

# The life history characteristics of *Neosebastes pandus* and the relationship between sexually dimorphic growth and reproductive strategy among Scorpaeniformes

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## Abstract

Scorpaeniformes are an important component of commercial and recreational fisheries world-wide. The *Neosebastes* species, found in the western Pacific and south-east Indian Ocean, have received little attention from a research perspective. Samples of the bighead gurnard perch, *Neosebastes pandus*, collected from the lower west and south coasts of Western Australia, were used to undertake the first comprehensive investigation of the biological characteristics of a *Neosebastes* species. Opaque zones in sectioned sagittal otoliths were validated as forming annually. Female *N. pandus* grow to a significantly larger size, on average, than males and dominate the largest size classes, while males, growing to a smaller size, accumulate in the intermediate size classes. Although males were far less numerous than females in those age classes in which both sexes were found, males and females attain similar maximum ages >25 years. *Neosebastes pandus* spawns over a brief period between May (austral late autumn) and July (austral mid-autumn) when water temperature and day length are declining. The mean monthly gonadosomatic indices (GSI,  $I_{GS}$ ) values of females during the spawning period are 37–50 times higher than those of males, which mature at an earlier age and smaller length compared to females. Histological examination of the ovaries of females indicate that their structure is consistent with “general” teleost ovarian anatomy and thus differs from *Scorpaena*, *Helicolenus* and *Sebastes* species whose ovaries are adapted for specialized reproductive modes. The reproductive strategy of *N. pandus* of maximizing the reproductive output of females, by this sex attaining a larger size than males and pair spawning (i.e., large disparity in  $I_{GS}$  values) demonstrates the close lineage between the *Neosebastes* and other Scorpaeniformes, such as the *Scorpaena*, *Helicolenus* and *Sebastes*.

## KEYWORDS

growth, longevity, maturity, Neosebastidae, otoliths, spawning

## 1 | INTRODUCTION

The Neosebastidae (gurnard perches) is one of the nine Scorpaeniforme families (Smith *et al.*, 2018). This family consists of two genera and 18 species, with the *Neosebastes* consisting of 12 of those species (Nelson *et al.*, 2016). Characterized by a prominent head

covered in strong spines and ridges, large eyes and mouth, as well as possessing venomous spines, the *Neosebastes* are found in waters between the west Pacific and south-east Indian Oceans, with seven species occurring in southern Australian waters (Gomon *et al.*, 2008). The bighead gurnard perch *Neosebastes pandus* (Richardson, 1842), the largest species in the *Neosebastes* genus, attaining a maximum

standard length of 480 mm, is endemic to southern Australian waters between Houtman Abrolhos Island (28.4°S, 113.5°E) and Kangaroo Island, South Australia (35.8°S, 137.2°E) and is most commonly found in water depths of 50–200 m (Gomon *et al.*, 2008; Hutchins & Swainston, 1986). A recent study of the diet of *N. pandus* from south-western Australia demonstrated that, while cephalopods, brachyurans and teleosts were the largest overall contributors to their diet, teleosts and polychaetes were more important to diets of *N. pandus* on the lower-west coast and south coasts, respectively. In addition, the more diverse diet of *N. pandus* on the lower-west coast compared to the south coast was attributed to differences in habitat between the two coasts (Greenwell *et al.*, 2018).

Although many other Scorpaeniformes, such as *Scorpaena*, *Helicolenus* and *Sebastes* species, are commercially important (Gertseva *et al.*, 2017; Paul & Horn, 2009; Stewart & Hughes, 2010), *Neosebastes* species are considered an incidental catch in commercial trawl and line fisheries. In addition, the vast majority of *Neosebastes* species, including *N. pandus*, caught by recreational fishers in Western Australia are released (Ryan *et al.*, 2015), presumably due to their venomous spines (Gomon *et al.*, 2008). Thus, the majority of our knowledge of the biological characteristics of Scorpaeniformes is restricted to those species that are commercial and/or recreationally important. The deeper water *Helicolenus* and *Sebastes* species have been shown to be moderately and very long-lived, attaining ages of up to ~50 (e.g., Abecasis *et al.*, 2006; Paul & Horn, 2009) and >100 years (Cailliet *et al.*, 2001; Gertseva *et al.*, 2017), respectively, while the shallow water *Scorpaena* species are shorter-lived, attaining ages of between 5 and 35 years (Scarcella *et al.*, 2011; Stewart & Hughes, 2010). A common feature of Scorpaeniformes is sexually dimorphic growth. While the females of *Platycephalus* (e.g., Coulson *et al.*, 2017; Gray & Barnes, 2015) and *Sebastes* (e.g., Heo *et al.*, 2015; Laidig *et al.*, 2003; Wyllie Echeverria, 1986) species typically grow larger than their males, the reverse is true for the majority of the studied *Scorpaena* (e.g., Bilgin & Çelik, 2009; Stewart & Hughes, 2010) and *Helicolenus* species (e.g., Kelly *et al.*, 1999; Massutí *et al.*, 2000; Paul & Horn, 2009).

Families within the Scorpaeniformes display a diverse range of reproductive strategies. Although the majority of species are gonochoristic, apart from some *Platycephalids* which exhibit protandrous hermaphroditism (e.g., Fujii, 1970, 1971; Shinomiya *et al.*, 2003), their reproductive strategy in regard to egg fertilization and the degree of “reproductive output” varies. For example, *Platycephalus* species exhibit external fertilization (oviparity) and the mean monthly gonadosomatic indices ( $I_{GS}$ ) during the spawning period for males, in most cases, are ~20–70% of those of their females (e.g., Coulson *et al.*, 2017; Jordan, 2001; Masuda *et al.*, 2000). While *Scorpaena* species are also oviparous, the mean  $I_{GS}$  values for males during the spawning period are often <5% of that of their females (e.g., Love *et al.*, 1987; Muñoz *et al.*, 2005; Stewart & Hughes, 2010). In addition, male *Scorpaena* species are known to release thick seminal fluid, proposed to keep spermatozoa together and facilitate fertilization of the eggs, which are released

by females in a gelatinous egg mass (Koya & Muñoz, 2007; Muñoz *et al.*, 2002a; Wourms, 1991). Although the disparity in “reproductive output” of female and male *Sebastes* (e.g., Colton & Larson, 2007; Love *et al.*, 1990) and *Helicolenus* (e.g., Muñoz & Casadevall, 2002) species parallels that of *Scorpaena* species, species of the former two genera exhibit internal fertilization. While *Helicolenus* species display an intermediate form of viviparity, releasing fertilized eggs in a gelatinous egg mass (e.g., Koya & Muñoz, 2007; Sequeira *et al.*, 2011), *Sebastes* species exhibit more advance viviparity, releasing live young (e.g., Boehlert & Yoklavich, 1984; Wourms, 1991).

In regard to the life history characteristics of Neosebastids, there is no published information on the biology of any species within this family. Thus, the present study was undertaken to determine the length and age compositions, growth, spawning period and length and age at maturity of *N. pandus* in south-western Australia. The results of this study were used to examine how the biology of *N. pandus* compares to other temperate Scorpaeniformes, specifically *Scorpaena*, *Helicolenus* and *Sebastes* species. The variety of the reproductive strategies displayed by Scorpaeniformes are discussed, particularly in relation to the extent of sexually dimorphic growth.

## 2 | MATERIALS AND METHODS

### 2.1 | Sampling regime

Samples of large ( $\geq 225$  mm total length) *N. pandus*, caught by commercial saucer scallop (*Amusium balloti* Bernardi, 1861) trawlers in waters off Rottnest Island (~32.0°S, 115.5°E) on the lower west coast of Western Australia, were collected as filleted frames, with their viscera intact, from fish processors or purchased as whole fish from a market between July and September 2012 (Austral winter and early spring), and January and May 2013 (Austral summer and autumn) (Supporting Information Table S1). An additional five individuals were collected in January 2015 from waters off Cape Naturaliste (~33.5°S, 115.0°E) by a commercial line fisher. Rottnest Island and Cape Naturaliste are hereafter collectively referred to as the “west coast”. Samples of *N. pandus* from a wider total length range (138–427 mm), kept specifically for the purpose of this study, were caught by a commercial saucer scallop trawler operating off Esperance (hereafter referred to as the “south coast”), on the south-eastern coast of Western Australia (~33.9°S, 121.9°E), in May and June 2013, June and September 2014, and May and July 2015 (Supporting Information Table S1). Very little, or no, commercial trawling occurs between October and January due to the seasonal closure of the scallop fishery (Kangas *et al.*, 2011). On both the west and south coasts, commercial trawling was undertaken predominantly at depths of 15–40 m, using a trawl net with a mesh size of 50 mm in the wings and 45 mm in the cod-end that was towed at a speed of approximately 6.5 km/h for 60–180 min (Jones *et al.*, 2010).

## 2.2 | Length and weight measurements

The total length ( $L_T$ ) of all fish was measured to the nearest 1 mm and the total weight ( $W_T$ ) of each whole fish was recorded to the nearest 0.1 g. Analysis of covariance (ANCOVA), employing  $W_T$  as the dependent variable,  $L_T$  as the independent variables and sex as the fixed factor was employed to determine if the relationships between  $W_T$  and  $L_T$  were significantly different between sexes (see Results). While the  $W_T$  of some *N. pandus* collected from fish processors were recorded prior to filleting ( $n = 82$ ), in the majority of cases when  $W_T$  was not recorded ( $n = 191$ ) the length–weight relationship was used to estimate the  $W_T$  of these individuals (see Results). The gonad mass ( $M_G$ ) of each fish, except for five fish from the west coast whose gonads had largely been removed during filleting, but whose sex could still be identified for four of those individuals, was recorded to the nearest 0.01 g.

## 2.3 | Age determination, growth and mortality

The left sagittal otolith from each *N. pandus* was embedded in clear epoxy resin and cut transversely through its primordium into ~0.3 mm sections using an Isomet Buehler low-speed saw. The resulting sections were cleaned, dried and mounted on glass microscope slides using DePX mounting adhesive and a cover slip. Images of each sectioned otolith were taken using an Olympus DP70 camera mounted on an Olympus BX51 compound microscope and employing transmitted light. Counts of opaque zones and all measurements for marginal increment analysis were made on the dorsal side of the otolith, along the edge (crista superior) bordering 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 (MI) 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 *N. pandus*. The MI was expressed as a proportion of either the distance between the primordium and the outer edge of the single opaque zone, when one such zone was present, or the distance between the outer edges of the two outermost opaque zones when two or more such zones were present. See Coulson *et al.* (2009, 2010) for detailed methodology for ageing and its validation. In addition, the approach described by Okamura and Semba (2009) was applied to determine, statistically, 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 (a) no cycle, (b) an annual cycle or (c) 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).

While the number of opaque zones in all otoliths were counted by the author, the number of such zones in the sectioned otoliths of 100 *N. pandus*, which essentially covered the entire age range of this species, were also counted independently by another experienced otolith reader (A. Cottingham). The level of precision between the counts of the two readers was assessed by calculating the coefficient of variation (CV):

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

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

Each fish was assigned an age based on the number of opaque zones in its otolith, but taking into account the date of capture of the fish, the “average” birth date (commencement of the spawning period) of 1 May (see Results) and the time of year when the single or outermost of those zones become delineated. Von Bertalanffy growth curves (vBGCs) were fitted to the  $L_T$  values at age of the females and males of *N. pandus*. The von Bertalanffy growth equation has the form,  $L_T = L_{T\infty}(1 - e^{-k(t-t_0)})$ , where  $L_T$  is the total length (mm) at age  $t$  (years),  $L_{T\infty}$  is the asymptotic total length (mm) predicted by the equation,  $k$  is the growth coefficient ( $\text{year}^{-1}$ ) and  $t_0$  is the hypothetical age (years) at which fish would have zero length. A likelihood-ratio test (Cerrato, 1990) was used to compare the vBGCs of females and males on each coast and the growth curves of corresponding sexes on the two coasts. The test statistic was determined as twice the difference between the log-likelihoods obtained by fitting a common growth curve to the  $L_T$  values at age for sex/region collectively and by fitting separate growth curves to the  $L_T$  values at age for each sex/region. The hypothesis that the growth of the two groups could be appropriately represented by a single growth curve was rejected at the  $\alpha = 0.05$  level of significance if the above test statistic exceeded  $\chi_a^2(q)$ , where  $q$  is the difference between the numbers of parameters in the two approaches, i.e., 6 (Cerrato, 1990). The log-likelihood,  $\lambda$ , for each curve, ignoring constants, was calculated as  $\lambda = (-n/2) \ln(ss/n)$ , where  $n$  is sample size,  $ss$  refers to the sum of the squared residuals between the observed and expected  $L_T$  values at age and  $\ln$  represents the natural logarithm. When comparing the vBGCs, the percentage difference between the  $L_T$  values at age, as determined by those curves, was also used as an indication of whether any significant difference was of significant biological difference, with a difference between  $L_T$  values at age of <5% being considered of limited biological significance (Coulson, 2019; Coulson *et al.*, 2010).

Mortality estimates for female and male of *N. pandus* were calculated using the combined age composition data for fish collected from commercial trawlers on the west and south coasts. The natural mortality ( $M$ ) of females and males was determined using both the equation for fish in Hoenig (1983), i.e.,  $M = \exp(1.46)t_{\max}^{-1.01}$ , and the refitted version of this equation calculated by Then *et al.* (2015), i.e.,  $M = 4.899t_{\max}^{-0.916}$ , in which  $t_{\max}$  is the maximum age of the respective

sex. Employing the age composition data for female and male *N. pandus* that had been combined for the corresponding sexes on each coast, total mortality ( $Z \text{ year}^{-1}$ ) was calculated from catch curves (Chapman & Robson, 1960) using the frequencies of the individuals of each sex in 1 year age classes, following that at which the age frequency peaked (Smith *et al.*, 2012). Estimates of  $Z$  for each sex were taken as the median value of 5000 point estimates, with approximate 95% confidence limits of the parameters calculated as the 2.5 and 97.5 percentiles of the bootstrap estimates.

## 2.4 | Duration and prevalence of spawning

The sex of all *N. pandus* were identified macroscopically, except for one fish from the west coast whose gonads were removed during filleting. As the reproductive data for *N. pandus* from neither the west nor south coasts encompass all months of the year, and the differences between the spawning periods of fish species on the lower west coast and south coasts exhibit little, if any, differences (e.g., Coulson, 2019; Coulson *et al.*, 2010), the data from both coasts were combined to determine the spawning period, and lengths and ages at maturity of females and males.

On the basis of their macroscopic characteristics, the ovaries or testes of all other fish were assigned to one of the following four maturity stages adapted from the criteria used by Laevastu (1965): I/II, immature/resting; III/IV, developing/maturing; V/VI, pre-spawning/spawning; VII/VIII, spent/recovering. Individuals with stages III–VIII gonads in each year were considered likely to become mature (stages III–V) or to have matured (VI–VIII) because of the relatively discrete spawning time (see Results and Discussion) and have thus been classified as mature for the purpose of determining size and age at maturity (see later). In each month of sampling, gonads from a subsample of 10 individuals of each sex, and which encompassed all gonad stages recorded in that month, were used to confirm histologically that gonads had been macroscopically assigned to the appropriate stage of maturity.

Mean monthly gonadosomatic indices ( $I_{GS}$ ) were determined for female and male *N. pandus* with  $L_T$  greater than or equal to their corresponding  $L_{T50}$  at maturity (see later), using the equation  $I_{GS} = M_G/M_T \times 100$ , where  $M_G$  is wet gonad mass and  $M_T$  is wet body mass. The prevalence of the females and males with gonads at each developmental stage in each month was used in conjunction with monthly trends exhibited by the  $I_{GS}$  to define the spawning period of *N. pandus* and helped elucidate its peak.

The  $L_T$  values at which 50% and 95% of female and male *N. pandus* ( $L_{T50}$  and  $L_{T95}$ , respectively) attain maturity, together with their 95% confidence limits, were determined by logistic regression analysis, as in previous studies (Coulson *et al.*, 2005, 2017). Logistic regression analyses for each sex were restricted to data obtained during the spawning period (i.e., May to July). The form of the logistic model relating the probability that a female or male *N. pandus* is mature to its  $L_T$  was

$$P = 1 / \{1 + \exp[-\log_e(19)(L_T - L_{T50}) / (L_{T95} - L_{T50})]\}^{-1},$$

where  $P$  is the proportion mature,  $L_T$  is the total length in millimetres and  $L_{T50}$  and  $L_{T95}$  are the total lengths in millimetres at which 50% and 95% of fish were mature, respectively. This model was fitted by maximizing the log likelihood in R (R CoreTeam, 2018). Resampling with replacement was employed to determine the 95% confidence limits for the logistic parameters. The same logistic regression analysis was used, when possible, to estimate the ages at which 50% ( $A_{50}$ ) and 95% ( $A_{95}$ ) of female and male *N. pandus* attain maturity.

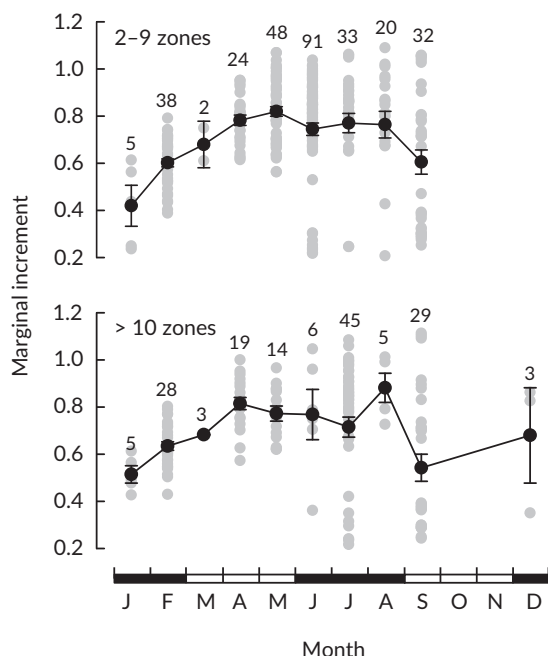
## 3 | RESULTS

### 3.1 | Validation of ageing using otoliths

The otolith of the smallest *N. pandus* (138 mm), caught in January (mid-summer), possessed a single opaque zone with a narrow translucent edge. The otoliths of the three small individuals (156–160 mm) caught in May (late autumn) and those of 10 small individuals (148–172 mm) caught in June (mid-winter) also possessed a single opaque zone, but their translucent edge was wider. Likewise, the otoliths of the majority of the 16 slightly larger fish (182–230 mm) caught in May and the 38 fish (170–229 mm) caught in June with two opaque zones possessed a very wide translucent margin, with the otoliths of seven of these fish also possessing an opaque margin. The otoliths of all three fish (185–213 mm) caught in September (early spring) with two opaque zones also possessed an opaque margin. As the spawning period for *N. pandus* is from May (late autumn) to July (mid-winter), when opaque zones are typically starting to form, or have formed, respectively, in the otoliths of fish species in south-western Australia (e.g., Coulson, 2019; Coulson *et al.*, 2010), it is presumed that the first opaque zone in the otoliths of *N. pandus* does not form until the second winter of life when the fish are ~12–15 months of age. It would thus follow that the smallest fish caught in January, May and June with a single opaque zone in their otoliths are ~21, 25 and 26 months old and those with two opaque zones caught in May, June and September are ~36, 37 and 42 months old.

The mean monthly marginal increments on otoliths of *N. pandus* with two to nine opaque zones increased from the minimum of 0.42 in January to 0.68 in March and remained elevated, i.e.,  $\geq 0.68$ , between April and August before declining to 0.61 in September (Figure 1). The mean monthly marginal increments on the otoliths of the species with  $\geq 10$  opaque zones followed essentially the same trend. The marginal increment for the otoliths of individual *N. pandus* indicates that the newly formed opaque zone becomes delineated from the edge of the otolith as early as June (mid-winter) and occurs until September (early spring) and January (mid-summer) (Figure 1).

The progressive increase and then single pronounced decline undergone during the year by the mean monthly marginal increments on sectioned otoliths of *N. pandus* with different numbers of opaque



**FIGURE 1** Individual marginal increment values (grey dots) and mean monthly marginal increments (black dots)  $\pm$  1 S.E. on sectioned sagittal otoliths of *N. pandus* 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

**TABLE 1** Akaike Information Criterion values for otoliths of *N. pandus* 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

	2–14 zones	$\geq 15$ zones
No cycle	191.1	356.9
Annual cycle	<b>165.2</b>	<b>301.1</b>
Biannual cycle	176.7	328.4

Note: Values in bold text are the smallest, for which the associated models were selected as best representing the data.

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 1). Thus, the AIC value of 165.2 and 301.1 for an annual cycle was less than that for no cycle or a biannual cycle for each of the two groups into which the otoliths had been pooled according to the number of their opaque zones, i.e., two to 14 and  $\geq 15$  opaque zones (Table 1). Furthermore, the difference between these two lowest AIC values and each of the other two AICs for the two groups of otoliths exceeded 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 of *N. pandus* can thus be used to age the individuals of this species.

The resultant CV of 4.5%, for the comparison between the age estimates of two readers, demonstrates an acceptable level of agreement between the counts of the two readers (Campana, 2001).

### 3.2 | Length–weight relationship, and length and age compositions

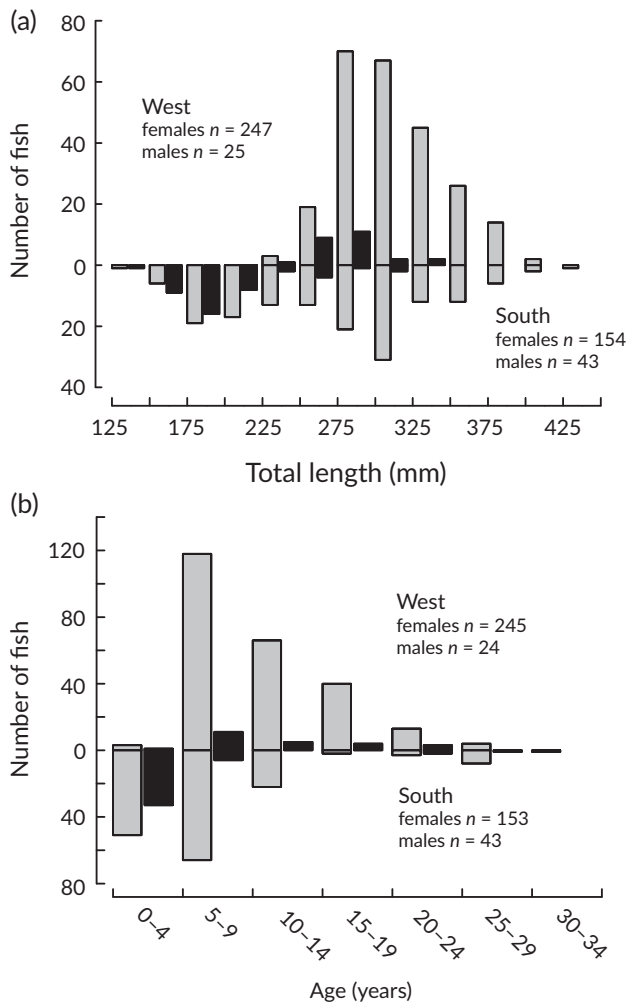
As there was no significant ( $P > 0.05$ ) difference between the length–weight relationships for females and males, the data for each sex were combined. The linear relationship between the natural logarithms of  $L_T$  and  $W_T$  for *N. pandus* is  $\ln W_T = 3.05(\ln L_T) - 11.18$  ( $P < 0.001$ ,  $r^2 = 0.94$ ,  $n = 279$ ). Female and male *N. pandus* caught in west coast waters ranged from 239 to 450 mm and 237 to 344 mm, respectively, and in age from 4 to 27 years and 4 to 23 years, respectively. Females and males caught in south coast waters ranged from 138 to 427 mm and 148 to 317 mm, respectively, and from 1 to 35 years and 2 to 28 years of age, respectively.

Both female and male *N. pandus* on the west coast were found in those length classes between 225 and 349 mm, but only females were found in any of the larger length classes (Figure 2a). On the south coast, females and males were found in the length classes between 125 and 324 mm, with females found exclusively in all larger length classes  $\geq 325$  mm (Figure 2a). On both coasts, in those length classes in which both females and males were present, females were more numerous in each case. On the west coast, although females and males were present in each age class between 5 and 24 years, only females were recorded in the oldest age class of 25–30 years (Figure 2b). Females and males were present in the two youngest age classes (i.e.,  $< 10$  years) on the south coast and also in the 20–24 and 25–29 years classes. Females were found exclusively in the 10–14 and 15–19 years classes, and also the oldest age class of 30–34 years (Figure 2b). On both coasts, the ratio of females to males in those age classes in which there were  $> 20$  fish was heavily skewed towards females, ranging from 4.3: 1 to 13.2: 1 on the west coast and 1.6: 1 to 11.0: 1 on the south coast. The overall female to male sex ratio was 10.2: 1 on the west coast and 3.6: 1 on the south coast.

### 3.3 | Growth and mortality

The likelihood ratio test for the vBGCs fitted to the lengths at age of female and male *N. pandus* on the west demonstrated that those curves were significantly different ( $P < 0.001$ ). Likewise, the vBGCs of females and males on the south coast were also significantly different ( $P < 0.001$ ). Although the vBGCs for the corresponding sexes from the two coasts were significantly different (females  $P < 0.001$ , males

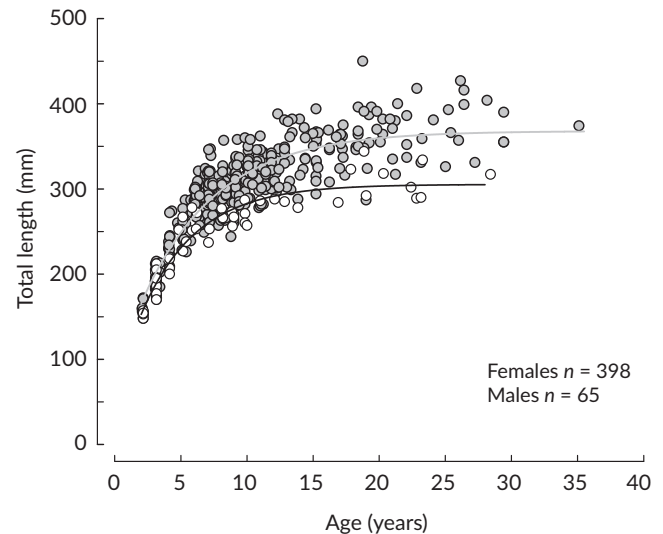




**FIGURE 2** (a) Length and (b) age-frequency distributions for female (grey bars) and male (black bars) *N. pandus* caught on the west and south coasts of Western Australia.  $n$  = sample size

$P < 0.05$ ), the percentage difference between the lengths at age were always  $<5\%$  for females and  $<2\%$  for males over the age range containing the majority of the data, i.e., females 5–15 years, males 5–10 years. Thus, as these differences were deemed to not be biologically significant, the length-at-age data for females and males from the two coasts were combined to describe the growth of each sex (Figure 3 and Table 2). Thus, on the basis of vBGCs, females attain  $L_T$  values of 248, 318, 347 and 359 mm at 5, 10, 15 and 20 years of age, respectively, while males attain  $L_T$  values of 231, 282, 298 and 303 mm, respectively (Figure 4).

Estimates for natural mortality ( $M$ ) for female and male *N. pandus* using the equation of Then *et al.* (2015) were  $0.19$  and  $0.23 \text{ year}^{-1}$ , respectively, and thus greater than  $0.12$  and  $0.15 \text{ year}^{-1}$ , respectively, obtained using the Hoenig (1983) equation. The median values for the catch curve estimate of total mortality ( $Z$ ) for females was the same (i.e.,  $0.19 \text{ year}^{-1}$ , 95% CI =  $0.17$ – $0.21$ ) as that for  $M$  obtained using the Then *et al.* (2015) data, while for males (i.e.,  $0.18 \text{ year}^{-1}$ , 95% CI =  $0.13$ – $0.25$ ) it lay between those  $M$  estimates for this sex.



**FIGURE 3** von Bertalanffy growth curves fitted to the total length (mm) at age of female (grey circles, grey solid line) and male (white circles, black solid line) *N. pandus*.  $n$  = sample sizes

**TABLE 2** The von Bertalanffy growth curve parameters  $L_\infty$ ,  $k$  and  $t_0$ , and their upper and lower 95% confidence limits, for female and male *N. pandus* derived from the total lengths at age of all aged individuals collected during the present study

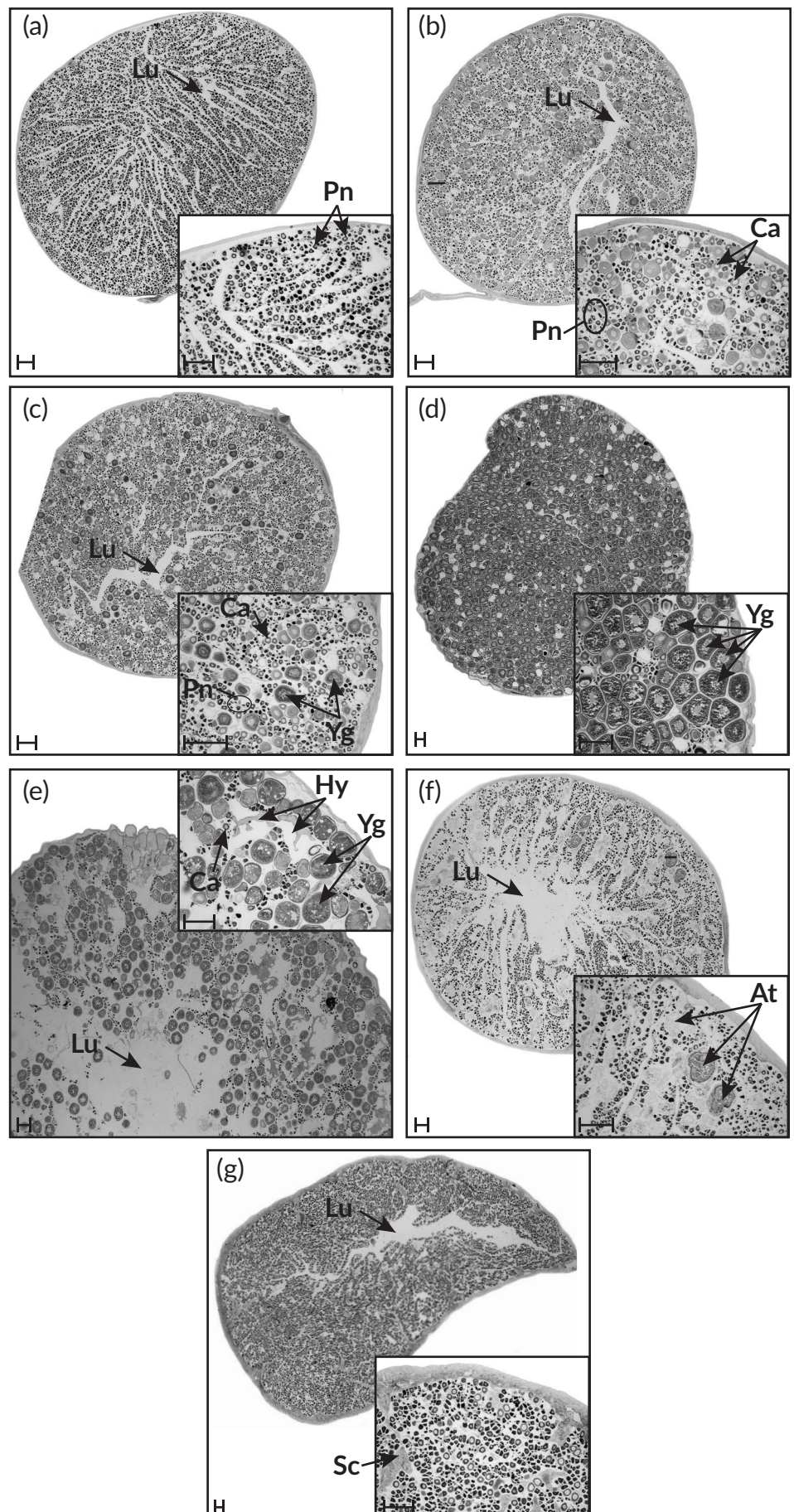
		$L_\infty$	$k$	$t_0$	$r^2$	$n$
Females	Estimate	368	0.18	−1.39	0.80	398
	Upper	379	0.20	−0.89		
	Lower	358	0.15	−2.03		
Males	Estimate	305	0.24	−0.89	0.92	65
	Upper	320	0.31	−0.22		
	Lower	293	0.18	−1.93		

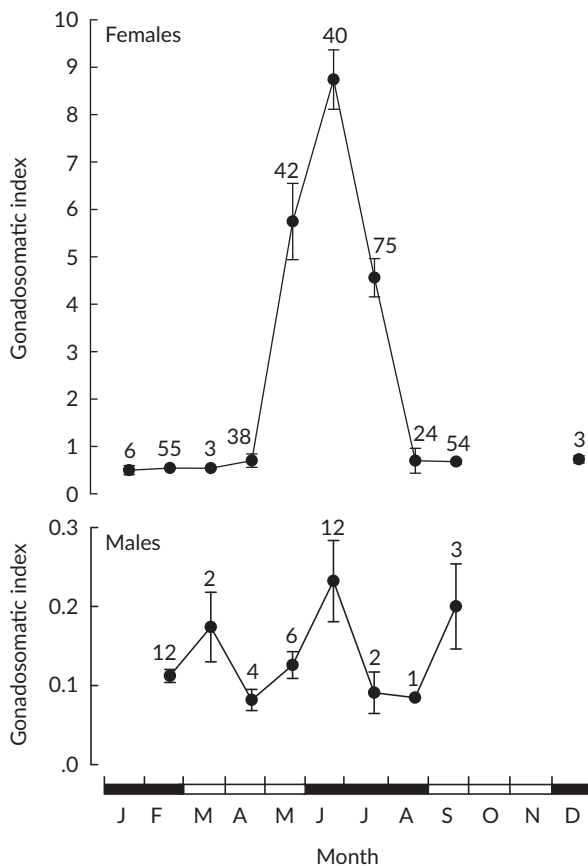
Note:  $r^2$  = coefficient of determination;  $n$  = sample size.

### 3.4 | Histological description of ovaries, and duration and prevalence of spawning

The ovaries of stage II (resting) *N. pandus* females possess a thin ovarian wall which encases a complex series of folds (lamellae), consisting exclusively of previtellogenic (Pn) oocytes that project inwards from the periphery of the ovary (Figure 4a). The presence of chromatin nucleolar (Ca) oocytes indicates the commencement of maturation and distinguishes stage III (developing) ovaries (Figure 4b), while the occurrence of many Ca oocytes and a few yolk granule (Yg) oocytes typifies stage IV (maturing) ovaries (Figure 4c). In stage V (pre-spawning) ovaries, large numbers of Yg oocytes are tightly packed together and are interspersed with Ca and Pn oocytes (Figure 4d). Stage VI (spawning) ovaries are very similar to stage V ovaries, except the former stage possess hydrated (Hy) oocytes (Figure 4e). Atretic oocytes (At) are a typifying feature of stage VII (spent) ovaries (Figure 4f), while stage VIII (recovering) ovaries, although organized

**FIGURE 4** Histological sections of each of the seven stages of development of the ovaries of female *N. pandus*. (a) Stage II (immature/resting), (b) stage III (developing), (c) stage IV (maturing), (d) stage V (prespawning), (e) stage VI (spawning), (f) stage VII (spent), (g) stage VIII (recovering). Lu, ovarian lumen; Pn, perinuclear oocytes; Ca, cortical alveoli oocytes; Yg, yolk granule oocytes; Hy, hydrated oocytes; At, atretic oocytes; Sc, scar tissue. All scale bars = 500  $\mu$ m



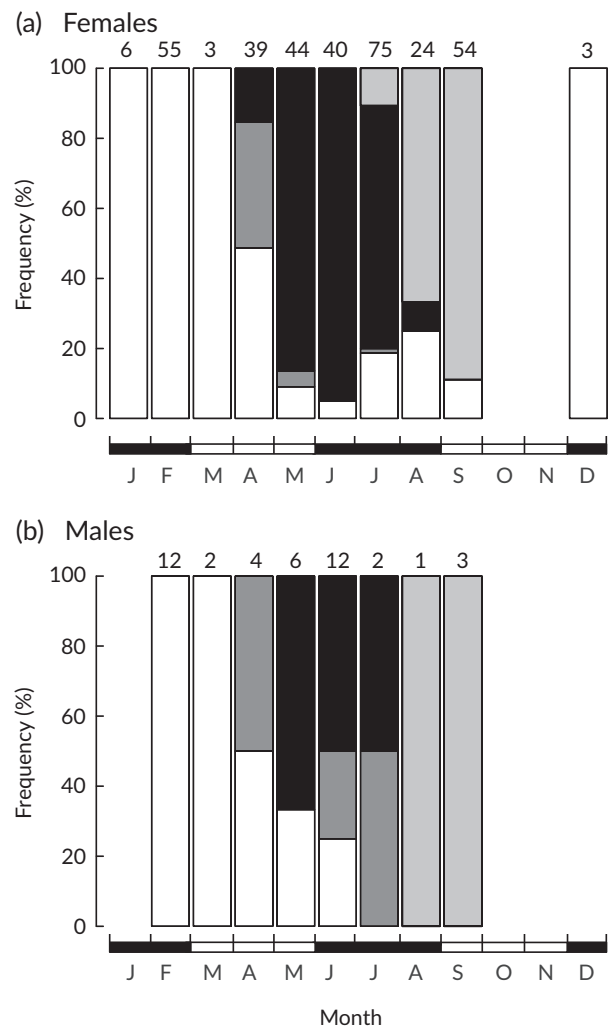


**FIGURE 5** Mean monthly gonadosomatic indices (GSI)  $\pm 1$  S.E. (black dots) for female and male *N. pandus*  $\geq$  than their respective  $L_{T50}$ s at maturity. Sample sizes are given above each mean. On the x axis closed rectangles refer to summer and winter months and the open rectangles to autumn and spring months

more like stage II ovaries, possess a much thicker ovarian wall and scar tissue within the ovary (Figure 4g). A central lumen is consistent in all stages of ovarian development, except in stage V and VI ovaries where it is less distinct due to the expansion of oocytes. In addition, in stages VI, V and VI, the Yg oocytes are always accompanied by earlier developmental stage oocytes (i.e., Pn and Ca oocytes), indicating that during the spawning period there is a consistent progression of oocytes through the maturation process.

The mean monthly  $I_{GS}$  values for female *N. pandus* ( $>L_{T50}$ ) remained very low ( $<1.0$ ) between January and April before increasing rapidly to 5.7 in May and to a maximum of 8.7 in June (Figure 5a). The mean monthly  $I_{GS}$  values for females declined to 4.5 in July and then back to very low levels again in August and September. The corresponding mean monthly  $I_{GS}$  values for male *N. pandus* ( $>L_{T50}$ ), while following a similar trend to that of their females, reaching a peak in June, were many magnitudes lower than those of their females (Figure 5b).

Female *N. pandus* with stage II ovaries were found exclusively between January and March (Figure 6a). The percentage frequency of occurrence of females with stage II ovaries declined to 50% in April, while individuals with stage III/IV or V/VI ovaries



**FIGURE 6** Monthly percentage frequencies of occurrence of sequential stages in the gonadal development of (a) female and (b) male *N. pandus*  $\geq$  their respective  $L_{T50}$ s at maturity. Stage II, white bars; stage III/IV, dark grey bars; stage V/VI, black bars; stage VII/VIII, grey bars

constituted 35% and 15% of females caught in that month. In May and June, the percentage frequency of occurrence of females with stage V/VI ovaries increased substantially to 86% and 95%, respectively. While females with stage V/VI ovaries were still dominant in July, females with stage VII/VII ovaries were first observed in this month, with their number increasing in August and September (Figure 6a). The prevalence of male *N. pandus* with gonads at different stages of development followed the trend displayed by the ovaries of females, with males with stage II testes being exclusively present in February and March, males with V/VI testes being most prevalent between May and July, and males with stage VII/VII testes occurring in August and September (Figure 6b).

The trends exhibited by the mean monthly  $I_{GS}$  values for females and males and the months when females and males with gonads at stages V/VI were present demonstrate that *N. pandus* spawns between May (late autumn) and July (mid-winter autumn). As 1 May



represents the commencement of the spawning period, it was chosen as the birth date for *N. pandus*.

### 3.5 | Length and age at maturity

The smallest mature female and male *N. pandus* collected during the spawning period were 195 and 182 mm, respectively. All seven females <175 mm collected during the spawning period were immature, as were the vast majority of females in the 175–199 and 200–224 mm length classes (Figure 7). The percentage of mature females increased from 42% in the 225–249 mm length class to 70% in the 250–274 mm length class, with most females in larger size classes being mature. While all males <175 mm were immature, ~40% of males between 175 and 224 mm were mature, as were all males ≥225 mm (Figure 7). The  $L_{T50}$  values, as determined by logistic

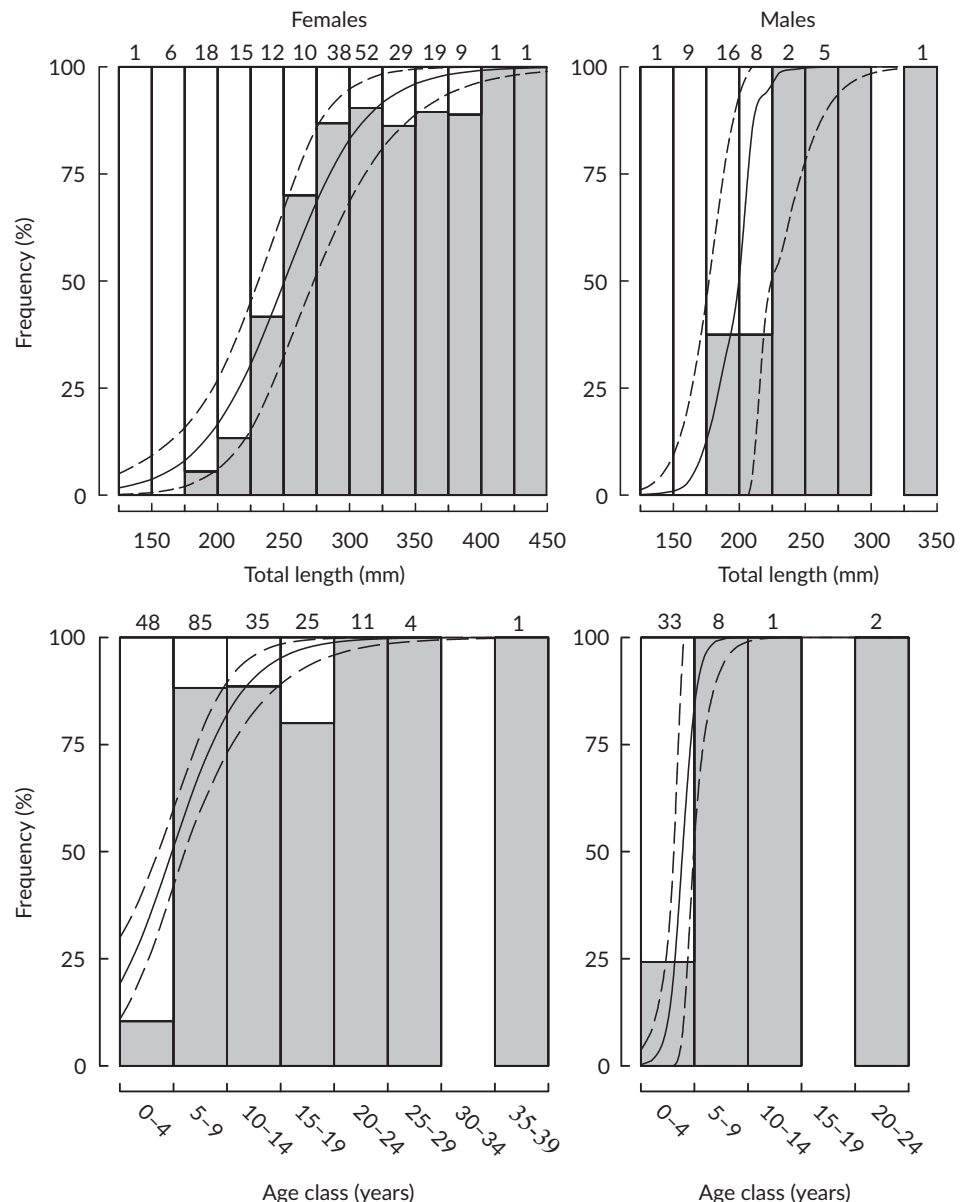
regression analysis, for female and male *N. pandus* were 251 and 199 mm, respectively (Table 3).

The youngest mature female and male *N. pandus* collected during the spawning period were both 3 years of age. While the majority of female and male *N. pandus* < 5 years were immature, the reverse was true for individuals of both sexes ≥5 years of age (Figure 7). The  $A_{50}$  values, as determined by logistic regression analysis, for female and male *N. pandus* were 4.9 and 3.9 years, respectively (Table 3).

## 4 | DISCUSSION

### 4.1 | Timing of formation of first opaque zone

Identifying, in particular, the timing of formation of the first growth (opaque) zone is central to age determination in any species, for if



**FIGURE 7** Percentage frequencies of occurrence of female and male *N. pandus* with mature gonads (grey histograms) in sequential 25 mm length classes and 5 year age classes in samples obtained during the peak spawning period, i.e., May to July. Logistic curves (solid line) and their 95% confidence limits (dashed lines) were derived from the probability that a fish at a given length or age is mature. Sample sizes for each length and age class are shown

**TABLE 3** Estimates of the total lengths ( $L_t$ , mm) and ages (A, years) at which 50% and 95% of female and male *N. pandus* are mature and their upper and lower 95% confidence limits

		$L_{t50}$	$L_{t95}$	$A_{50}$	$A_{95}$
Females	Estimate	251	342	4.9	14.9
	Upper	273	384	6.0	18.9
	Lower	230	300	3.5	12.0
Males	Estimate	199	220	3.9	5.8
	Upper	230	275	4.9	7.9
	Lower	176	202	3.1	3.9

incorrectly done it can lead to ageing errors (Campana, 2001; Campana & Neilson, 1985). This is particularly relevant to fish species that spawn just prior to, or during, winter when the opaque zone in otoliths is formed. In south-western Australia, water temperature between May (late autumn) and July (mid-winter) is falling and close to its minimum (see Figure 1 in Coulson *et al.*, 2012). During colder months when somatic and otolith growth slows, although fewer organic fibres are deposited in otoliths, the ratio of the organic portion compared to the inorganic portion (*i.e.*, calcium carbonate) is higher due to calcification being reduced (Pannella, 1971). Thus, the denser mesh of these organic fibres forms the opaque zone, which appears dark when otolith sections are viewed with transmitted light or white when viewed against a black background with reflected light. As the spawning period of *N. pandus* extends from May to July, the very small otoliths of recently “born” individuals will be entirely opaque until water temperature, and thus growth, increases in late spring and summer, when the first translucent zone begins to form. It is therefore proposed that it is not until after the second winter of life that the first discrete opaque zone becomes visible in the otoliths of *N. pandus* when the fish are ~12–15 months old. The formation of the first opaque zone in the second winter of life by *N. pandus* parallels that for other fish species in south-western Australia, such as *Arripis georgianus* (Valenciennes 1831), *Achoerodus gouldii* (Richardson 1843), *Nemadactylus valenciennesi* (Whitley 1937), *Scorpaenopsis aequipinnis* Richardson 1848 and *Cheilodactylus rubrolabiatus* Allen & Heemstra 1976, who all exhibit spawning periods between early autumn and late winter (Coulson, 2019; Coulson *et al.*, 2009, 2010, 2012; Fairclough *et al.*, 2000a, 2000b).

## 4.2 | Sex ratio and time of spawning

The length and age compositions and the growth patterns of *N. pandus* demonstrate that, while females grow to larger sizes than their males, both sexes attain similar maximum ages. Faster growth exhibited by females will facilitate them moving through smaller size classes and accumulating in the larger size classes, while males, growing slower and to a smaller size, will accumulate in the intermediate size classes. This is particularly evident on the south coast, where small *N. pandus* were specifically kept for this study. The trend in a

sex ratio becoming increasingly biased towards females with increasing length parallels that observed in several other Scorpaeniformes (Bilgin & Çelik, 2009; Coulson *et al.*, 2017; Masuda *et al.*, 2000). The larger size of female *N. pandus* would make this sex more vulnerable to capture in trawl nets, such as those used to catch scallops. Although it would be expected that female *N. pandus* would experience a higher total (Z) mortality rate, the median Z values for both sexes were almost identical. This parallels the situation for a suite of platycephalids in south-western Australia for which point estimates of Z for both sexes were either very similar or those estimates for females were markedly higher than those for males (Coulson *et al.*, 2017). The greater number of female European Hake *Merluccius merluccius* (Linnaeus, 1758) in the larger size classes, in comparison to males, was proposed to be due to differences in mortality as well as growth of the two sexes (Cerviño, 2014).

The short, 3-month, late autumn to mid-winter spawning period exhibited by *N. pandus* is identical to that for *Scorpaenopsis aequipinnis* in southern Western Australia and overlaps with other fish species from this region such as *Sillaginodes punctatus* (Cuvier 1829), *A. gouldii*, *N. valenciennesi*, *C. rubrolabiatus*, *A. georgianus* and *C. gerrardi* (Günther 1887) (Coulson, 2019; Coulson *et al.*, 2009, 2010, 2012, 2019; Fairclough *et al.*, 2000a; Hyndes *et al.*, 1998). Gonadal recrudescence in *N. pandus*, as in *S. aequipinnis* and *A. georgiana*, is initiated when day length is declining and water temperature starts to decline (see Figure 1 in Coulson *et al.*, 2012). This parallels the typical situation with temperate fish species that spawn in winter and thus when water temperatures are low (Lam, 1983). The timing of spawning by *N. pandus* may also be influenced by the presence of the pole-ward flowing Leeuwin Current (LC), which is strongest in winter months and proposed to transport the eggs and larvae of other teleosts to nursery grounds in waters off the south coast of Western Australia (Coulson *et al.*, 2010, 2019; Fairclough *et al.*, 2000a).

## 4.3 | Histological structure of ovaries and disparity of female and male gonad size

The ovarian structure of the *Sebastes*, *Helicolenus* and *Scorpaena* differ as a result of the reproductive strategies. The internal fertilizing and live-bearing *Sebastes* possess cystovarian Type II-1 ovaries in which the lamella-like stroma extend from the ovarian hilus on the dorsal side of the ovary and the ovarian cavity is located on the ventral side of the ovary (Koya & Muñoz, 2007; McMillan, 2007). Although *Helicolenus* species exhibit internal fertilization of oocytes before ovulation and *Scorpaena* exhibit external fertilization, the structure of the ovaries, referred to as cystovarian Type II-3 ovaries (Koya & Muñoz, 2007), of species in these two genera are very similar. In both cases, the ovarian lamellae protrude radially from the stroma that originates from the anterior part of the ovary, which contains a centrally located artery and veins, and is suspended freely inside the lumen (Muñoz *et al.*, 1999; Muñoz *et al.*, 2002b; Stewart & Hughes, 2010). In addition, the wall of the ovaries of such species contains three layers, with the inner layer consisting of epithelial cells that secrete gelatinous

material in which, in the case of the *Scorpaena*, the oocytes are embedded during ovulation (Stewart & Hughes, 2010). The histological sections of the ovaries of *N. pandus* show that the epithelial lining of the ovary forms a complex series of folds (lamellae) that project inwards into the centre of the ovary cavity (lumen), which becomes increasingly concealed as the oocytes mature and become larger (Figure 4d). This type of ovarian structure is consistent with "general" teleost ovarian anatomy (Franchi, 1962; Hoar, 1969; Wourms, 1981) and is consistent with other broadcast spawning species such as *Chrysophrys auratus* (Forster 1801) and *Nelusetta ayraudi* (Quoy & Gaimard 1824) (Mackie *et al.*, 2009; Miller & Stewart, 2013).

The disparity in the mean monthly  $I_{GS}$  values for female and male *N. pandus*, particularly during the spawning months, indicates that this species spawns in pairs, or at least spawns in small groups. While the possession of far smaller testes by males in comparison to the size of the ovaries of their females is a characteristic often associated with pair-spawning hermaphroditic species (e.g., Coulson *et al.*, 2009; Sadovy, 1996; Sadovy & Colin, 1995; Shapiro *et al.*, 1993), it is a trait exhibited by many gonochoristic species as well (e.g., Moore *et al.*, 2007; French *et al.*, 2014; Coulson *et al.*, 2016). A similar disparity in the  $I_{GS}$  values between females and males to that observed in *N. pandus* is also exhibited by some species from other closely related families, such as *Scorpaena guttata* Girard, 1854, *Scorpaena porcus* Linnaeus, 1758, *Scorpaena cardinalis* Solander & Richardson 1842, and *Scorpaena notata* Rafinesque, 1810 (Bilgin & Çelik, 2009; Love *et al.*, 1987; Muñoz *et al.*, 2005; Ordines *et al.*, 2009; Stewart & Hughes, 2010). While the females of *S. guttata*, from the Southern Californian Bight, and *S. porcus* also grow to a larger size than their males, further paralleling the situation with *N. pandus*, the reverse is true for *S. cardinalis* and *S. notata*. The large disparity in the  $I_{GS}$  values between females and males of *N. pandus* and other *Scorpaena* species may be an adaptation towards a reproductive strategy of internal fertilization exhibited by the closely related *Helicolenus* and *Sebastes* (e.g., Sequeira *et al.*, 2003; Wourms, 1991), as this strategy does not require males to produce/store large volumes of sperm (Pavlov & Emel'yanova, 2013).

#### 4.4 | Sexual dimorphism and reproductive strategy

The difference in the length compositions and growth between female and male *N. pandus* also indicates that there have been selective pressures for females to attain a larger size than males, which parallels the sexual dimorphism exhibited by many closely related *Platycephalus*, *Sebastes* and *Sebastolobus* species (e.g., Coulson *et al.*, 2017; Lenarz & Wyllie Echeverria, 1991; Orlov & Abramov, 2010). As the number of eggs produced and released by females (i.e., fecundity) in gonochoristic species is proportional to the body cavity volume of the fish, larger size in females is considered a life history strategy for supporting increasing egg production (Beckman *et al.*, 1989; Conover, 1984; Palumbi, 2004; Roff, 1983). While females growing to a greater size than males and pair spawning appears to be the strategy for *N. pandus* to increase reproductive

output, the *Scorpaena*, *Helicolenus* and *Sebastes* species have adopted increasing degrees of reproductive investment to maximize the fertilization rates of eggs and survival of young.

To increase the survivorship of eggs, the females of *Scorpaena* species, which are typically smaller than their males, release eggs in a buoyant gelatinous coating (Koya & Muñoz, 2007; Muñoz *et al.*, 2002b). In addition, group-release of sperm in thick seminal fluid by the males of *Scorpaena* species during pair spawning is proposed to keep spermatozoa together and facilitate fertilization of the whole egg mass (Koya & Muñoz, 2007; Muñoz *et al.*, 2002a; Wourms, 1991). The females of *Helicolenus* species, like the females of *Scorpaena* species, release their eggs in a gelatinous mass (Koya & Muñoz, 2007; Sequeira *et al.*, 2011). However, *Helicolenus* species exhibit zygoparity, whereby eggs are internally fertilized and released at the early-celled developmental stage, and larvae hatch in the external environment (Boehlert & Yoklavich, 1984; Koya & Muñoz, 2007; Sequeira *et al.*, 2003; Wourms, 1991). The reproductive strategies outlined above would mean that the females of *Scorpaena* and *Helicolenus* species do not need to produce as many eggs as other broadcast spawning teleosts and so typically do not grow to a size larger than their males (e.g., Kelly *et al.*, 1999; Neves *et al.*, 2015; Paul & Horn, 2009; Stewart & Hughes, 2010). In addition, a larger size attained by males would benefit this sex when competing for access to females and/or spawning sites (Ng *et al.*, 2003; Parker, 1992). *Sebastes* species exhibit a more advanced form of viviparity in which larvae at birth are well developed, supported by remnant yolk, but able to feed (Boehlert & Yoklavich, 1984; Pavlov & Emel'yanova, 2013; Wourms, 1991). In *Sebastes* species, the larger size attained by females in comparison to their males (e.g., Laidig *et al.*, 2003; Love *et al.*, 1990; Saborido-Rey *et al.*, 2004) is thought to be an adaptation to maximize the number of eggs produced (Wyllie Echeverria, 1986). In addition, considering that these species are internal bearers and internally developed embryos are larger than eggs, it would make sense for females to be larger. Thus, among the *Scorpaena*, *Helicolenus*, *Sebastes* and *Neosebastes*, sexually dimorphic growth is used to benefit the sex that attains the greatest advantage by being larger.

## 5 | CONCLUSIONS

This study is the first comprehensive investigation of the biological characteristics of a *Neosebastes* species. The attainment of a larger size by female *N. pandus*, in comparison to their males, in conjunction with a large disparity in the mean monthly  $I_{GS}$  values of females and males during the spawning period suggests this species possesses a reproductive strategy that maximizes the reproductive output of females and the fertilization of their eggs by males through pair spawning. The reproductive strategy of other closely related Scorpaeniformes, such as *Scorpaena*, *Sebastes* and *Helicolenus* species, has developed to focus on increasing the rate of egg fertilization, whether this is by males growing to a larger size and thereby gaining

exclusive access to females and/or by protecting eggs in a gelatinous mass or internal fertilization.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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