs.).

Comprehensive surveys of the larval fish communities in offshore waters of south-western and south-eastern Australia failed to catch any larvae of *P. recurvirostris*, *P. gallipavo* or *P. hutchinsi* or of any other pentacerotid (Neira, 2005; Muhling & Beckley, 2007; Keane & Neira, 2008; Muhling *et al.*, 2008). Some *P. gallipavo* and *P. recurvirostris* with $L_T < 150$ mm have been caught by trawling at depths of 52–140 m in south-eastern Australia (G. Moore, S. Morrison, M. Gomon, D. Bray & A. Hay, pers. comm.). It is thus tentatively suggested that the larvae and juveniles of these *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi*, which were spawned in southern waters of Western Australian, may be carried southwards into Antarctic waters or eastwards to south-eastern Australia.

In summary, this study demonstrates that the otoliths of *P. recurvirostris*, *P. gallipavo* and *P. hutchinsi* require sectioning to reveal the full complement of their growth zones and therefore be able to be used for ageing. The results thus obtained reveal that these species, and particularly *P. recurvirostris* and *P. hutchinsi*, are long-lived, contrasting markedly with the far lower maximum ages recorded for *P. wheeleri* and *P. richardsoni*. The three south-western Australian pentacerotids exhibit little or no growth during most of their life. The duration and time of year of spawning and sex ratio of *P. gallipavo* differ from those of *P. recurvirostris* and *P. hutchinsi*, implying that the former species has been subjected to different selection pressures. The sometimes very marked differences in the biological characteristics, and especially longevity, now

recorded for species of pentacerotid from four genera emphasize that there is a need to elucidate the basis for these divergent life cycle traits.

Special thanks are due to S. Flynn (All Seas Fish Supply, Esperance) for providing samples of boarfish caught by commercial fishers, and to E. Ashworth for her assistance in confirming the reliability of growth zone counts within sectioned otoliths. S. Morrison and G. Moore (Western Australian Museum), M. Gomon and D. Bray (Victorian Museum) and A. Hay (Australian Museum) kindly provided details on their collections of boarfishes. Particular gratitude is also expressed to the two referees whose detailed and constructive comments led to a greatly improved manuscript. Financial support was provided by Murdoch University.

References

- Beamish, R. J. (1979). Differences in the age of Pacific Hake (*Merluccius productus*) using whole otoliths and sections of otoliths. *Journal of the Fisheries Research Board of Canada* **36**, 141–151.
- Bedford, B. C. (1983). A method of preparing sections of large numbers of otoliths embedded in black polyester resin. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **41**, 4–12.
- Boehlert, G. W. & Sasaki, T. (1988). Pelagic biogeography of the armorhead *Pseudopentaceros wheeleri*, and recruitment to isolated seamounts in the North Pacific Ocean. *Fishery Bulletin* **86**, 453–465.
- Borets, L. A. (1980). The distribution and structure of the range of Boarfish *Pentaceros richardsoni*. *Journal of Ichthyology* **20**, 141–143.
- Braccini, M., McAuley, R. & Rowland, F. (2013). Temperate demersal gillnet and demersal longline fisheries status report. In *Status Reports of the Fisheries and Aquatic Resources of Western Australia 2012/13: The State of the Fisheries* (Fletcher, W. J. & Santoro, K., eds), pp. 271–284. Perth: Department of Fisheries.
- Burnham, K. P. & Anderson, D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. New York, NY: Springer.
- Campana, S. E. (2001). Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *Journal of Fish Biology* **59**, 197–242.
- Campana, S. E., Valentin, A. E., MacLellan, S. E. & Groot, J. B. (2016). Image-enhanced burnt otoliths, bomb radiocarbon and the growth dynamics of redfish (*Sebastes mentella* and *S. fasciatus*) off the eastern coast of Canada. *Marine and Freshwater Research*. doi: 10.1071/MF15002
- Cerrato, R. M. (1990). Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Canadian Journal of Fisheries and Aquatic Sciences* **47**, 1416–1426.
- Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1208–1210.
- Chapman, D. & Robson, D. S. (1960). The analysis of a catch curve. *Biometrics* **16**, 354–368.
- Clarke, M. W., Kelly, C. J., Connolly, P. L. & Molloy, J. P. (2003). A life history approach to the assessment and management of deepwater fisheries in the Northeast Atlantic. *Journal of Northwest Atlantic Fishery Science* **31**, 401–411.
- Cossington, S., Hesp, S. A., Hall, N. G. & Potter, I. C. (2010). Growth and reproductive biology of the foxfish *Bodianus frenchii*, a very long-lived and monandric protogynous hermaphroditic labrid. *Journal of Fish Biology* **77**, 600–626.
- Coulson, P. G., Hesp, S. A., Hall, N. G. & Potter, I. C. (2009). The western blue groper (*Achoerodus gouldii*), a protogynous hermaphroditic labrid with exceptional longevity, late maturity, slow growth, and both late maturation and sex change. *Fishery Bulletin* **107**, 57–75.
- Coulson, P. G., Hesp, S. A., Potter, I. C. & Hall, N. G. (2010). Life cycle characteristics of the blue morwong *Nemadactylus valenciennesi*, compared with those of other species of Cheilodactylidae. *Marine and Freshwater Research* **61**, 104–118.

- Coulson, P. G., Potter, I. C. & Hall, N. G. (2012). The biological characteristics of *Scorpius aequipinnis* (Kyphosidae), including relevant comparisons with those of other species and particularly of a heavily exploited congener. *Fisheries Research* **125**, 272–282.
- Ewing, G. P., Lyle, J. M., Murphy, R. J., Kalish, J. M. & Ziegler, P. E. (2007). Validation of age and growth in a long-lived temperate reef fish using otolith structure, oxytetracycline and bomb radiocarbon methods. *Marine and Freshwater Research* **58**, 944–955.
- Fischer, A. J., Baker, M. S. Jr., Wilson, C. A. & Nieland, D. L. (2005). Age, growth, mortality, and radiometric age validation of gray snapper (*Lutjanus griseus*) from Louisiana. *Fishery Bulletin* **103**, 307–319.
- French, B., Potter, I. C., Hesp, S. A., Coulson, P. G. & Hall, N. G. (2014). Biology of the harlequin fish *Othos dentex* (Serranidae), with particular emphasis on sexual pattern and other reproductive characteristics. *Journal of Fish Biology* **84**, 106–132.
- Gomon, M. F., Bray, C. D. & Kuiter, R. H. (Eds) (2008). *Fishes of Australia's Southern Coast*. Sydney: Reed New Holland.
- Grandcourt, E. M., Al Abdessalaam, T. Z. & Francis, F. (2006). Age, growth, mortality and reproduction of the blackspot snapper, *Lutjanus fulvivflamma* (Forsskål, 1775), in the southern Arabian Gulf. *Fisheries Research* **78**, 203–210.
- Hesp, S. A., Potter, I. C. & Hall, N. G. (2002). Age and size composition, growth rate, reproductive biology, and habitats of the West Australian dhufish (*Glaucosoma hebraicum*) and their relevance to the management of this species. *Fishery Bulletin* **100**, 214–227.
- Hoinig, J. M. (1983). Empirical use of longevity data to estimate mortality-rates. *Fishery Bulletin* **81**, 898–903.
- Humphreys, R. L. (2000). Otolith-based assessment of recruitment variation in a North Pacific seamount population of armorhead *Pseudopentaceros wheeleri*. *Marine Ecology Progress Series* **204**, 213–223.
- Humphreys, R. L., Winans, G. A. & Tagami, D. T. (1989). Synonymy and life history of the North Pacific pelagic armorhead, *Pseudopentaceros wheeleri* Hardy (Pisces: Pentacerotidae). *Copeia* **1989**, 142–153.
- Hutchins, B. & Swainston, R. (1986). *Sea Fishes of Southern Australia. Complete Field Guide for Anglers and Divers*. Smithfield: Swainston Publishing.
- Hyndes, G. A., Loneragan, N. R. & Potter, I. C. (1992). Influence of sectioning otoliths on marginal increment trends and age and growth estimates for the flathead *Platycephalus speculator*. *Fishery Bulletin* **90**, 276–284.
- Keane, J. P. & Neira, F. J. (2008). Larval fish assemblages along the south-eastern Australian shelf: linking mesoscale non-depth-discriminate structure and water masses. *Fisheries Oceanography* **17**, 263–280.
- Kim, S. Y. (2012). Phylogenetic systematics of the family Pentacerotidae (Actinopterygii: order Perciformes). *Zootaxa* **3366**, 1–111.
- Kiyota, M., Nishida, K., Murakami, C. & Yonezaki, S. (2016). History, biology, and conservation of Pacific endemics 2. The North Pacific armorhead, *Pentaceros wheeleri* (Hardy, 1983) (Perciformes, Pentacerotidae). *Pacific Science* **70**, 1–20.
- Kokko, H. & Monaghan, P. (2001). Predicting the direction of sexual selection. *Ecology Letters* **4**, 159–165.
- Kvarnemo, C. & Ahnesjö, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution* **11**, 404–408.
- Kvarnemo, C. & Merilaita, S. (2006). Mating distribution and its temporal dynamics affect operational sex ratio: a simulation study. *Biological Journal of the Linnean Society* **89**, 551–559.
- Laevastu, T. (1965). *Manual of Methods in Fisheries Biology*. Rome: FAO.
- Lam, T. J. (1983). Environmental influences on gonadal activity in fish. In *Fish Physiology*, Vol. IXB (Hoar, W. S. & Randall, D. J., eds), pp. 65–116. London: Academic Press.
- López-Abellán, L. J., Santamaría, M. T. G. & González, J. F. (2008). Approach to ageing and growth back-calculation based on the otolith of the southern boarfish *Pseudopentaceros richardsoni* (Smith, 1844) from the south-west Indian Ocean seamounts. *Marine and Freshwater Research* **59**, 269–278.
- Marino, G., Azzurro, E., Massari, A., Finoia, M. G. & Mandich, A. (2001). Reproduction in the dusky grouper from the southern Mediterranean. *Journal of Fish Biology* **58**, 909–927.

- Moore, S. E., Hesp, S. A., Hall, N. G. & Potter, I. C. (2007). Age and size compositions, growth and reproductive biology of the breaksea cod *Epinephelides armatus*, a gonochoristic serranid. *Journal of Fish Biology* **71**, 1407–1429.
- Muhling, B. A. & Beckley, L. E. (2007). Seasonal variation in horizontal and vertical structure of larval fish assemblages off south-western Australia, with implications for larval transport. *Journal of Plankton Research* **29**, 967–983.
- Muhling, B. A., Beckley, L. E., Koslow, J. A. & Pearce, A. F. (2008). Larval fish assemblages and water mass structure off the oligotrophic south-western Australian coast. *Fisheries Oceanography* **17**, 16–31.
- Mundy, B. C. & Moser, H. G. (1997). Development of early stages of pelagic armorhead *Pseudopentaceros wheeleri* with notes on juvenile *P. richardsoni* and larval *Histiogaster typus* (Pisces, Percoidae, Pentacerotidae). *Bulletin of Marine Science* **61**, 241–269.
- Neira, F. J. (2005). Summer and winter plankton fish assemblages around offshore oil and gas platforms in south-eastern Australia. *Estuarine, Coastal and Shelf Science* **63**, 589–604.
- Newman, S. J. (2002). Growth rate, age determination, natural mortality and production potential of the scarlet seaperch, *Lutjanus malabaricus* Schneider 1801, off the Pilbara coast of north-western Australia. *Fisheries Research* **58**, 215–225.
- Okamura, H. & Semba, Y. (2009). A novel statistical method for validating the periodicity of vertebral growth band formation in elasmobranch fishes. *Canadian Journal of Fisheries and Aquatic Sciences* **66**, 771–780.
- Patrick, W. S., Spencer, P., Link, J., Cope, J., Field, J., Kobayashi, D., Lawson, P., Gedamke, T., Cortés, E., Ormseth, O. & Bigelow, K. (2010). Using productivity and susceptibility indices to assess the vulnerability of United States fish stocks to overfishing. *Fishery Bulletin* **108**, 305–322.
- Peres, M. B. & Haimovici, M. (2004). Age and growth of southwestern Atlantic wreckfish *Polyprion americanus*. *Fisheries Research* **66**, 157–169.
- Romanov, E. V. (ed.) (2003). Summary and Review of Soviet and Ukrainian Scientific and Commercial Fishing Operations on the Underwater Ridges of the Southern Indian Ocean. *FAO Fisheries Circular* No. 991. Rome: FAO.
- Sadovy, Y. (1996). Reproduction of reef fishery species. In *Reef Fisheries* (Polunin, N. V. C. & Roberts, C. M., eds), pp. 15–59. London: Chapman & Hall.
- Smith, M. W., Then, A. Y., Wor, C., Ralph, G., Pollock, K. H. & Hoenig, J. M. (2012). Recommendations for catch-curve analysis. *North American Journal of Fisheries Management* **32**, 956–967.
- Somerton, D. A. & Kikkawa, B. S. (1992). Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on Southeast Hancock Seamount. *Fishery Bulletin* **90**, 756–769.
- Then, A. Y., Hoenig, J. M., Hall, N. G. & Hewitt, D. A. (2015). Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. *ICES Journal of Marine Science* **72**, 82–92.
- Uchiyama, J. H. & Sampaga, J. D. (1990). Age estimation and composition of pelagic armorhead *Pseudopentaceros wheeleri* from Hancock Seamounts. *Fishery Bulletin* **88**, 217–222.
- Wakefield, C. B., Newman, S. J. & Molony, B. W. (2010). Age-based demography and reproduction of hapuku, *Polyprion oxygeneios*, from the south coast of Western Australia: implications for management. *ICES Journal of Marine Science* **67**, 1164–1174.
- Weber, M. J., Brown, M. L., Wahl, D. H. & Shoup, E. (2015). Metabolic theory explains latitudinal variation in common carp populations and predicts responses to climate change. *Ecosphere* **6**, 1–16.
- Yanagimoto, T. & Humphreys, R. L. Jr. (2005). Maturation and reproductive cycle of female armorhead *Pseudopentaceros wheeleri* from the southern Emperor-northern Hawaiian Ridge Seamounts. *Fisheries Science* **71**, 1059–1068.

Electronic References

- Anon. (2008). Boarfish (Pentacerotidae). *Status of the Fisheries Resources in NSW 2006/07*. NSW Department of Primary Industries, Sydney. pp. 2. Available at www.dpi.nsw.gov.au/_data/assets/pdf_file/0008/221012/Status-of-Fisheries-Resources-in-NSW-2006-07.pdf

- Anon. (2010). Federal Register, Vol. 75, No. 217, Wednesday, November 10, 2010, Rules and Regulations. Available at www.gpo.gov/fdsys/pkg/FR-2010-11-10/pdf/2010-28325.pdf#page=1 (last accessed 29 January 2016).
- Anon. (2015). National Marine Fisheries Service – 3rd Quarter 2015 update. Table A. Summary Of Stock Status for FSSI Stocks. Available at www.fisheries.noaa.gov/sfa/fisheries_eco/status_of_fisheries/archive/2015/third/q3_2015_stock_status_tables.pdf (last accessed 23 December 2015).
- Eschmeyer, W. N. & Fricke, R. (Eds) (2016). Catalog of Fishes: Genera, Species, References. Available at <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp/> (last accessed 29 January 2016).
- Koopman, M. T., Brown, L. P. & Gason, A. S. H. (2008). Integrated Scientific Monitoring Program – Great Australian Bight Trawl Fishery Annual Report 2006. *Report to Australian Fisheries Management Authority, Project No. R03/1552*. Marine and Freshwater Research Institute, Queenscliff, Victoria. pp. 35. Available at www.afma.gov.au/wp-content/uploads/2010/06/R2006-0611_GABTF.pdf
- Lyle, J. M., Bell, J. D., Chuwen, B. M., Barrett, N., Tracey, S. R. & Buxton, C. D. (2014). Assessing the impacts of gillnetting in Tasmania: implications for by-catch and biodiversity. *FRDC Report 2010/016*. Institute for Marine and Antarctic Studies, University of Tasmania, Hobart. Available at frdc.com.au/research/final-reports/Pages/2010-016-DLD.aspx
- Sasaki, T. (1986). Development and present status of Japanese trawl fisheries in the vicinity of seamounts. In *Environment and Resources of Seamounts in the North Pacific* (Uchida, R. N., Hayasi, S. & Boehlert, G. W., eds), pp. 21–30. *NOAA Technical Report NMFS 43*. Available at www.cbd.int/doc/meetings/mar/ebsa-np-01/other/ebsa-np-01-submission-noaa-02-en.pdf