Abstract—The Indian halibut (*Psettodes erumei*) is an important flatfish species in tropical and subtropical waters of the northern Indian Ocean. However, inappropriate aging methods used in previous studies of Indian halibut limited the use of age and growth data from those studies. This study highlights the importance of correct aging methods and identification of sexually dimorphic growth, particularly if growth characteristics are used to estimate mortality rates. Counts of opaque zones in whole otoliths of Indian halibut were almost always fewer than those in their corresponding sections, particularly for older individuals. Multiple validation methods have been used to demonstrate that opaque zones form annually in otoliths of Indian halibut. Although the frequency of females increased with size, because of sexually dimorphic growth, males attained a greater maximum age (16 versus 11 years). Because of the greater ages and rapid early growth of Indian halibut described in this study, natural mortality estimates calculated by using the Pauly equation, particularly for males, were higher than estimates derived from the same equation in previous studies, which employed growth parameter estimates based on ages derived from whole otoliths, vertebrae, or monthly length–frequency trends and, typically, did not account for sexually dimorphic growth. In northwestern Australia, spawning in Indian halibut commences when water temperature and day length begin to increase and occurs between early spring and late summer.

Biological characteristics of the primitive flatfish Indian halibut (*Psettodes erumei*) from the tropical northeastern Indian Ocean, including implications of the use of incorrect aging methods on mortality estimates

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Globally, flatfish species (flounders, halibuts, and soles) are an important group of fish species, contributing over 1 million metric tons (t) to world fisheries production in 2014 (FAO[1]; Nelson et al., 2016). The Indian halibut (*Psettodes erumei*) is a moderate-sized flatfish distributed in tropical and subtropical waters of the Indian and western Pacific Oceans, where it is an important component of trawl fisheries (Mathew et al., 1992; Vivekanandan et al., 2003). The annual catch of Indian halibut from 3 of the tropical fishing regions designated by the Food and Agricultural Organization of the United Nations ranged from ~15,000 to ~30,000 t between 2000 and 2011 (Gibson et al., 2015). In waters of India, where the majority of previous research on Indian halibut has been carried out (e.g., Pradhan, 1962; Hussain, 1990; Mathew et al., 1992; Gilanshahi et al., 2012), this species

constituted ~1300 t of the total flatfish catch in 2012 (Nair and Gopalakrishnan, 2014). Although most flatfish have eyes on the right-hand (dextral) or left-hand side (sinistral) of the mouth (Nelson et al., 2016), a few species, including the Indian halibut and its 2 congeners, have varying proportions of dextral to sinistral polymorphism (Hubbs and Hubbs, 1945; Policansky, 1982). In addition, spiny dorsal and pelvic fin rays, vertebrae number, mouth structure, and upright swimming behavior are characteristics that separate *Psettodes* species from other flatfishes and why they are considered the most primitive form of flatfish (Hubbs and Hubbs, 1945; Platt, 1983).

The importance of choosing the appropriate aging structure and then validating the periodicity of growth increments has been made clear (Beamish and McFarlane, 1983; Campana, 2001), as have the implications of not doing so (c.f. Mace et al., 1990; Smith et al., 1995). Previous age estimates for Indian halibut have been derived from counting growth rings in

vertebrae (Edwards and Shaher, 1991), scales (Druzhinin and Petrova, 1980), and whole otoliths (Das and Mishra, 1990), and none of those methods were validated; ages also have been estimated by examining trends displayed by monthly length frequencies (Silvestre and Garces, 2004; Gilanshahi et al., 2012). The use of vertebrae to age fish has been associated with large discrepancies in age estimates between readers (e.g., Esteves et al., 1995; Filmalter et al., 2009) and interpretation difficulties (e.g., Baker and Timmons, 1991; Marriott and Cappo, 2000; Khemiri et al., 2005). Although scales have been shown to be a useful aging structure for which removal is not lethal (e.g., Robillard and Marsden, 1996; Khan and Khan, 2009), the accuracy of ages derived from counts of growth zones on scales is questionable (Beamish and McFarlane, 1983). Even though whole otoliths are suitable to age short-lived species (e.g., Fairclough et al., 2000; Kornis et al., 2017), for many fishes, including a number of flatfishes, it has been acknowledged that ages based on whole otoliths are often underestimated (e.g., Campana, 1984; Forsberg[2]; Stevens et al., 2005; Albert et al., 2009).

Previous estimates of the instantaneous rate of natural mortality (M) for Indian halibut, calculated by using the Pauly (1980) empirical equation, range from 0.51 to 0.76 year^{-1} (Edwards and Shaher, 1991; Silvestre and Garces, 2004; Gilanshahi et al., 2012) and are higher than the median value of 0.41 year^{-1} for members of the Pleuronectidae (Froese and Pauly[3]). The fact that the landings of Indian halibut in waters of India have declined by ~70% over the past 30 years, even as the overall catch of flatfishes has increased over the same period (Nair and Gopalakrishnan, 2014), indicates that the level of fishing pressure on this species may have been too high, possibly as a result of management advice based on unreliable age estimates.

This study was undertaken to determine the biological characteristics, including age, growth trends, timing and duration of spawning, and lengths and ages at maturity, of Indian halibut in waters off northwestern Australia. Because of the now known unreliability of the aging structures or methods that have previously been used to age Indian halibut in other regions, this study aimed to provide sound age estimates based on proven and validated aging methods, thereby facilitating accurate estimates of growth and of both natural and total mortality. The data were also used to test the hypothesis that, as reported for many other flatfishes (e.g., Stevens et al., 2005; Félix et al., 2011; Black et al., 2013), male Indian halibut grow faster than females, and females grow to a larger size. Furthermore, it has been hypothesized that the beginning of the spawning period for

Indian halibut, like that of other subtropical species, is associated with increasing day length and water temperatures (Lam, 1983).

Materials and methods

Sample collection and fish measurements

Large (>250 mm in total length [TL]) Indian halibut were purchased whole from a wholesale market in Perth, Australia, in each month between February 2014 and December 2015, such that 20–50 fish were collected for each calendar month. These fish were taken as bycatch by commercial bottom trawlers that deployed standard stern trawling gear (a single net with extension sweeps) at depths of 50–200 m in the eastern Indian Ocean off the Pilbara coast in northwestern Australia (approximately between 19°S, 120°E and 20°S, 116°E), where the catch is largely composed of lutjanid and lethrinid species (Wakefield et al.[4]; Newman et al.[5]). Additional smaller individuals, 35–215 mm TL), caught in August 2015 and September 2017, were provided by the Western Australian Department of Primary Industry and Regional Development. These fish were caught during research surveys off the Pilbara coast, by using an otter trawl with net mesh sizes of 229 mm (9 in) in the wings and 110 mm (4.3 in) in the pocket.

The TL and total body mass of each Indian halibut was measured to the nearest 1 mm and 0.1 g, respectively. The eye side (i.e., right or left) of each fish was recorded, and the sagittal otoliths of each fish were removed, cleaned, dried, and stored in envelopes.
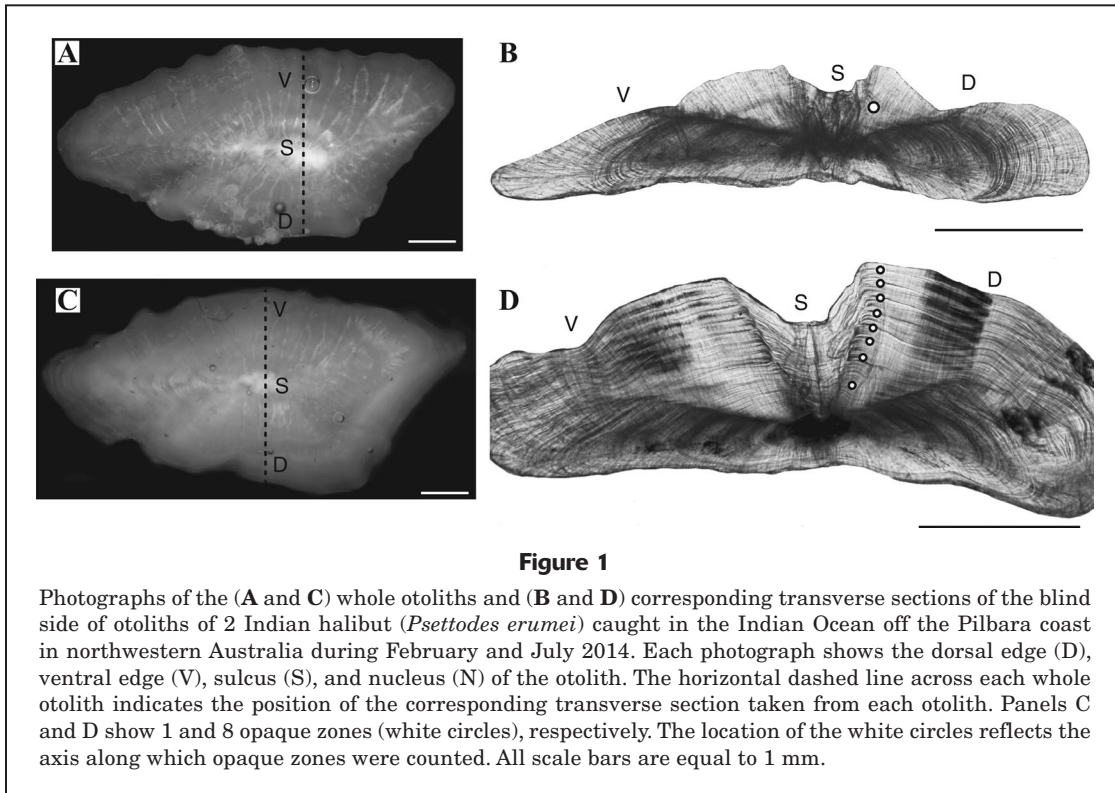
Mean monthly sea-surface temperatures in waters off the Pilbara coast, for the 1° grid block of 19–20°S, 117–118°E, were calculated from monthly values in 2010–2015 obtained from the Koninklijk Nederlands Meteorologisch Instituut Climate Explorer (available from website), which employs data from Reynolds optimum interpolation analysis of sea-surface temperatures (Reynolds et al., 2007). Daily lengths of days for the town of Karratha (~22°S, 117°E), on the Pilbara coast, obtained from timeanddate.com (day length data available from website), were employed to generate mean monthly day lengths for 2014 and 2015.

[2] Forsberg, J. E. 2001. Aging manual for Pacific halibut: procedures and methods used by the International Pacific Halibut Commission. Tech. Rep. 46, 50 p. [Available from website.]

[3] Froese, R., and D. Pauly (eds.). 2017. FishBase, vers. 12/2017. World Wide Web electronic publication. [Available from website, accessed January 2018.]

[4] Wakefield, C. B., S. Blight, S. R. Dorman, A. Denham, S. J. Newman, J. Wakeford, B. W. Molony, A. W. Thomson, C. Syers, and S. O'Donoghue. 2014. Independent observations of catches and subsurface mitigation efficiencies of modified trawl nets for endangered, threatened and protected megafauna bycatch in the Pilbara fish trawl fishery. Fish. Res. Rep. 244, 33 p. West. Aust. Dep. Fish., North Beach, Australia. [Available from website.]

[5] Newman, S., C. Wakefield, C. Skepper, D. Boddington, R. Jones, and P. Dobson. 2017. North coast demersal resource status report 2016. *In* Status reports of the fisheries and aquatic resources of Western Australia 2015/16: the state of the fisheries (W. J. Fletcher, M. D. Mumme, and F. J. Webster, eds.), p. 144–152. West. Aust. Dep. Fish., Perth, Australia. [Available from website.]

Figure 1

Photographs of the (**A** and **C**) whole otoliths and (**B** and **D**) corresponding transverse sections of the blind side of otoliths of 2 Indian halibut (*Psettodes erumei*) caught in the Indian Ocean off the Pilbara coast in northwestern Australia during February and July 2014. Each photograph shows the dorsal edge (D), ventral edge (V), sulcus (S), and nucleus (N) of the otolith. The horizontal dashed line across each whole otolith indicates the position of the corresponding transverse section taken from each otolith. Panels C and D show 1 and 8 opaque zones (white circles), respectively. The location of the white circles reflects the axis along which opaque zones were counted. All scale bars are equal to 1 mm.

Otolith preparation and age determination

The otolith corresponding to the *blind side* of each Indian halibut (i.e., the side of the fish facing downward and therefore having no eyes) was selected for aging purposes because it has been proven that the blind-side otolith in some flatfishes provides a clearer interpretation of growth zones than the eye-side otolith (Lear and Pitt, 1975; Forsberg[2]; Armsworthy and Campana, 2010). The whole blind-side otoliths of 272 fish were each placed in a black dish with low viscosity immersion oil, with the ventral side facing upward, and photographed under reflected light by using a Leica DFC 425 camera (Leica Microsystems Inc.[6], Buffalo Grove, IL) mounted on a Leica MZ7.5 dissecting microscope (Leica Microsystems Inc.). Captured images were viewed by using Leica Application Suite, vers. 4.3 (Leica Microsystems Inc.), enabling opaque zones in each otolith to be marked and counted. The number of opaque zones in the whole blind-side otoliths were counted on a single occasion by the primary reader (senior author).

Those same otoliths were cleaned, dried, and embedded in a clear epoxy resin, along with the blind-side otoliths from another 265 individuals, and cut transversely through the primordium into sections of ~250–300 μm with a low-speed diamond saw (IsoMet Low Speed Precision Cutter, Buehler Ltd., Lake Bluff, IL). Otolith sections

were then mounted on microscope slides by using DePeX mounting adhesive (VWR International LLC, Radnor, PA) and a coverslip. Digital images of each sectioned otolith were taken, by using a 12-MP Olympus DP70 camera (Olympus Corp., Tokyo, Japan) mounted on an Olympus BX51 compound microscope (Olympus Corp.) and by employing transmitted light.

Counting of opaque zones on the digital images of sectioned otoliths was facilitated by the use of Leica Application Suite, which enabled such zones to be marked and readily counted and the distances required for marginal increment analysis to be measured with confidence (Coulson et al., 2021). Opaque zones on the edge of the dorsal side of the otolith section, closest to the sulcus, were counted (Fig. 1). Measurements for marginal increment analysis were recorded to the nearest 0.01 mm and taken on an axis perpendicular to the opaque zones on the dorsal side.

To validate that a single opaque zone is formed annually in the otoliths of Indian halibut, we analyzed trends observed throughout the year by using the mean monthly marginal increments (MI) on sectioned otoliths (i.e., the distance between the outer edge of the single or outermost opaque zone and the otolith periphery). When one opaque zone is present, the MI was expressed as a proportion of the distance between the primordium and the outer edge of the single opaque zone. When 2 or more opaque zones were present, the MI was expressed as a proportion of the distance between the outer edges of the 2 outermost opaque zones. An approach based on the methods

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[6] Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

of Okamura and Semba (2009) was applied to determine the periodicity of occurrence of otoliths of Indian halibut with marginal increments falling within the lower 30th percentile of values for each category of zone counts (Coulson et al., 2016, 2017). For this analysis, binomial models linked with von Mises circular distributions were fitted by assuming 1) no cycle, 2) an annual cycle, or 3) a biannual (twice yearly) cycle. When compared by using the Akaike information criterion (AIC), the model with the lowest value was deemed to best represent the data (Burnham and Anderson, 2002).

The number of opaque zones in all sectioned otoliths were counted twice by the primary reader, with the counts from the second read considered the most accurate. The level of precision between the primary reader's second counts and those of a second experienced reader (J. Poad) for a subsample of 280 otoliths was assessed by calculating the coefficient of variation (CV) (Chang, 1982; Campana, 2001):

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

where CV_j = the age precision estimate for the jth fish;
  X_{ij} = the ith age determination for the jth fish;
  X_j = the mean age estimate for the jth fish; and
  R = the number of times each fish is aged.

Growth and sex ratio

Each Indian halibut was assigned an age, on the basis of the number of opaque zones in sectioned otoliths, the date of capture of the fish, the "average" birth date (i.e., the approximate midpoint of the spawning period; see the "Reproductive biology" subsection in the "Results" section) of 1 December, and the time of year when the outermost opaque zone typically becomes delineated in the otoliths. Growth was described by fitting von Bertalanffy growth curves to the lengths at age of the females and males, with estimates of von Bertalanffy growth function (VBGF) parameters, and their 95% confidence limits, obtained by using a nonlinear function in R, vers. 3.4.1 (R Core Team, 2017). The VBGF used was as follows:

$$L = L_\infty\left(1 - e(-k(t - t_0))\right), \qquad (2)$$

where L = the total length (in millimeters) at age t (in years),
  L_∞ = the estimated asymptotic total length (in millimeters);
  k = the growth coefficient (year^{-1}); and
  t_0 = the hypothetical age (in years) at which fish have zero length.

A likelihood-ratio chi-square test was used to compare the growth curves from the VBGF for female and male Indian halibut. The test statistic was twice the difference between the log-likelihoods obtained by fitting growth curves to the lengths at age for each sex, separately, and by fitting

a common growth curve to all lengths at age regardless of sex (Cerrato, 1990). The hypothesis that the growth of the 2 groups could be represented by a single growth curve was rejected at the level of significance (α) of 0.05 if the previously mentioned test statistic exceeded $\chi^2_\alpha(q)$, where q is the difference between the numbers of parameters in the 2 approaches, for example, a difference of 3 numbers (Cerrato, 1990). The log-likelihood (λ) for each curve, ignoring constants, was calculated as follows:

$$\lambda = (-n/2) \ln(ss/n), \qquad (3)$$

where n = sample size; and
  ss = the sum of the squared residuals between the observed and expected lengths at age.

Chi-square tests were used to determine whether the ratio of females to males in each of the main TL and age classes, as well as the sex ratio for all TLs and ages collectively, differed significantly from parity.

Spawning time and maturation

When identifiable as ovaries or testes, the mass of the gonads of each Indian halibut was weighed to the nearest 0.01 g. On the basis of its macroscopic characteristics, each ovary was allocated to one of the following 4 groups of maturity stages adapted from the criteria used by Laevastu (1965): virgin and immature or resting (stages 1 and 2); developing and maturing (stages 3 and 4); prespawning and spawning (stages 5 and 6); and spent and recovering (stages 7 and 8). Ovaries at stages 3–7 in each year were considered likely to become mature (stages 3–5) or to have matured (stages 6–7) during that year; therefore, for convenience, ovaries at these stages are referred to as *mature*. The prevalence of females and males with gonads at each developmental stage in each month was determined.

Because all female Indian halibut >300 mm TL collected during the spawning period possessed mature gonads, the mean monthly gonadosomatic indices (GSIs) for females were determined by using all individuals greater than this length. For males, the mean monthly GSIs were determined by using individuals with lengths greater than or equal to the TLs at which 50% of the males attained maturity (L_{50}) (see the "Lengths and ages at maturity" subsection in the "Results" section). For both sexes, the mean monthly GSI was determined by using this equation:

$$GSI = (GM / TM) / TM \times 100, \qquad (4)$$

where GM = wet gonad mass, and
  TM = wet total body mass.

To confirm the macroscopic gonoad staging, histological sections were prepared from the gonads of a subsample of the Indian halibut collected in each month; the subsample of fish had a wide range of lengths, and their gonads were at all maturity stages found in fish in that month. Depending on the size of the gonads, they were placed in Bouin's fixative for 24–48 h, prior to being dehydrated in a series of increasing concentrations of ethanol. The mid-region

of each gonad was next embedded in paraffin wax, cut into 6-µm transverse sections, and stained with Mallory's trichrome.

The TLs at which 50% and 95% of males reached maturity, together with their 95% confidence limits, were determined by using logistic regression analysis, as has been done in similar studies for other species (Coulson et al., 2005, 2009). Fish were considered mature (i.e., about to spawn, spawning, or just spawned) if they possessed gonads at a maturity level between stage 3 and stage 8. The spawning period is defined as the consecutive months in which ≥50% of fish possessed gonads at stage 5 or 6, together with elevated mean monthly GSIs. Logistic regression analysis was restricted to males obtained during the spawning period, from September through February (see the "Reproductive biology" subsection in the "Results" section). The form of the logistic model relating the probability that a male Indian halibut is mature to its TL is as follows:

$$P = \{1 + e[-\ln(19)\,(L - L_{50})/(L_{95} - L_{50})]\}^{-1}, \qquad (5)$$

where P = proportion mature;
$\quad L$ = total length in millimeters;
$\quad L_{50}$ = total lengths in millimeters at which 50% of fish were mature; and
$\quad L_{95}$ = total lengths in millimeters at which 95% of fish were mature.

Mortality estimates

In northwestern Australia, the Indian halibut is considered a bycatch species and is caught in very low numbers in a fishery that targets larger bodied, more valuable lutjanids, lethrinids, and serranids (WADF[7]). This low level of catch is indicated, for example, by the total weight of Indian halibut available on market days at the wholesale market in Perth typically ranging only between 5 and 15 kg (senior author, personal observ.), with all fish available on a particular day, in some instances, being purchased for this study. Therefore, the sizes and ages of fish collected for this study are assumed to be representative of the population of this species in northwestern Australia.

Estimates of the M of females and males were calculated from their maximum individual ages, by using both the Hoenig (1983) and Hoenig$_{NLS}$ (Then et al., 2015) equations, with the estimates from the latter equation recognized as the more reliable (Maunder and Piner, 2015). The estimates of M, derived with the Hoenig (1983) equation, are provided to make comparisons possible because this equation has been widely used in previous studies. To further enable comparisons with previous studies (Edwards and Shaher, 1991; Silvestre and Garces, 2004; Gilanshahi et al., 2012), M was also estimated by using the Pauly (1980) empirical

equation for length and by using a water temperature of 27°C (i.e., the mean annual sea-surface temperature for waters off the Pilbara coast).

For catch curve analysis, only those age classes consisting of individuals 1 year older than the age at full recruitment for each sex (i.e., 4 years) were used (Ricker, 1975), with the remaining age classes assigned an age relative to the age at full recruitment (i.e., the first fully recruited age was assigned the age of zero). Total mortality (Z) for fully recruited fish was estimated by using the Chapman and Robson (1960) approach, as implemented in the chapmanRobson function of the FSA package (vers. 0.8.6; Ogle, 2016) in R.
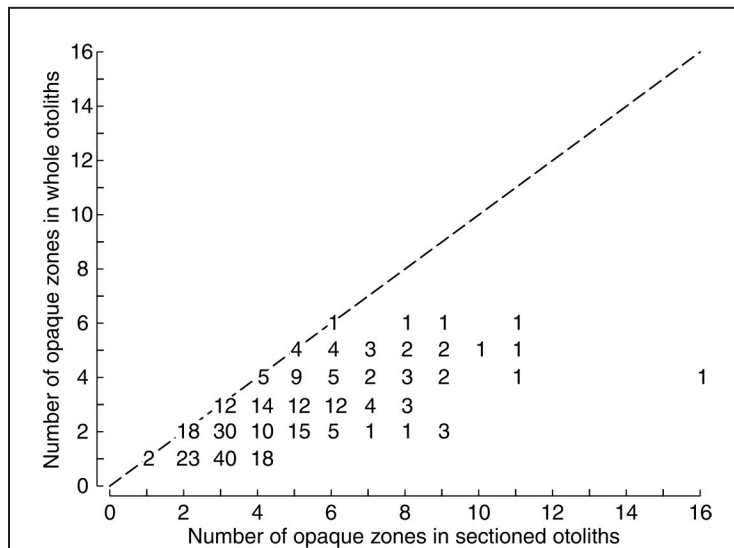
Results

Whole versus sectioned otoliths

Although a single opaque zone was visible in all of the whole otoliths whose sections also possessed a single opaque zone, the level of agreement between the opaque zone counts for whole otoliths and for their corresponding sections decreased rapidly (Fig. 2). For example, the same number of opaque zones were visible in only 4 of the 41 otoliths in which 5 opaque zones were visible in their sections. There was no agreement in opaque counts when the number of opaque zones in sections was ≥7. In the most severe case, only 4 opaque zones were clearly visible in a whole otolith whose corresponding section revealed 16 opaque zones (Fig. 2).

Validation of aging methods

The mean monthly MIs on sectioned otoliths of Indian halibut with 2–4 opaque zones remained ≤0.41 between January and March before increasing to 0.49 in May and to a maximum of 0.57 in July (Fig. 3). The mean monthly MI remained at elevated levels in August and September, before declining rapidly to a minimum in December. The mean monthly MIs for otoliths with ≥5 opaque zones in other months of the year followed a similar trend, increasing from low levels in January to a maximum in September, before declining to lower levels in December (Fig. 3). The single pronounced decline and then progressive increase of the mean monthly MIs during the year for otoliths with different numbers of opaque zones indicates that a single opaque zone is formed annually in the otoliths of Indian halibut. The validity of the notion that the mean monthly MIs followed a single cycle during the year is substantiated by the results in this study from circular distribution models (Okamura and Semba, 2009; Coulson et al., 2016). For otoliths with 2–4 opaque zones and ≥5 opaque zones, the accompanying AIC values of 302 and 169, respectively, for an annual cycle were less than the AIC values of 309 and 183 for no cycle and 312 and 182 for a biannual cycle; in addition, the difference between the former value and the AIC values of the latter 2 cycles exceeded 2, the number required to

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[7] WADF (Western Australia Department of Fisheries). 2010. A bycatch action plan for the Pilbara fish trawl interim managed fishery. Fish. Manage. Pap. 244, 24 p. West. Aust. Dep. Fish., Perth, Australia. [Available from website.]

Figure 2

Bias plot of opaque zone counts showing the level of agreement between the counts of the number of opaque zones in whole otoliths and their corresponding sections from Indian halibut (*Psettodes erumei*) caught as bycatch by commercial trawlers between February 2014 and December 2015 and with an otter trawl during research surveys between August 2015 and September 2017 off the Pilbara coast in northwestern Australia. Values represent the number of individual otoliths. The diagonal dashed line represents perfect agreement between counts of the 2 readers.

identify definitively the best model in terms of the Kullback–Leibler distance for the 2 groups of otoliths (Burnham and Anderson, 2002). The number of opaque zones in sectioned otoliths can, therefore, be used for aging individual Indian halibut.

The sectioned otoliths of 5 small Indian halibut (135–196 mm TL) caught in August (late winter) contained a large, central opaque region and a surrounding wide translucent area, and, in 2 cases, an opaque edge. The sectioned otoliths of several similarly sized fish (151–211 mm TL) and of larger individuals (272–310 mm TL), caught in the same month, possessed the same characteristics but, in addition, contained 1 and 2 recently formed and diffuse opaque zones, respectively, that had become delineated from the otolith edge through the presence of a narrow, translucent zone at the otolith margin. The patterns of opacity within the otoliths of several small Indian halibut provide strong evidence that the first opaque zone is formed during the first winter of life, when Indian halibut are on average ~8 months old. Therefore, those Indian halibut caught in August with a wide translucent zone surrounding the nucleus and with an opaque zone on, or just delineated from, the edge of the otolith were ~9 months old. Those fish with 2 opaque zones in their otoliths, the second being recently deposited, were therefore ~21 months old.

The resultant CV of 1.85% indicates a high level of agreement between the counts of opaque zones for each otolith

by each reader, falling well below the reference level of 5% for correspondence recommended by Campana (2001).
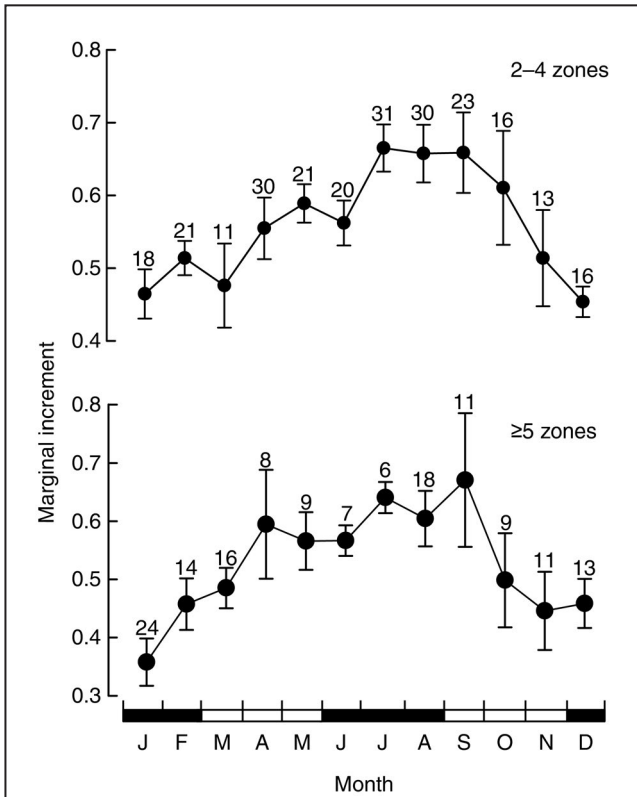
Length and age compositions and growth

The numbers of female and male Indian halibut <250 mm TL, all of which were largely collected in trawl nets during research surveys, were very similar (Fig. 4). Although males were far more abundant in the length classes of 250–299 mm TL and 300–349 mm TL, caught by commercial trawlers, females were considerably more abundant than males in the length class of 350–399 mm TL. The 2 largest length classes were composed of females exclusively (Fig. 4). The ratios of females to males in the 3 length classes of the commercially caught fish that contained both sexes, 250–299 mm TL, 300–349 mm TL, and 350–399 mm TL, were 0.2:1.0, 0.8:1.0, and 12.8:1.0, respectively. For all 3 of these length classes, the sex ratio was significantly different from parity (the χ^2 statistic for each class was 53.0, 4.1, and 56.8, respectively, with $P>0.05$ for all of them). The TLs of the largest female and male were 469 and 380 mm TL, respectively, with these fish also having the greatest total body mass for their sex, 1773 and 752 g, respectively.

Male Indian halibut were more abundant in the youngest and 3 oldest age classes in which both sexes were present, but females were more abundant in the age class of 4–5 years (Fig. 3). A single male constituted the oldest age class of 16–17 years. The ratio of females to males in each age class that contained ≥20 individuals varied from 0.6:1.0 in the age classes of 6–7 years and 8–9 years to 1.3:1.0 in the age class of 4–5 years. However, for no age class was the sex ratio significantly different from parity (χ^2=0.6–3.1, $P>0.05$). The maximum ages recorded for female and male Indian halibut were 11 and 16 years, respectively.

The length–mass relationships for the female and male Indian halibut were not significantly different ($P=0.24$); therefore, the length–mass data for both sexes were pooled and described by using this equation:

$$\ln TM = 3.17(\ln L) - 12.20 \qquad (6)$$

(coefficient of determination [r^2]=0.99, sample size [n]=544). The von Bertalanffy growth curves for female and male Indian halibut provide good fits to the lengths at ages for the individuals of each sex (Fig. 5), as indicated by the high values for the r^2 for each sex (Table 1). The von Bertalanffy growth curves for females and males, which were significantly different ($P<0.001$), increasingly diverged with increasing age, a pattern that is reflected in the values for L_∞ and k (Table 1). On the basis of estimates from the VBGF, females attained lengths of 196, 322, 379, and 392 mm TL at 1, 3, 6, and 9 years of age compared with
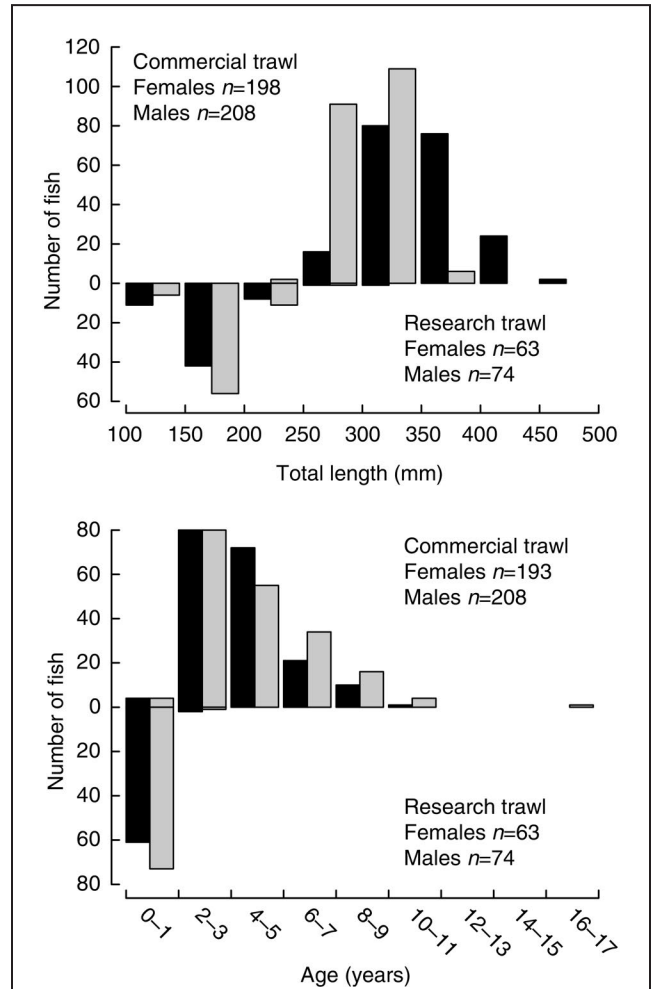
Figure 3

Mean monthly marginal increments of sectioned otoliths, with 2–4 opaque zones and with ≥5 opaque zones, from Indian halibut (*Psettodes erumei*) caught by commercial trawlers between February 2014 and December 2015 and during research surveys between August 2015 and September 2017) off the Pilbara coast in northwestern Australia. Error bars indicate standard errors of the mean. Sample sizes are given above error bars. Black bars on the *x*-axis indicate summer and winter months, and open bars indicate autumn and spring months.

Figure 4

Length–frequency and age–frequency distributions for female (black bars) and male (gray bars) Indian halibut (*Psettodes erumei*) caught as bycatch by commercial trawlers between February 2014 and December 2015 and with an otter trawl during research surveys between August 2015 and September 2017 in the Indian Ocean off the Pilbara coast in northwestern Australia. *n*=sample size.

the lengths of 201, 287, 314, and 318 mm TL, respectively, attained by males at the same ages.

Reproductive biology

Mean monthly temperatures in offshore waters, adjacent to the Pilbara coast, increased steadily from a minimum of 24.4°C in August (late winter) to a maximum of 30.0°C in March (mid-autumn) before declining to 25.6°C in June (early winter) (Fig. 6). Day length was shortest in June (early winter) and longest in December (early summer) (Fig. 6).
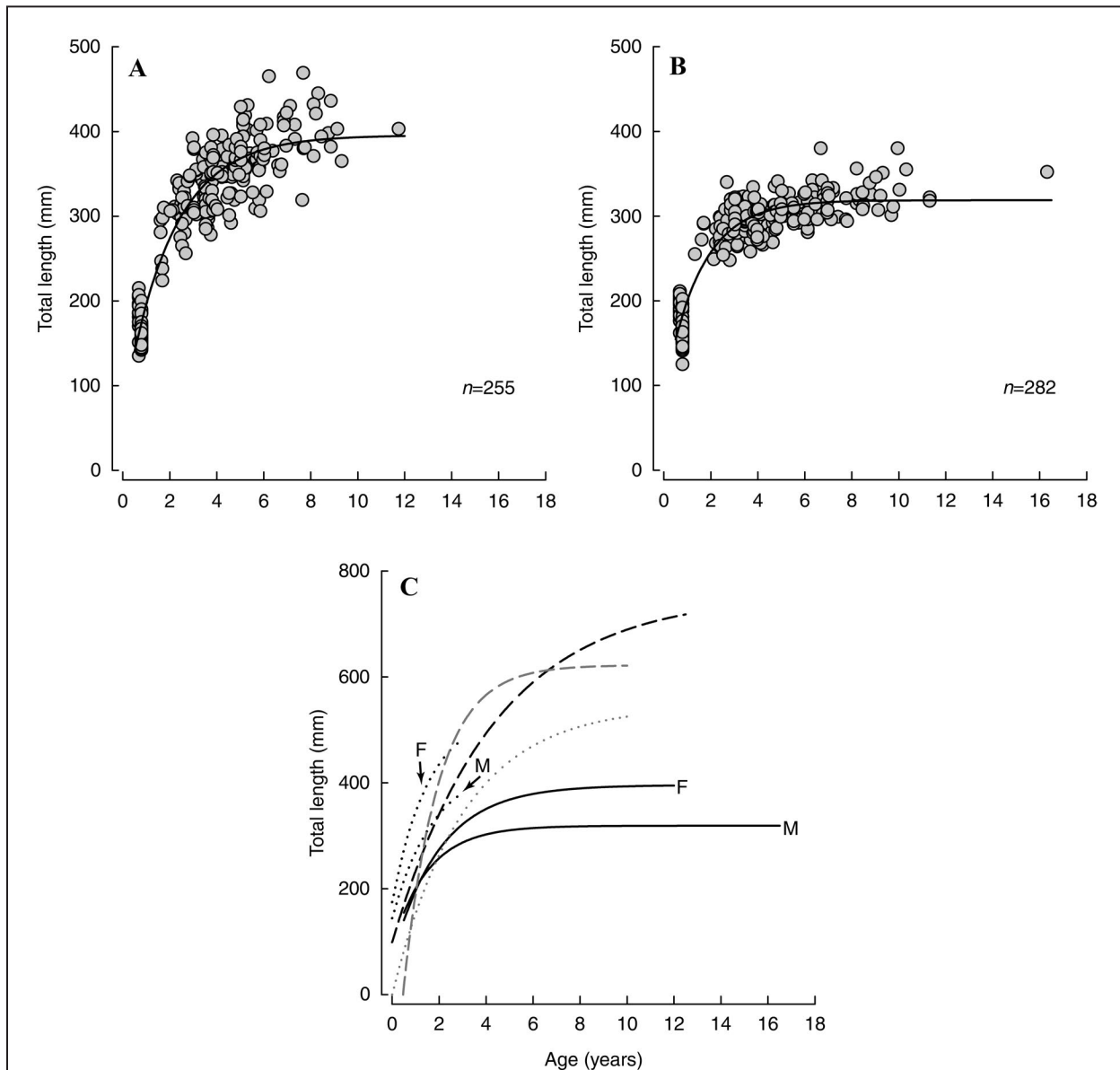
The mean monthly GSI for female Indian halibut rose sharply from 0.6 in July to a well-defined maximum of 6.6 in October. Although it declined to 4.0 and 4.7 in December and January, respectively, the mean monthly GSI for females remained at levels >4.0 until February, after which it declined precipitously to 1.2 in April and to a minimum of 0.6 in June (Fig. 6). The mean monthly GSI for male Indian halibut followed the same trend.

All female Indian halibut sampled from May through July possessed ovaries that were either immature or resting (stage 2) or spent and recovering (stages 7 and 8). The frequency of females with ovaries at such stages declined in August, when those with mature or spawning ovaries (stages 5 and 6) were first present (Fig. 7). The vast majority of females sampled between September and February had ovaries in stages 5 and 6. Although ~45% of females in March also possessed ovaries in those stages, a similar proportion of females had ovaries in stages 7 and 8. The frequency of females with such ovaries increased to ~92% in April (Fig. 7). The trends in the frequency of occurrence of male Indian halibut with testes at different stages of development followed closely that of the females, in that males with mature or spawning

Figure 5

von Bertalanffy growth curves fit to total lengths at age for (**A**) female and (**B**) male Indian halibut (*Psettodes erumei*) caught by commercial trawlers in February 2014–December 2015 and during research surveys in August 2015–September 2017 off the Pilbara coast in northwestern Australia. Samples sizes (*n*) are given for each graph. (**C**) Comparisons of growth curves fit to the lengths at age of female (F) and male (M) Indian halibut from northwestern Australia (solid black lines) and from the northwestern Bay of Bengal (dotted black lines) (Das and Mishra, 1990) and of growth curves fit to the lengths at age of females and males combined from Brunei (dotted gray line) (Silvestre and Garces, 2004), the Gulf of Aden (dashed gray line) (Edwards and Shaher, 1997), and the Persian Gulf (dashed black line) (Gilanshahi et al., 2012). Growth curves from Gilanshahi et al. (2012) and Silvestre and Garces (2004) were derived from trends in monthly length frequencies, and curves from Das and Mishra (1990) and Edwards and Shaher (1997) are based on individual fish aged by using whole otoliths and vertebrate, respectively.

testes (stages 5 and 6) largely dominated samples collected between September and February.

Although the prevalence of female and male Indian halibut with gonads at stages 5–8 between September and February increased, the abundance of individuals with gonads at stages 3 and 4 declined markedly or were not even present. Still, female and male Indian halibut with gonads at stages 3 and 4 more than likely become mature during the spawning season. Therefore, fish with gonads at stages 3 and 4 and at stages 5–8 were collectively regarded as mature for the purposes of estimating length and age at maturity. Trends in the GSIs and prevalences of females and males

Table 1

Estimates of parameters of the von Bertalanffy growth function (VBGF) for female (F) and male (M) Indian halibut (*Psettodes erumei*) caught in the Indian Ocean off the Pilbara coast in northwestern Australia by commercial trawlers as bycatch between February 2014 and December 2015 and during research surveys with an otter trawl between August 2015 and September 2017. The parameters are the asymptotic length (L_∞) in total length, growth coefficient (k), and hypothetical age at which fish have zero length (t_0). The upper and lower 95% confidence limits, coefficient of determination (r^2), and sample size (n) are provided for each estimate. Values were derived from the total lengths at age of individuals. The VBGF parameters obtained for Indian halibut in other studies are provided for comparison. The values for L_∞ and k from Gilanshahi et al. (2012) and Silvestre and Garces (2004) were derived from trends in monthly length frequencies, and those from Edwards and Shaher (1997) and Das and Mishra (1990) are based on individual fish aged by using vertebrae and whole otoliths, respectively.

| | | | VBGF parameter | | | | |
| | | | L_∞ | k | t_0 | | |
Source	Sex	Value	(mm)	(year^{-1})	(years)	r^2	n
This study	F	Estimate	395	0.49	−0.38	0.88	255
		Upper	407	0.57	−0.22		
		Lower	384	0.42	−0.55		
	M	Estimate	319	0.66	−0.51	0.88	282
		Upper	324	0.76	−0.33		
		Lower	313	0.56	−0.69		
Edwards and Shaher (1997)	Both		622	0.68	0.46		
Silvestre and Garces (2004)	Both		545	0.33			
Gilanshahi et al. (2012)	Both		745	0.23	−0.61		
Das and Mishra (1990)	F		535	0.64	−0.61		
	M		436	0.56	−0.72		

with mature or spawning gonads (stages 5 and 6) indicate that the spawning period for Indian halibut in northwestern Australia extends from September through February.

Lengths and ages at maturity

Because all female Indian halibut with TLs <225 mm that were caught during the spawning period were immature and all those with TLs >300 mm had mature gonads (stages 3–8), no attempt was made to determine an L_{50} for this sex (Fig. 8). All male Indian halibut <250 mm TL that were caught during the spawning period, except 2 individuals (163 and 164 mm TL), were immature (Fig. 7). The percentage of mature males increased sharply to 50% and 85% in the length classes of 250–274 and 275–299 mm TL, with all males ≥300 mm TL being mature. The L_{50} and L_{95}, and their upper and lower 95% confidence intervals (CIs), for male Indian halibut were estimated to be 268 mm TL (95% CI: 250–288 mm TL) and 284 mm TL (95% CI: 255–325 mm TL), respectively.

All females and most males that were ≤1 year old and caught during the spawning period were immature (Fig. 7). In contrast, all females that were 2–9 years old and most males that were 2–10 years old, and caught during the spawning period, were mature. This result indicates that, generally, female and male Indian halibut do not mature until they are almost 2 years old.
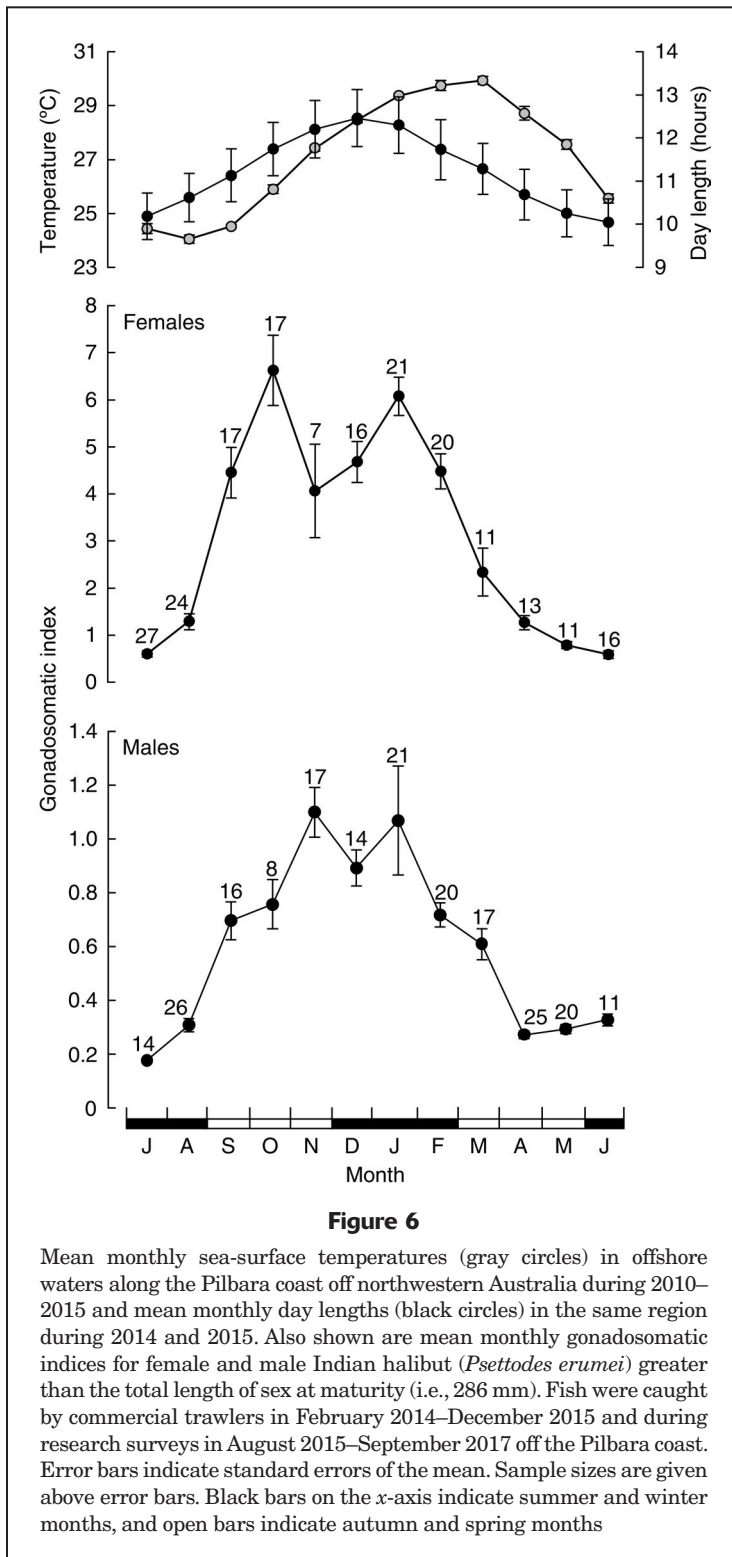
Mortality

Estimates for M of female and male Indian halibut, derived by using the Pauly (1980) equation and the respective VBGF parameters, were far higher than those derived by using either the Hoenig (1983) equation or the Then et al. (2015) equation, both of which use the maximum age of each sex (Table 2). In addition, the M values estimated by using the equation of Then et al. (2015) were slightly greater than those derived by using the Hoenig (1983) equation, noting that, through cross validation, Then et al. (2015) established that their equation provided a better estimate of published values of M than other equations that they tested. The catch curve estimates of Z for both sexes were slightly less than the corresponding estimates of M derived from use of the Then et al. (2015) equation (Table 2).

Discussion

Method of aging

The results of the comparison between the number of opaque zones in whole otoliths and the number in their corresponding sections indicate that ages of Indian halibut estimated from counts of opaque zones in whole otoliths, even when the numbers of such zones are few, are

Figure 6

Mean monthly sea-surface temperatures (gray circles) in offshore waters along the Pilbara coast off northwestern Australia during 2010–2015 and mean monthly day lengths (black circles) in the same region during 2014 and 2015. Also shown are mean monthly gonadosomatic indices for female and male Indian halibut (*Psettodes erumei*) greater than the total length of sex at maturity (i.e., 286 mm). Fish were caught by commercial trawlers in February 2014–December 2015 and during research surveys in August 2015–September 2017 off the Pilbara coast. Error bars indicate standard errors of the mean. Sample sizes are given above error bars. Black bars on the *x*-axis indicate summer and winter months, and open bars indicate autumn and spring months
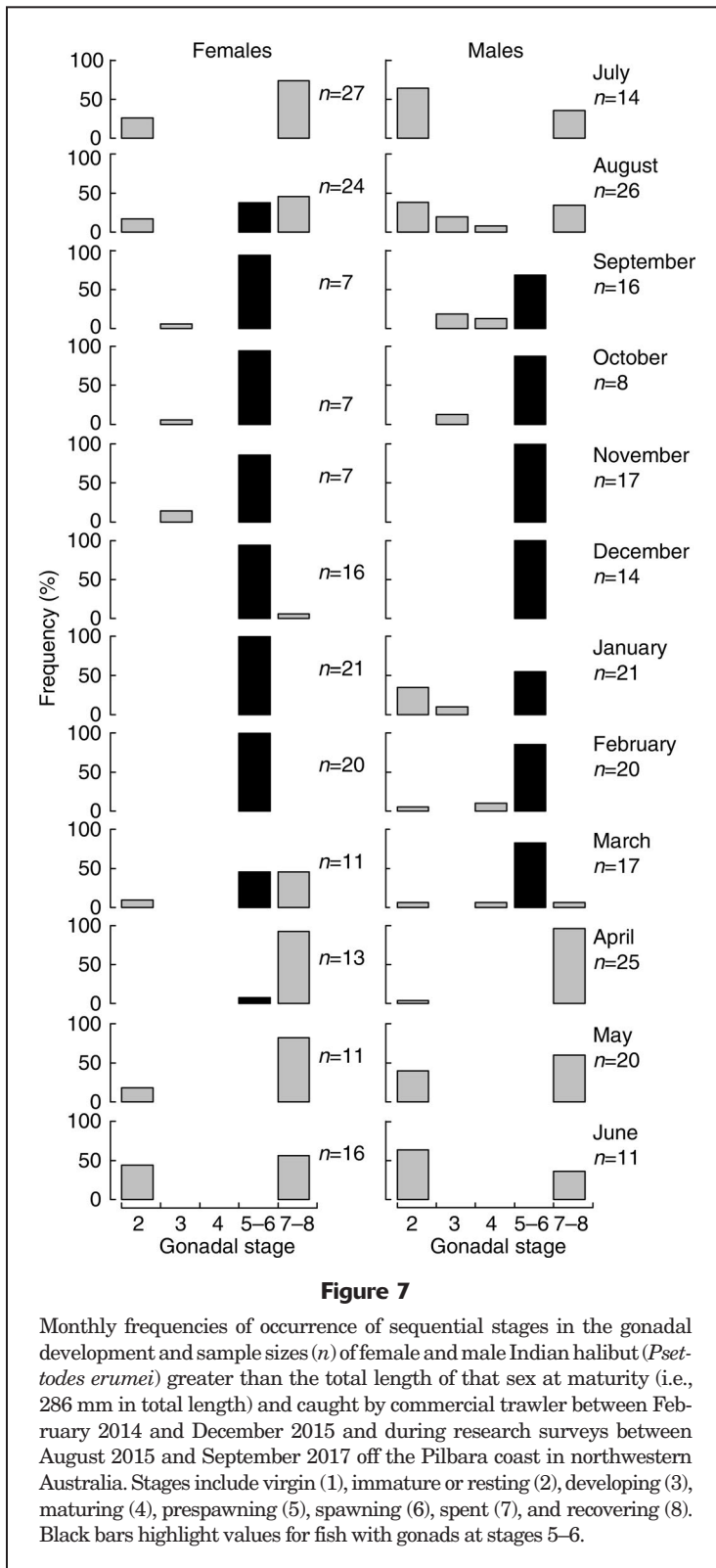
flounder (*Platichthys stellatus*) (Campana, 1984), New Zealand brill (*Colistium guntheri*) and *C. nudipinnis* (Stevens et al., 2005), marbled flounder (*Pseudopleuronectes yokohamae*) (Lee et al., 2009), and turbot (*Scophthalmus maximus*) (Yoneda et al., 2007). The finding of a maximum age of 16 years for Indian halibut from northwestern Australia, from use of sectioned otoliths in this study, indicates that this species is much longer lived than the maximum age of 3 years that has been obtained for this species in waters of northeastern India by using whole otoliths (Das and Mishra, 1990). The maximum age determined in our study also is slightly older than the age of 12.4 years that has been obtained for this species in the Persian Gulf by analyzing trends in monthly length frequencies (Gilanshahi et al., 2012).

In other regions, Indian halibut have been caught as large as 640 and 705 mm TL (Hussain, 1990; Gilanshahi et al., 2012) and, because of the sexually dimorphic growth of this species, are most likely to be females. Considering that the oldest female (11 years old) collected in this study was only 403 mm TL, it is not unreasonable to expect that Indian halibut may attain ages ≥20 years. However, in those regions where Indian halibut is an important component of the commercial catch, regions such as those in the Arabian Sea, Persian Gulf, Gulf of Oman, and Bay of Bengal, fish ages have been determined by counts of growth zones in vertebrae or whole otoliths (Das and Mishra, 1990; Hussain, 1990; Edwards and Shaher, 1991). These apparently unvalidated aging methods have led to estimates of a maximum age of only 3 years that, if employed in mortality estimates when developing management plans for this species, would grossly overestimate the resilience of this species to fishing pressure (see the "Mortality" subsection later in this section). Therefore, we recommend that, for those regions where Indian halibut account for an important component of the fishery, age estimates be determine from sectioned otoliths. Although analysis of trends in monthly length–frequency data by Gilanshahi et al. (2012) has provided a more realistic estimate of maximum age, for a species in which growth is negligible for a large proportion of their adult life, this method of aging is not recommended (e.g., Morales-Nin, 1989).

Growth

Results from comparisons of the von Bertalanffy growth curves indicate that female and male Indian halibut have different growth patterns, with females attaining a larger size at age than males. This pattern of sexually dimorphic growth is a common feature of many flatfishes, including those of the Paralichthyidae and Pleuronectidae

considerably underestimated. Although this species is not long-lived, the thickness, and therefore the opacity, of otoliths prevent annuli from being readily detected when otoliths are read whole; similar results have been reported for other flatfish species, such as the starry

Figure 7

Monthly frequencies of occurrence of sequential stages in the gonadal development and sample sizes (*n*) of female and male Indian halibut (*Psettodes erumei*) greater than the total length of that sex at maturity (i.e., 286 mm in total length) and caught by commercial trawler between February 2014 and December 2015 and during research surveys between August 2015 and September 2017 off the Pilbara coast in northwestern Australia. Stages include virgin (1), immature or resting (2), developing (3), maturing (4), prespawning (5), spawning (6), spent (7), and recovering (8). Black bars highlight values for fish with gonads at stages 5–6.
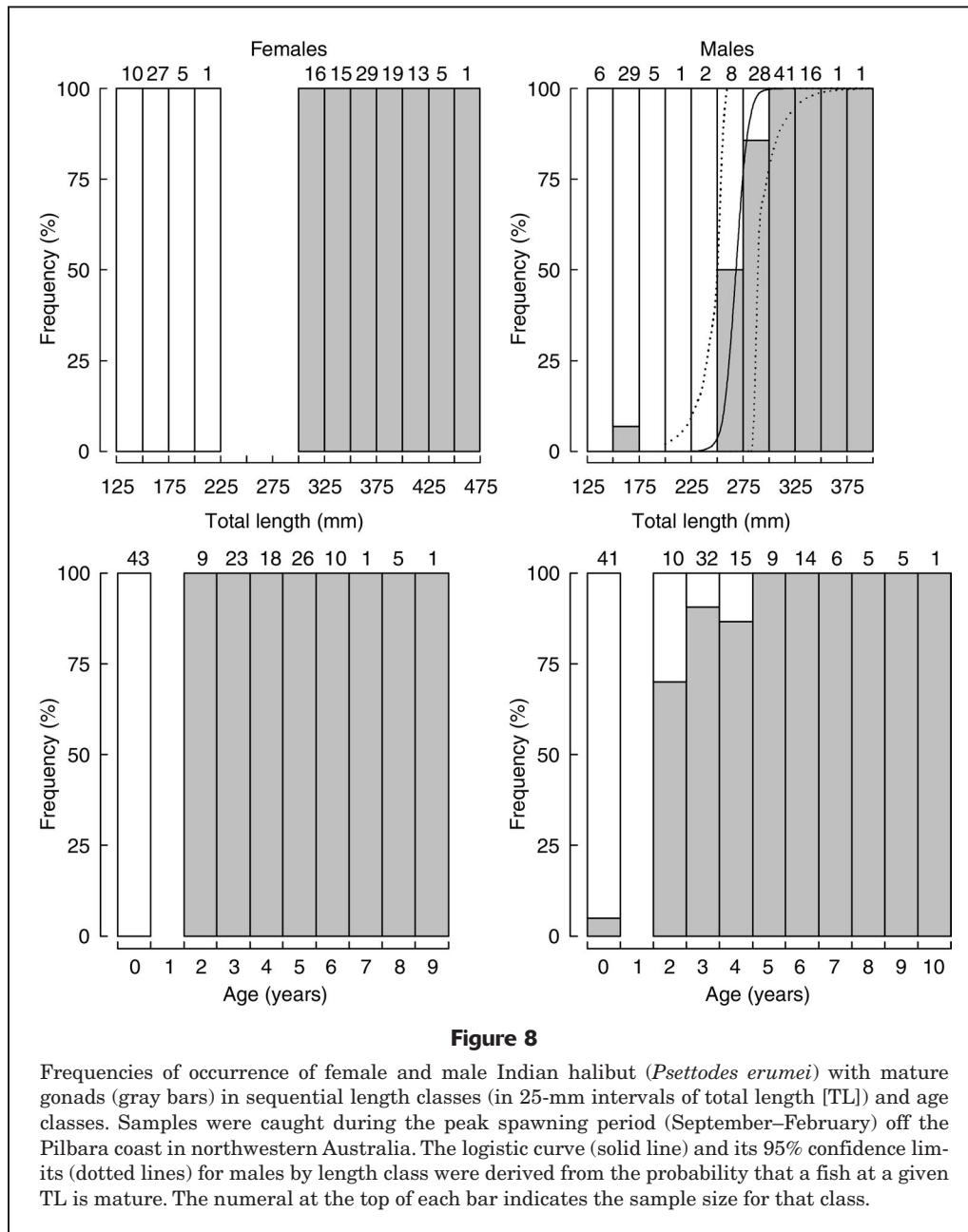
Indian halibut no difference was assumed, and growth curves were fit to data for females and males combined (Fig. 4; Hussain, 1990; Edwards and Shaher, 1991; Gilanshahi et al., 2012).

The results of this study indicate that the early growth of females and males is similarly rapid, with the majority of growth occurring in the first 3–4 years of life. Although findings from previous growth studies indicate rapid early growth as well, they also indicate that growth is sustained, with little or no asymptote (Table 1, Fig. 5). The discrete length modes of individual age groups identified in monthly length–frequency data of fast growing, short-lived species enable programs, such as the systems of methods known as electronic length–frequency analysis (ELEFAN) and multiple length–frequency analysis (MULTIFAN), to be valuable alternatives for determining fish growth (e.g., Morales-Nin and Aldebert, 1997; Bellido et al., 2000; Campana, 2001). If applied to long-lived, slow-growing species, however, these tools involve the use of the well-defined length modes of the youngest cohorts of a species to fit a growth model to all fish (Campana, 2001). Species that have a broad spawning period are also not suitable for such analysis because the long spawning period results in age cohorts with a wide length distribution that obscures the distinction between those cohorts (Morales-Nin and Ralston, 1990).

Spawning

Latitude, and therefore water temperature, influences the timing and duration of the spawning period of fishes (e.g., Gray et al., 2012; Wakefield et al., 2015). The commencement of the spawning period for Indian halibut in late winter or early spring is typical of temperate species (e.g., Hyndes and Potter, 1997; Morato et al., 2007; Gray and Barnes, 2015; Coulson et al., 2017), in which an increasing photoperiod or rising temperatures stimulate gonadal recrudescence (Lam, 1983). However, the timing of the spawning period of Indian halibut through spring and summer is also similar to that of a range of teleost species in tropical and subtropical waters (e.g., Mackie, 2000; Sumpton and Brown, 2004; Grandcourt et al., 2006; Russell and McDougall, 2008).

Results from reproductive studies of Indian halibut in the Arabian Sea by Hussain (1990), at a latitude (~24–25°N) higher than that considered in this study, indicate that the spawning period for Indian halibut occurred early and was far more restricted, from March (boreal early spring) through May (boreal late spring), than the spawning period observed in this study. However, Ramanathan and Natarajan (1979) determined that, at the far lower latitude of ~11°N in the Arabian Sea, Indian halibut had a more extended spawning period, from May through

(e.g., MacNair et al., 2001; Fischer and Thompson, 2004; Pearson and McNally, 2005; Yoneda et al., 2007). Das and Mishra (1990) identified a difference in length at age of the 2 sexes (Fig. 4), but in the other previous studies of

Figure 8

Frequencies of occurrence of female and male Indian halibut (*Psettodes erumei*) with mature gonads (gray bars) in sequential length classes (in 25-mm intervals of total length [TL]) and age classes. Samples were caught during the peak spawning period (September–February) off the Pilbara coast in northwestern Australia. The logistic curve (solid line) and its 95% confidence limits (dotted lines) for males by length class were derived from the probability that a fish at a given TL is mature. The numeral at the top of each bar indicates the sample size for that class.

September (boreal mid-autumn), a period that is similar in terms of timing and duration to that found in this study for fish from northwestern Australia at ~19–20°S. In contrast, in the Bay of Bengal at latitudes of 19–20°N, Indian halibut spawn from August (boreal late summer) through December (boreal early winter) (Pradhan, 1962; Das and Mishra, 1990), similar to the spawning time of other teleosts in that region (Rao, 1983). The difference in the timing and duration of the spawning period of Indian halibut in the Bay of Bengal, compared with those of fish in similar latitudes off northwestern Australia and in the Arabian Sea may be related to the influence of the monsoons and freshwater input into coastal waters in the region of Bay of Bengal.

During the summer monsoon season, the Bay of Bengal becomes highly stratified, with a surface layer of freshwater because weaker winds prevent vertical mixing (Prasanna Kumar et al., 2002; Sengupta et al., 2006). In contrast, coastal upwelling along the southern part of the west coast of India and upwelling, wind-driven mixing, and lateral advection in open-ocean waters (Bauer et al., 1991; Lee et al., 2000; Prasanna Kumar et al., 2001; Krishnakumar and Bhat, 2008) make the Arabian Sea more productive. Off northwestern Australia, where the nutrient-deficient Leeuwin Current is the dominant oceanographic feature (Cresswell and Golding, 1980; Koslow et al., 2008), rainfall and terrestrial input from rivers is limited (Molony et al., 2011). Although in other regions, the increase in water

Table 2

Maximum age, natural mortality (*M*), and total mortality (*Z*) for female (F) and male (M) Indian halibut (*Psettodes erumei*) caught by commercial trawlers between February 2014 and December 2015 and during research surveys between August 2015 and September 2017 in northwestern Australia. Estimates of *M* were calculated by using the Pauly (1980), Hoenig (1983), and Then et al. (2015) equations, and estimates of *Z* (provided with standard errors in parentheses) were calculated by using the catch curve method of Chapman and Robson (1960). Estimates of *M* from Gilanshahi et al. (2012) and Silvestre and Garces (2004) were based on estimates of von Bertalanffy growth function parameters, asymptotic length and growth coefficient, derived from trends in monthly length frequencies, and those from Edwards and Shaher (1997) are based on individual fish aged by using vertebrae. Estimates of *Z* from Gilanshahi et al. (2012) and Silvestre and Garces (2004) were derived from length-converted catch curves.

			M			*Z*
Source	Sex	Max. age	Pauly (1980)	Hoenig (1983)	Then et al. (2015)	Chapman and Robson (1960)
This study	F	11	1.02	0.40	0.55	0.39 (0.09)
This study	M	16	1.31	0.28	0.39	0.32 (0.07)
Edwards and Shaher (1997)	Both		0.76			
Silvestre and Garces (2004)	Both		0.73			0.85
Gilanshahi et al. (2012)	Both		0.51			1.20

temperature from its winter minimum may provide a cue for the onset of gonadal development for Indian halibut, in the Bay of Bengal, it appears that spawning may be delayed until the post-monsoon period, when primary productivity is greatest (Choudhury and Pal, 2010) and when suitable prey for recently spawned larvae is abundant.

Mortality

The estimates of *M* for females, and particularly for males, derived in this study by using the Pauly (1980) equation were far higher than the values derived by using the same method in previous studies (Table 2). Because *k* is used for the Pauly (1980) equation, the resultant value for *M* reflects the accuracy of the estimates of that parameter. The results of the studies carried out by Silvestre and Garces (2004) and Gilanshahi et al. (2012) indicate that the growth of Indian halibut is slow and does not reach an asymptote (Fig. 4C), as reflected by lower values for *k* from those studies: 0.33 year^{-1} and 0.23 year^{-1}, respectively, in comparison with *k* values from our study. In the cases of those studies, the use of *k* to estimate *M* for Indian halibut is not suitable, firstly because *k* is not reliably estimated (i.e., monthly length–frequency data) and secondly because the estimated *k* values reflect a species that never reaches its asymptotic length (Kenchington, 2014). Although in our study *k* was estimated reliably by using individual length at (validated) ages, the fact that females and males grew rapidly in the first 2–3 years, after which growth slowed appreciably, also prohibits those *k* values for each sex from being employed to estimate *M* (Kenchington, 2014).

Direct estimates of *Z* should always exceed the true *M* value. Results from this study indicate that indirect estimates of *M* for female and male Indian halibut, derived from the Hoenig$_{NLS}$ equation of Then et al. (2015), exceed the estimates of *Z* and are therefore considered overestimates (Coulson et al., 2017). However, indirect estimates of *M* for each sex derived by using the equation of Hoenig (1983) are more consistent with those of *Z*. The similarity in values of *Z* and *M*, from the Hoenig (1983) equation, is consistent with the fact that, in northwestern Australia, the Indian halibut is a bycatch species. This similarity in mortality values parallels the mortality estimates for 4 of 5 platycephalid species from southwestern Australia that are caught as bycatch in commercial fisheries that target other species, as part of the catch in multispecies commercial fisheries, or as catch in low numbers in a recreational fishery (Coulson et al., 2017).

The use of mortality estimates that supposedly reflect a species that has high natural mortality, when those estimates are based on underestimates of age, may lead fisheries managers to set catch limits higher than is suitable for a species that actually has far lower natural mortality rates. It is, therefore, imperative that the management of Indian halibut in those regions where this species accounts for a significant proportion of catch, and the management of species that have similar life history characteristics (i.e., sexually dimorphic growth, rapid initial growth, and medium longevity), is based on a sound understanding of their biology, determined by using proven and validated techniques.

Conclusions

This study is the first comprehensive investigation of the biological characteristics of Indian halibut. The greater

number of opaque zones visible in sectioned otoliths compared with the number visible in the corresponding whole otolith indicates the importance of identifying the correct aging structure and preparation methods to enable the provision of reliable fish ages. The maximum age of 16 years observed in this study was much greater than the previous estimate of 3 years from whole otoliths. In addition, this study found that Indian halibut have sexually dimorphic growth, a finding that has implications for the use of growth characteristics to estimate natural mortality. Although the Indian halibut is a bycatch species in the trawl fishery in northwestern Australia, in other regions of the northern Indian Ocean, this species is far more important. In those regions, the information provided in this study, in particular the ages, growth characteristics, and mortality estimates, will be important to fisheries agencies for developing appropriate management plans for Indian halibut.

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