

Life-history characteristics of Theodore's threadfin bream, *Nemipterus theodorei* (Ogilby, 1916), and the yellow-lip butterfly bream, *Nemipterus aurifilum* (Ogilby, 1910), from southern Queensland, Australia

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ABSTRACT

Theodore's threadfin bream (*Nemipterus theodorei*) and the yellow-lip butterfly bream (*Nemipterus aurifilum*) are two of the most common nemipterids in eastern Queensland. These two species are caught incidentally and at times retained for sale as 'permitted' species in Australia's largest trawl fishery, the Queensland East Coast Otter Trawl Fishery (QECOTF). Despite their prevalence, little biological information is available for these species. This paper reports key life-history characteristics of these nemipterids. Growth and length-at-maturity parameters were estimated from samples collected in southern Queensland. Growth parameters were estimated using back-calculation of fork length (FL) from otolith increment data and modelled within a Bayesian framework to overcome bias resulting from the small number of larger, older animals in the retained bycatch. The von Bertalanffy growth function (VBGF) was identified as the most appropriate growth model with significant differences in sex-specific growth rates evident for both species. Maximum ages were six and four years for *N. theodorei* and *N. aurifilum* respectively, with individuals maturing within their first year of life. The length-at-maturity for females was 91 mm FL and 77 mm FL for *N. theodorei* and *N. aurifilum* respectively. Increased reproductive activity was observed in the austral spring and summer months. The results from this study can be used to assess the ecological risk posed to these species by the QECOTF.

The QECOTF is the largest trawl fishery in Australia. Logbook data indicate that, in 2022, 269 vessels fished 28,362 days and landed approximately 5,412 t of product. In the period 2011–2014, approximately 21,000 t, or 71%, of the catch was discarded annually (Wang et al. 2020), and the discarded portion of the catch was comprised of hundreds of species, most of which were small and displayed poor discard survival (Courtney et al. 2008; Courtney et al. 2014; Courtney et al. 2006). Several nemipterid species were found in the discards and, at times, have an occurrence frequency as high as 79% of trawls (Courtney et al. 2007). Nemipterids, also referred to as threadfin bream, are distributed throughout tropical and sub-tropical regions of the Indo-West Pacific area and inhabit mud and sand substrates (Russell 1990). Two of the most common nemipterids caught in the QECOTF are Theodore's threadfin bream (*Nemipterus theodorei*), and the yellow-lip butterfly bream (*Nemipterus aurifilum*) (Fig. 1). Both species are endemic to eastern Australia, with *N. theodorei* occurring in depths from 19–410 m (Russell 1990) and *N. aurifilum* in depths greater than 90 m (Courtney et al. 2014). As *N. theodorei* is the larger of the two species, it dominates nemipterid landings, although large *N. aurifilum* are also landed. Within the QECOTF, fishers can retain up to 198 L (~200 kg) of nemipterids per fishing trip: however, this limit was imposed without an assessment of nemipterid stocks.

At present, the QECOTF imposes an unknown level of fishing mortality on nemipterids. Jacobsen et al. (2018) noted that the general life-history characteristics of the nemipterid's biology provided the family with some level of resilience against exploitation, but to date there are no studies detailing the life-history biology of any nemipterid species in Queensland. Therefore, the aim of this study was to investigate the life-history population characteristics of *N. theodorei* and *N. aurifilum*, with an emphasis on growth and maturity parameters.



Figure 1. A *Nemipterus theodorei* B *Nemipterus aurifilum*

MATERIALS AND METHODS

Sample capture and processing: Trawl-caught specimens of *N. theodorei* and *N. aurifilum* were obtained during research charters (Courtney et al. 2006; Courtney et al. 2007) and opportunistic sampling of commercial catches between April 2000 and November 2002. Samples were collected in Queensland waters between Yeppoon (23°07.728' S, 150°44.661' E) and Coolangatta (28°09.844' S, 153°32.942' E), in depths from 20–165 m, and frozen whole at sea for later processing (Fig. 2). In the laboratory, frozen samples were thawed and the total weight (± 0.1 g), fork length (FL ± 1 mm), sex, gonad weight (GW ± 0.1 g) and reproductive stage (see Table 1) were recorded. Fork length, rather than total length, was used as a more reliable measure of fish size, due to damage to caudal fins during capture and freezing. Finally, sagittal otolith pairs were removed, air-dried and placed into labelled vials.

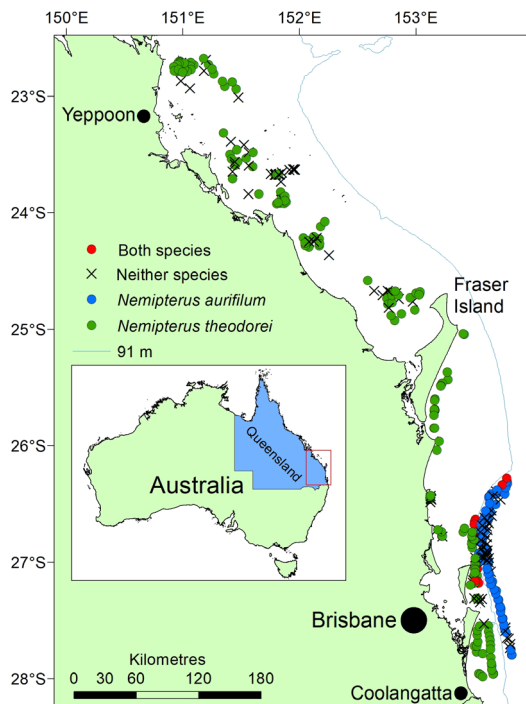


Figure 2. Locations of trawls undertaken as part of previous research (Courtney et al. 2007) from which *Nemipterus theodorei* and *Nemipterus aurifilum* samples were obtained in southern Queensland.

Table 1. Criteria for macroscopic classification of female nemipterid gonads based on Haddy and Pankhurst (1998).

Stage	Classification	Macroscopic appearance
1	Immature	Ovary small, clear threads. Sex indeterminable
2	Regressed	Ovary enlarging but still clear
3	Vitellogenic	Ovary enlarging with opaque oocytes visible through epithelium
4	Hydrated	Ovary enlarged with opaque and hydrated oocytes visible through epithelium
5	Ovulated	Eggs in the oviduct can be extruded with gentle pressure
6	Spent	Ovary flaccid and bloody

Ageing: The methods used to determine age and growth were based on those used in previous studies (Campbell et al. 2022; Campbell & Rigby 2022), and these studies provide a more thorough description of these methods. A summary of the methods used is provided below.

Whole sagittal otoliths were weighed, set in resin, and sectioned with a Gemmasta faceting saw. Two to four 350 μ m sections closest to the otolith primordia were selected and mounted onto a microscope slide. The sections were viewed under a dissecting microscope with transmitted light, and age was estimated by counting the number of band pairs. An annual band pair was defined as one wide translucent band and one narrow opaque band. From the primordium, a transect was laid from the primordium, ventral to the sulcus, to the otolith edge. Distances from the primordium to the outside edge of each opaque band and otolith edge (i.e. otolith radius) were determined using the image analysis system described by Morison et al. (1998).

Counts were made without the researcher's knowledge of the size or sex of the individual and 25% of the sections were randomly selected for a second estimate of age to determine intra-reading variability using two methods: 1) percent agreement (PA); and 2) average percent error (APE, Beamish & Fournier 1981). Further, Bowker's test of symmetry was used to assess bias between reads.

Marginal increment ratio: To determine the periodicity of band formation, monthly marginal increment ratio (MIR) was calculated following Natanson et al. (1995), who defined MIR as $MIR = (OR - OR_n)/(OR_n - OR_{n-1})$, where OR is the otolith radius, OR_n is the radius of the last opaque band and OR_{n-1} is the radius of the 2nd last opaque band. Following Simpfendorfer et al. (2000), MIR was compared between months using the Kruskal–Wallis one-way analysis of variance on ranks. Edge type was qualitatively assessed to provide further evidence of band formation periodicity (Cailliet et al. 2006). Edge type was classified into three levels: ‘new’, ‘intermediate’ and ‘wide’. A ‘new’ edge was one where an opaque zone occurred at the distal edge of the otolith irrespective of the width of the opaque zone. An edge of an otolith with any translucence visible beyond the last complete band pair (i.e. $MIR < 0.25$) was categorised as ‘intermediate’ and ‘wide’ if the width of the translucent band beyond the last opaque zone was $\geq 1/4$ the width of the previous translucent band (i.e. $MIR \geq 0.25$).

Growth: Back-calculation of fork length used the linear-modified Dahl-Lea method (Francis 1990) as follows:

$$L_a = L_c \times \left(\frac{b + mOR_a}{b + mOR_c} \right)$$

where L_a is the back-calculated length at age, L_c is the length at capture; OR_a is the otolith radius at age a ; OR_c is the otolith radius at capture; and b and m are sex-specific coefficients of the linear regression between OR_c and L_c . A final age adjustment was performed based on edge type, where all 0+ fish and individuals with otolith edges classified as wide had their age adjusted by +1.

Three growth functions were used to estimate mean length-at-age: von Bertalanffy growth function (VBGF), logistic function and Gompertz function (Table 2). Growth parameters were estimated in a Bayesian framework using Markov chain Monte Carlo (MCMC) methods (Smart & Grammer 2021). In all instances, the length-at-age-zero (L_0) was estimated, rather than the age when length is zero (i.e. t_0).

Table 2. Equations of the three candidate growth functions used to assess the growth of 314 *Nemipterus theodorei* and 181 *Nemipterus aurifilum* caught in south-east Queensland, Australia, between April 2000 and November 2002. **Note:** L_t is the length (mm) at age t (years); L_∞ is the asymptotic length (mm); L_0 is the length (mm) at $t = 0$; and k , g_1 and g_2 are coefficients (year⁻¹) of the respective growth functions to be estimated.

Model	Classification
von Bertalanffy	$L_t = L_0 + (L_\infty - L_0)(1 - e^{-kt})$
Gompertz function	$L_t = L_0 \times e^{\left(Ln \left(\frac{L_\infty}{L_0} \right) (1 - e^{-g_1 t}) \right)}$
Logistic function	$L_t = \left(\frac{L_\infty \times L_0 (e^{(g_2 t)})}{L_\infty \times L_0 (e^{(g_2 t - 1)})} \right)$

Bayesian models were fit using the ‘BayesGrowth’ package (Smart 2020, accessed 18 February 2021) using R statistical software (R Core Team, Version 3.6.1, accessed 24 March 2022), in accord with methods described by Smart and Grammer (2021). The ‘BayesGrowth’ package uses the Stan computer program (Carpenter et al. 2017), via the ‘Rstan’ package (Stan Development Team 2020) to perform MCMC using No U-Turn Sampling (NUTS). Four MCMC chains with 10,000 simulations, with a burn-in period of 5,000 simulations, were used to determine parameter posterior distributions. Model convergence was assessed using the Gelman–Rubin test and diagnostic plots generated using the ‘Bayesplot’ package (Gabry 2020, accessed 18 February 2021) in R.

The models were fitted with a normal residual error structure (σ). The prior distributions of the L_∞ parameters were informed by the datasets under review. The largest male *N. theodorei* was 289 mm FL and the largest female was 275 mm FL. Given this information, priors for L_∞ were set at $L_\infty \sim N(289, 14.45)$ for males, and $L_\infty \sim N(275, 13.75)$ for females. Using the same method, the priors of L_∞ for *N. aurifilum* were set at $L_\infty \sim N(228, 11.40)$ for males, and $L_\infty \sim N(196, 9.80)$ for females. In accord with Smart and Grammer (2021), the prior for the L_0 parameter was $L_0 \sim N(0, 0.001)$ for both species. A non-informative prior was used for σ and a common non-informative prior was used for the growth coefficients of candidate models (k , g_1 and g_2 , Table 2).

An upper bound was nominated for the uniform distributions of σ and k of 100 and 3.0 year⁻¹, respectively. The common non-informative prior for the growth coefficients allowed for comparison of the three candidate growth functions, each with identical priors. Leave-one-out-information criterion weights (LOOICw), calculated within the 'BayesGrowth' package using the 'loo' R package (Vehtari et al. 2020), were used to determine the most appropriate candidate model. The candidate model with the highest LOOICw was considered the most appropriate.

Differences in growth parameters between sexes were assessed by comparing 10,000 posterior estimates of L_{∞} , k and L_0 of each sex. A frequency histogram of a vector, representing the difference between the two vectors of interest (e.g., male L_{∞} and female L_{∞}), was generated and a significant difference was detected if zero was not within the 95% confidence interval of the distribution of this vector (Campbell & Rigby 2022).

Maturity: The length-at-maturity (L_{50}) of female *N. theodorei* and *N. aurifilum* was determined using generalised linear modelling (GLM) in R, via a binomial distribution with a logit link function.

Maturity (0, 1) was the response variable, with all females with stage 3 gonads (see Table 1) or higher deemed to be mature (1), and FL added as a continuous explanatory variable. Age-at-maturity (t_{50}) was calculated by substituting the L_{50} into the respective appropriate growth functions. Further, gonadosomatic index (GSI) was calculated using the equation: GSI (%) = (gonad weight/total weight) × 100. Mean monthly GSI was calculated using only individuals with gonads categorised as stage 2 to stage 6 (see Table 1).

RESULTS

Of the 314 *N. theodorei* assessed, 170 were male (range = 52 – 289 mm FL; mean (SE) = 155.80 ± 2.51 mm) and 127 were female (range = 65 – 275 mm FL; mean (SE) = 145.10 ± 2.90 mm). Sex was indeterminable for 17 individuals due to immaturity or damaged gonads. Two-sample *t*-tests indicated males were significantly larger than females ($t = 2.0842$, d.f. = 268.35, $P < 0.05$) (Fig. 3a). Of the 181 *N. aurifilum* assessed, 84 were male (range = 79 – 228 mm FL; mean (SE) 126.03 ± 2.54 mm), 78 were female (range = 75 – 196 mm FL; mean (SE) 124.03 ± 2.63 mm), and sex was indeterminable for the remaining 19 individuals. Two-sample *t*-tests indicated no significant difference in size between sexes of *N. aurifilum* ($t = 0.578$, d.f. = 157.83, $P = 0.564$) (Fig. 3b).

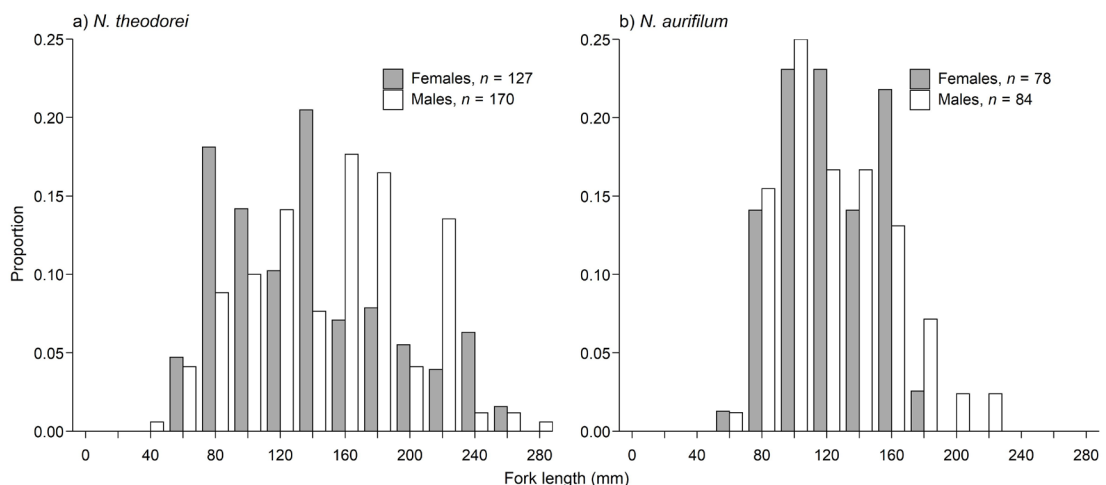


Figure 3. Length–frequency (FL, mm) distribution for **A** 297 *Nemipterus theodorei* and **B** 162 *Nemipterus aurifilum*, caught in south-east Queensland, Australia, as a function of sex.

Ageing: Generally, ageing between reads was consistent for both species (*N. theodorei*: PA = 75%, APE = 6.83; *N. aurifilum*: PA = 83%, APE = 2.53) with the age bias plot revealing little variation from the 1:1 line of equivalence (Supplementary Fig. 1). Further, Bowker’s test of symmetry showed no between-reader bias for *N. theodorei* ($\chi^2 = 3.01$, d.f. = 6, $P = 0.808$) and *N. aurifilum* ($\chi^2 = 0.14$, d.f. = 2, $P = 0.931$). The oldest male (six years) and female (four years) for *N. theodorei* were similar in size, measuring 273 and 275 mm FL respectively. In contrast, *N. aurifilum* had lower maximum ages, with males and females reaching three and four years of age respectively, and the oldest male measuring 207 mm FL, compared to the oldest female measuring 184 mm FL.

Marginal increment ratio: For *N. theodorei*, mean MIR was lowest in the austral summer (Supplementary Fig. 2a). The Kruskal–Wallis test on ranks for *N. theodorei* indicated that there was no difference in mean MIR among months ($\chi^2 = 6.022$, d.f. = 4, $P = 0.198$). The proportion of otoliths with narrow edges was highest in November and lowest in January for *N. theodorei*.

In contrast, the MIR for *N. aurifilum* was lowest during the austral winter (Supplementary Fig. 2b). Again, the Kruskal–Wallis test on ranks indicated that the MIR was independent of month ($\chi^2 = 8.039$, d.f. = 5, $P = 0.154$). Narrow edges were more likely in September and least likely in June for *N. aurifilum*. These proportions were reflected in the MIR, however due to the underrepresentation of a full seasonal profile of MIR values, the Kruskal–Wallis test on ranks failed to detect a significant difference in mean monthly MIR for both species.

Growth: As the relationship between L_c and OR_c varied significantly ($P < 0.001$) between sexes in both species, species- and sex-specific regressions were used for back-calculation. After back-calculation, a total of 665 and 349 observations of length-at-age were generated to assess growth in *N. theodorei* and *N. aurifilum* respectively. Trace plots for each parameter indicated respective models converged sufficiently (Supplementary Fig. 3, Supplementary Fig. 4) and the Gelman–Rubin test statistic was ~1 in all cases. For both species, the VBGF was found to best fit the combined observed and back-calculated length-at-age data (Table 3, LOOICw = 1).

Species/ sex	LOOIC/ LOOICw	L_∞ (mm)	L_0 (mm)	k (year ⁻¹)	σ
<i>N. theodorei</i>					
All	5882.61 / 1	292.6 (280.8 – 304.8)	0	0.46 (0.43 – 0.49)	20.1 (19.1 – 21.3)
Female		277.7 (262.8 – 294.3)	0	0.49 (0.44 – 0.53)	20.4 (18.7 – 22.2)
Male		299.6 (285.4 – 314.6)	0	0.45 (0.41 – 0.49)	19.5 (18.2 – 21.0)
<i>N. aurifilum</i>					
All	3174.21 / 1	214.5 (201.9 – 228.0)	0	0.69 (0.62 – 0.77)	22.5 (20.9 – 24.3)
Female		193.5 (180.8 – 206.9)	0	0.87 (0.76 – 1.00)	20.4 (18.1 – 23.0)
Male		218.5 (203.4 – 234.3)	0	0.68 (0.60 – 0.77)	22.0 (19.9 – 24.5)

Table 3. Mean parameter estimates for the von Bertalanffy growth function used to assess the growth of 314 *Nemipterus theodorei* and 181 *Nemipterus aurifilum* caught in south-east Queensland, Australia, between April 2000 and November 2002. After back-calculation, a total of 665 *N. theodorei* and 349 *N. aurifilum* length-at-age measures were assessed. The parameter estimates shown are the mean values of the posterior distributions of the respective parameters generated by the ‘BayesGrowth’ package via R statistical software. **Note:** L_∞ is the asymptotic length (mm); L_0 is the length (mm) at $t = 0$; k is the growth coefficient of the von Bertalanffy function (see Table 1); and σ is the estimated residual error. Numbers in parentheses are the 95% credible interval of the respective parameters from their posterior distributions.

For *N. theodorei*, the L_{∞} was significantly higher for males than for females (Fig. 4, Supplementary Table 1, Supplementary Fig. 3): the VBGF parameters for males were $L_{\infty} = 306.0$ mm FL, $L_0 = 0.0$ mm FL, $k = 0.44$ year⁻¹, and for females were $L_{\infty} = 275.8$ mm FL, $L_0 = 0.0$ mm FL, $k = 0.49$ year⁻¹ (Table 3).

Similarly, significant differences were detected in L_{∞} and k between *N. aurifilum* males and females (Fig. 5, Supplementary Table 1, Supplementary Fig. 4): the VBGF parameters for males were $L_{\infty} = 221.9$ mm FL, $L_0 = 0.0$ mm FL, $k = 0.66$ year⁻¹, and for females were $L_{\infty} = 193.3$ mm FL, $L_0 = 0.0$ mm FL, $k = 0.88$ year⁻¹ (Table 3).

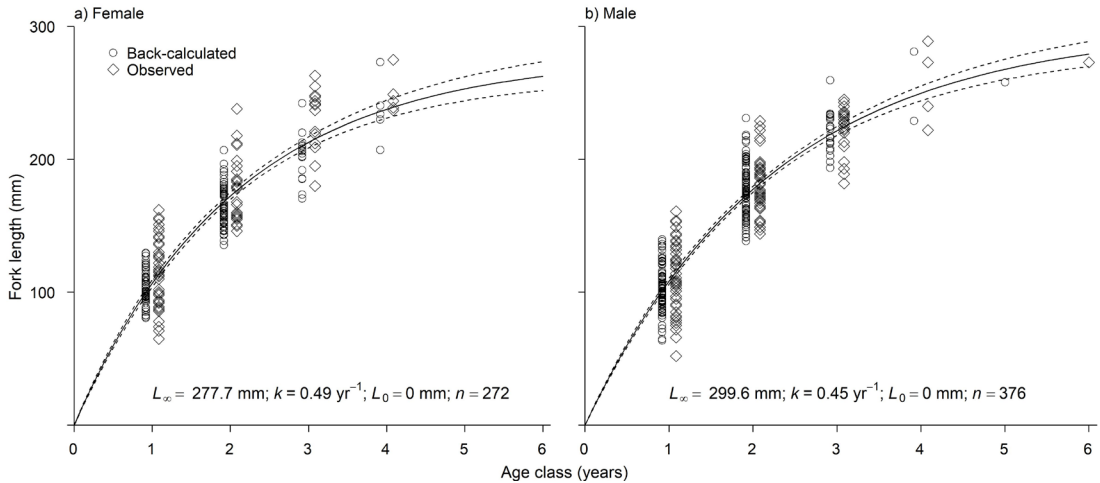


Figure 4. von Bertalanffy growth curve for *Nemipterus theodorei* **A** females and **B** males, caught in south-east Queensland, Australia, between April 2000 and November 2002. Both the observed and back-calculated lengths-at-age are shown, which resulted in 272 measures of length-at-age for females and 376 for males. Values are offset for illustrative purposes only. Priors were set at $L_{\infty} \sim N(289, 14.45)$ and $L_{\infty} \sim N(275, 13.75)$ for *N. theodorei* males and females respectively. Length-at-birth for both sexes was set at $L_0 \sim N(0, 0.001)$. Dashed lines represent 95% credible intervals.

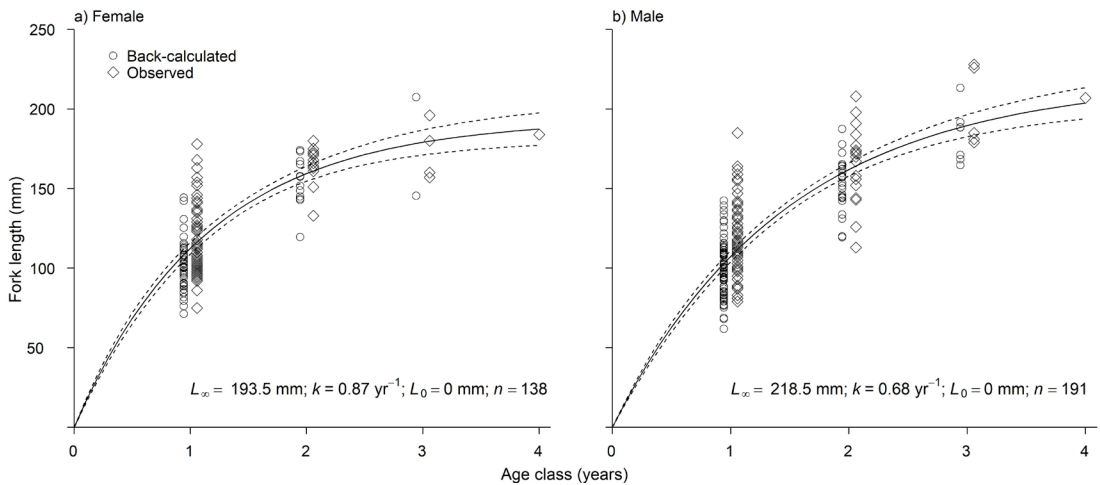


Figure 5. von Bertalanffy growth curve for *Nemipterus aurifilum* **A** females and **B** males, caught in south-east Queensland, Australia, between April 2000 and November 2002. Shown are both the observed and back-calculated lengths-at-age which resulted in 138 measures of length-at-age for females and 191 for males. Values are offset for illustrative purposes only. Priors were set at $L_{\infty} \sim N(228, 11.40)$ and $L_{\infty} \sim N(196, 9.80)$ for males/combined and females respectively. Length-at-birth for both sexes was set at $L_0 \sim N(0, 0.001)$. Dashed lines represent 95% credible intervals.

Maturity: No female *N. theodorei* were found to be in spawning (stage 5) condition. The proportion of female *N. theodorei* with hydrated ovaries (stage 4) was highest in the austral spring and summer (Fig. 6). In contrast, spawning female *N. aurifilum* were sampled throughout several months over the austral spring, summer, and autumn. Mean monthly GSI values were variable and were elevated (>2%) in September, October, January, and February for *N. theodorei* and February for *N. aurifilum* (Fig. 6).

In both species, GSI was lowest in the austral winter (Fig. 7). The logistic regressions indicated the length-at-maturity of female *N. theodorei* and *N. aurifilum* was $L_{50} = 91$ mm FL and $L_{50} = 77$ mm FL, respectively (Fig. 8). Using these values in the respective VBGFs, age-at-maturity for *N. theodorei* and *N. aurifilum* was $t_{50} = 0.82$ year (~9.8 months) and $t_{50} = 0.58$ year (~6.9 months), respectively.

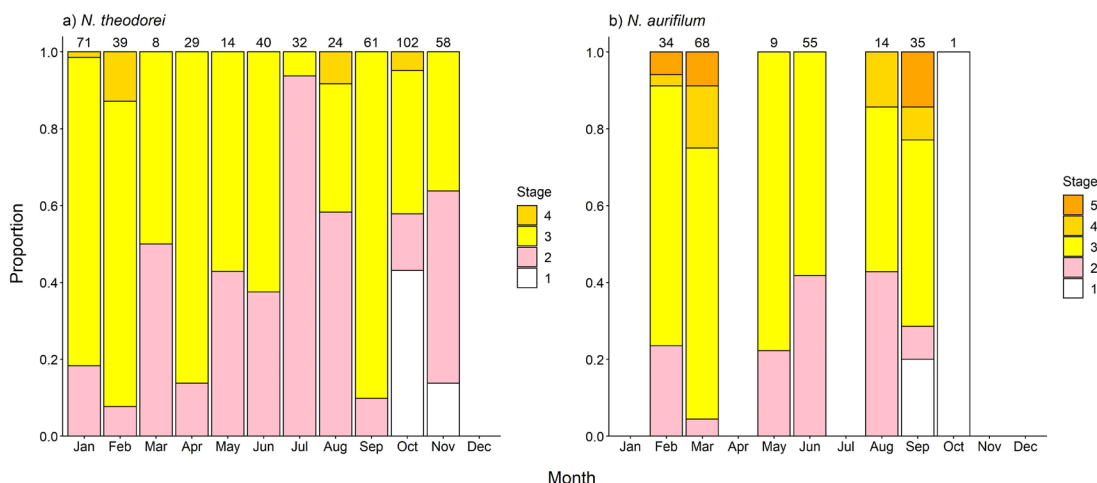


Figure 6. Female gonad stage as a function of month for **A** *Nemipterus theodorei* and **B** *Nemipterus aurifilum*. Numbers above each bar represent the number of animals in each month. Gonad stage was categorised according to Haddy and Pankhurst (1998).

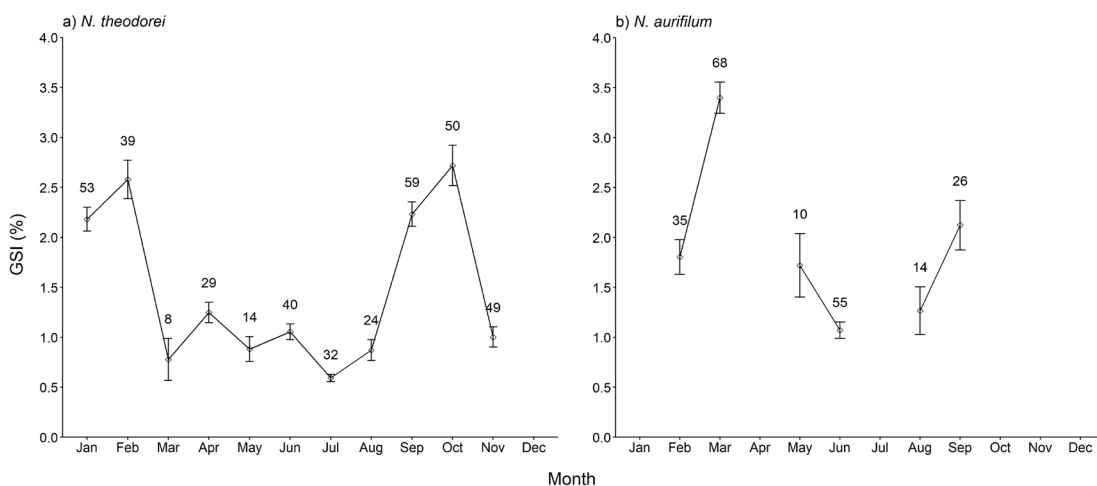


Figure 7. Gonadosomatic index (GSI, %) for **A** *Nemipterus theodorei* and **B** *Nemipterus aurifilum* as a function of month. Error bars are standard errors.

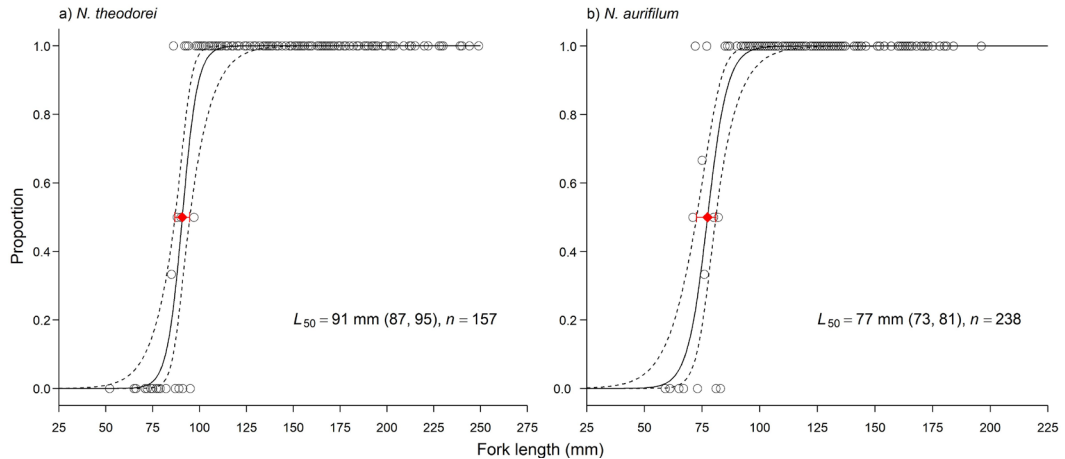


Figure 8. Mean length-at-maturity, in millimetres, for **A** *Nemipterus theodorei* and **B** *Nemipterus aurifilum*. Dashed lines are 95% confidence intervals. The hollow circles represent the observed proportion mature for each fork length and the red points represent the L_{50} of each species.

DISCUSSION

These results represent the first estimates of life-history parameters for *N. theodorei* and *N. aurifilum* published in primary literature and are consistent with previous research that shows nemipterids are fast growing, short-lived, and early to mature (Eggleston 1972; Sainsbury & Whitelaw 1984; Vivekanandan 1991). In accord with previous research on other nemipterid species (Erguden et al. 2010; Granada et al. 2004a), male *N. theodorei* and *N. aurifilum* grew larger than females.

Assessing the differences in the sex-specific L_c/OR_c relationship ensures the reliability of the back-calculation method. Munday et al. (2004) found that the relationship between somatic and otolith growth can differ between sexes, and sex-specific back-calculation should be used. Preliminary analysis, using a single L_c/OR_c relationship for both sexes of *N. theodorei*, resulted in no significant difference for L_∞ between sexes (data not shown). However, a re-examination of the L_c/OR_c relationship for both species revealed that it is sex-specific. Back-calculating lengths using the sex-specific regression parameters produced a significant difference in the L_∞ parameter as a function of sex for *N. theodorei*. This highlights the need to assess L_c/OR_c in species that exhibit sexually divergent growth.

The rates at which *N. theodorei* and *N. aurifilum* reach asymptotic size are higher than those published for other nemipterids. Granada et al. (2004a) reported k values for male and female *Nemipterus bathybius* in Japan of 0.16 year⁻¹ ($L_\infty = 231.0$ mm TL) and 0.34 year⁻¹ ($L_\infty = 274.0$ mm TL) respectively. Erguden et al. (2010) reported lower VBGF growth coefficients of $k = 0.22$ year⁻¹ ($L_\infty = 355.8$ mm TL) and $k = 0.22$ year⁻¹ ($L_\infty = 342.0$ mm TL) for male and female *Nemipterus randalli* respectively. Growth coefficients of $k = 0.218$ year⁻¹ ($L_\infty = 331.5$ mm TL) (Innal et al. 2015) and $k = 0.18$ year⁻¹ ($L_\infty = 330.0$ mm TL) (ElHaweet 2013) have also been reported for *N. randalli* from Turkey and Egypt respectively. The higher growth coefficients derived in the current study may be a result of the methods used to estimate the growth parameters. Forcing the function through the origin (i.e. setting $L_0 = 0$ as a prior) is likely to increase the slope of the derived growth curve and the resultant value of k . For example, substituting $t = 0$ into the VBGF reported for male *N. bathybius* by Granada et al. (2004a) results in a FL of 63 mm, which is problematic. Granada et al. (2004a) suggested that further studies on young fish were necessary to improve the fitting of length-at-age data to smaller fish.

The use of back-calculation techniques in the current study, combined with the use of prior information to estimate the growth parameters in Bayesian framework, overcomes the potential bias associated with a lack of smaller, younger fish (Smart & Grammer 2021). Differences in published growth coefficients may also be attributed to temporal and geographical variations and species-specific differences.

Maximum age estimates in this current study were found to be ~six years for *N. theodorei* and ~four years for *N. aurifilum*. These are at the upper range of maximum ages reported for other nemipterids. Previous studies have reported a maximum age of three years for *N. randalli* in Turkish waters (Erguden et al. 2010), four years for *N. bathybius* in the waters of Hong Kong (Eggleston 1972) and three years for *Nemipterus marginatus* in the South China Sea (Pauly & Martosubroto 1980), although the identification of this species is uncertain (Russell 1991). Further, Kao (1979) reported a maximum longevity of five years for *Nemipterus virgatus* in the East and South China Seas.

Gonad stage and GSI indicate both *N. theodorei* and *N. aurifilum* spawn over extended periods throughout the austral spring, summer, and early autumn. This is consistent with the timing and duration of spawning in other nemipterids reported in previous studies. For example, *N. randalli* (Murty 1984), *Nemipterus japonicus* (Raje 1996) and *Nemipterus bipunctatus* (Mohan & Velayudhan 1986, as *Nemipterus delagoae*) were all found to spawn in the austral spring and summer. Similarly, *N. bathybius* was found to spawn in the boreal summer (Granada et al. 2004b). In all species, spawning occurs over a prolonged period.

There is scant published life-history information for nemipterids, and other species caught incidentally in the QECOTF. Most species that are caught as bycatch in the QECOTF are considered to be at low risk of overfishing (Jacobsen et al. 2018) because they are assumed to exhibit fast growth and early maturity. However, very few species have published life-history information, requiring the use of proxies when assessing risk. There is, therefore, a need to attain life-history information for the bycatch species to assess population status. The ecological

risk to nemipterids and other bycatch species from the QECOTF has declined since the late 1990s due significant reductions in fishing effort (Wang et al. 2020). In addition, several bycatch reduction devices, which were mandated in the fishery in the early 2000s, are also likely to reduce the risk to some bycatch species. In particular, square codend bycatch reduction devices, constructed from large (~100 mm stretched) mesh, have been shown to significantly reduce the catch of nemipterids (Courtney et al. 2008). This particular device, however, is not suitable for use where *N. theodorei* and *N. aurifilum* predominantly occur, and as a result fishers use other less effective devices.

CONCLUSION

This study has increased the scientific knowledge of two common species, *N. theodorei* and *N. aurifilum*. Like other nemipterids, *N. theodorei* and *N. aurifilum* exhibit fast growth, mature in the first year of life and live to a maximum of six and four years, respectively. Both species are common in trawl bycatch in southern Queensland. However, the life-history characteristics derived suggest both species are resilient to current levels of trawl effort. The estimates of growth and length-at-maturity can be used when assessing future fishery impacts on these species.

ACKNOWLEDGEMENTS

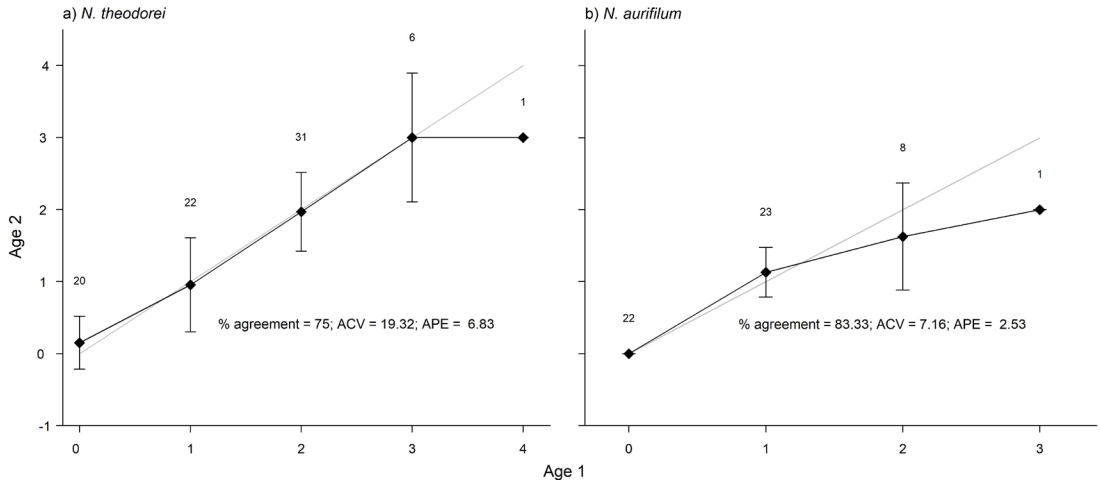
This study was funded by the Fisheries Research and Development Corporation (FRDC Project No. 2000/170), and the Queensland Department of Agriculture and Fisheries (DAF), and we thank them for their continuing support of fisheries research in Queensland. Darren Roy and Mark Tonks processed samples in the laboratory, and we thank them for their many hours in the Southern Fisheries Centre's wet lab. We are grateful to Corey Green for ageing the samples at the Central Ageing Facility. Tony Sterling provided samples and we thank him for his valuable contribution to this study. We sincerely thank Zalee Bates and Pat Abbott for their continued diligence in sourcing and supplying relevant literature and assisting with Endnote-related issues.

LITERATURE CITED

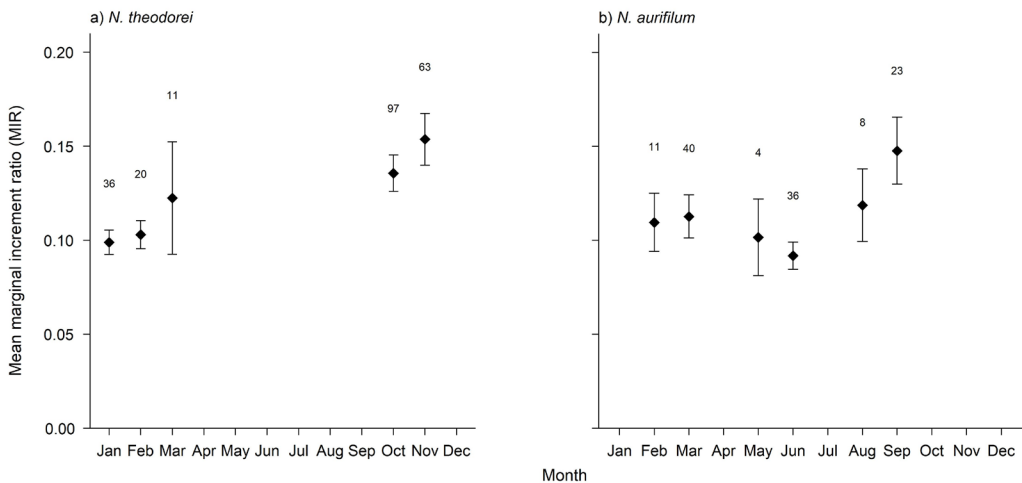
- Beamish, R. & Fournier, D. (1981). A method for comparing the precision of a set of age determinations. *Canadian Journal of Fisheries and Aquatic Sciences*. **38**(8), 982–983. <https://doi.org/10.1139/f81-132>.
- Cailliet, G.M., Smith, W.D., Mollet, H.F., & Goldman, K.J. (2006). Age and growth studies of chondrichthyan fishes: the need for consistency in terminology, verification, validation, and growth function fitting. *Environmental Biology of Fishes*. **77**, 211–228. <https://doi.org/10.1007/s10641-006-9105-5>.
- Campbell, M.J., McLennan, M.F., Nicolson, J.R., Garland, A., Prosser, R.M., & Midgley, R.F. (2022). Improving estimates of growth for pearl perch (*Glaucosoma scapulare*) in Queensland, Australia. *Aquaculture, Fish and Fisheries*. **3**(1), 71–80. <https://doi.org/10.1002/aff2.90>.
- Campbell, M.J. & Rigby, C.L. (2022). A re-examination of the growth of the gummy shark (*Mustelus antarcticus*) from Queensland, Australia. *Marine and Freshwater Research*. **73**(11), 1399–1403. <https://doi.org/10.1071/MF22066>.
- Carpenter, B., Gelman, A., Hoffman, M.D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M., Guo, J., Li, P., & Riddell, A. (2017) *Stan: A Probabilistic Programming Language*, Version 2017-01-11.
- Courtney, A., Campbell, M.J., Roy, D.P., Tonks, M.L., Chilcott, K.E., & Kyne, P.M. (2008). Round scallops and square meshes: a comparison of four codend types on the catch rates of target species and bycatch in the Queensland (Australia) saucer scallop (*Amusium balloti*) trawl fishery. *Marine and Freshwater Research*. **59**(10), 849–864. <https://doi.org/10.1071/MF08073>.
- Courtney, A.J., Campbell, M.J., Tonks, M.L., Roy, D.P., Gaddes, S.W., Haddy, J.A., Kyne, P.M., Mayer, D.G., & Chilcott, K.E. (2014). Effects of bycatch reduction devices in Queensland's (Australia) deepwater eastern king prawn (*Melicertus plebejus*) trawl fishery. *Fisheries Research*. **157**, 113–123. <https://doi.org/10.1016/j.fishres.2014.03.021>.
- Courtney, A.J., Tonks, M.L., Campbell, M.J., Roy, D.P., Gaddes, S.W., Kyne, P.M., & O'Neill, M.F. (2006). Quantifying the effects of bycatch reduction devices in Queensland's (Australia) shallow water eastern king prawn (*Penaeus plebejus*) trawl fishery. *Fisheries Research*. **80**(2-3), 136–147. <https://doi.org/10.1016/j.fishres.2006.05.005>.
- Courtney, A.J., Haddy, J.A., Campbell, M.J., Roy, D.P., Tonks, M.L., Gaddes, S.W., Chilcott, K.E., O'Neill, M.F., Brown, I.W., McLennan, M., Jebreen, E.J., van der Geest, C., Rose, C., Kistle, S., Turnbull, C.T., Kyne, P.M., Bennett, M.B., & Taylor, J. (2007). Bycatch weight, composition and preliminary estimates of the impact of bycatch reduction devices in Queensland's trawl fishery, rep. no. Fisheries Research and Development Corporation (FRDC) Final Report 2000/170. (Queensland Department of Primary Industries and Fisheries, Brisbane, Queensland). https://www.daf.qld.gov.au/_data/assets/pdf_file/0007/75769/BycatchFinalReport2007-FullReport.pdf.
- Eggleston, D. (1972). Patterns of biology in Nemipteridae. *Journal of the Marine Biological Association of India*. **14**(1), 357–364.
- ElHaweet, A.E.A. (2013). Biological studies of the invasive species *Nemipterus japonicus* (Bloch, 1791) as a Red Sea immigrant into the Mediterranean. *The Egyptian Journal of Aquatic Research*. **39**(4), 267–274. <https://doi.org/10.1016/j.ejar.2013.12.008>.
- Erguden, D., Turan, C., Gurlek, M., Yaglioglu, D., & Gungor, M. (2010). Age and growth of the Randall's threadfin bream *Nemipterus randalli* (Russell, 1986), a recent Lessepsian migrant in Iskenderun Bay, northeastern Mediterranean. *Journal of Applied Ichthyology*. **26**(3), 441–444. <https://doi.org/10.1111/j.1439-0426.2009.01387.x>.
- Francis, R.I.C.C. (1990). Back-calculation of fish length: a critical review. *Journal of Fish Biology*. **36**(6), 883–902. <https://doi.org/10.1111/j.1095-8649.1990.tb05636.x>.
- Gabry, J.T.M. (2020) bayesplot: Plotting for Bayesian Models. R package version 1.7.2, <https://mc-stan.org/bayesplot>.
- Granada, V.P., Masuda, Y., & Matsuoka, T. (2004a). Age and growth of the yellowbelly threadfin bream *Nemipterus bathybius* in Kagoshima Bay, southern Japan. *Fisheries Science*. **70**(3), 497–506. <https://doi.org/10.1111/j.1444-2906.2004.00831.x>.
- Granada, V.P., Masuda, Y., & Matsuoka, T. (2004b). Annual reproductive cycle and spawning frequency of the female yellowbelly threadfin bream *Nemipterus bathybius* in Kagoshima Bay, southern Japan. *Aquaculture Science*. **52**(4), 329–340. <https://doi.org/10.11233/aquaculturesci1953.52.329>.
- Haddy, J.A. & Pankhurst, N.W. (1998). Annual change in reproductive condition and plasma concentrations of sex steroids in black bream, *Acanthopagrus butcheri*, (Munro) (Sparidae). *Marine and Freshwater Research*. **49**(5), 389–397. <https://doi.org/10.1071/MF97239>.

- Innal, D., Aksu, M., Akdoganbulut, D., Kisin, B., Can Unal, M., Oztop, M., Dogangil, B., & Pek, E. (2015). Age and growth of *Nemipterus randalli* from Antalya Gulf, Turkey. *International Journal of Fisheries and Aquatic Studies*. **2**(4), 299–303.
- Jacobsen, I., Zeller, B., Dunning, M., Garland, A., Courtney, T., & Jebreen, E.J. (2018). An ecological risk assessment of the southern Queensland east coast otter trawl fishery and river and inshore beam trawl fishery. (Department of Agriculture and Fisheries, Brisbane, Queensland). https://www.daf.qld.gov.au/_data/assets/pdf_file/0004/1402672/Sth-QLD-Trawl-ERA-Final.pdf.
- Kao, C. (1979). Age and growth of golden thread, *Nemipterus virgatus*, (Houttuyn), from the East and the South China Seas. *Acta Oceanologica Taiwanica*. **9**, 97–110.
- Mohan, M. & Velayudhan, A. (1986). Spawning biology of *Nemipterus delagoae* (Smith) at Vizhinjam. *Journal of the Marine Biological Association of India*. **28**(1&2), 26–34.
- Morison, A.K., Robertson, S.G., & Smith, D.C. (1998). An integrated system for production fish aging: image analysis and quality assurance. *North American Journal of Fisheries Management*. **18**(3), 587–598. [https://doi.org/10.1577/1548-8675\(1998\)018<0587:AISFPF>2.0.CO;2](https://doi.org/10.1577/1548-8675(1998)018<0587:AISFPF>2.0.CO;2).
- Munday, P.L., Hodges, A.L., Choat, J.H., & Gust, N. (2004). Sex-specific growth effects in protogynous hermaphrodites. *Canadian Journal of Fisheries and Aquatic Sciences*. **61**(3), 323–327. <https://doi.org/10.1139/f04-057>.
- Murty, V. (1984). Observations on the fisheries of threadfin breams (Nemipteridae) and on the biology of *Nemipterus laponicus* (block) from Kakinada. *Indian Journal of Fisheries*. **31**(1), 1–18.
- Natanson, L.J., Casey, J.G., & Kohler, N.E. (1995). Age and growth estimates for the dusky shark, *Carcharhinus obscurus*, in the western North Atlantic Ocean. *Fishery Bulletin*. **93**(1), 116–126.
- Pauly, D. & Martosubroto, P. (1980). The population dynamics of *Nemipterus marginatus* (Cuvier & Val.) off Western Kalimantan, South China Sea. *Journal of Fish Biology*. **17**(3), 263–273. <https://doi.org/10.1111/j.1095-8649.1980.tb02760.x>.
- R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Version 3.6.1. <http://www.R-project.org/>.
- Raje, S.G. (1996). Some observations on the biology of *Nemipterus mesoprion* (Bleeker) from Veraval (Gujarat). *Indian Journal of Fisheries*. **43**(2), 157–162.
- Russell, B.C. (1990). Nemipterid fishes of the world. *FAO Fisheries Synopsis*. **12**(125), 1.
- Russell, B.C. (1991). Description of a new species of *Nemipterus* (Pisces: Perciformes; Nemipteridae) from the western Pacific, with re-descriptions of *Nemipterus marginatus* (Valenciennes), *N. mesoprion* (Bleeker) and *N. nematopus* (Bleeker). *Journal of Natural History*. **25**(5), 1379–1389. <https://doi.org/10.1080/00222939100770861>.
- Sainsbury, K.J. & Whitelaw, A.W. (1984). Biology of peron's threadfin bream, *Nemipterus peronii* (Valenciennes), from the north west shelf of Australia. *Australian Journal of Marine and Freshwater Research*. **35**(2), 167–185. <https://doi.org/10.1071/MF9840167>.
- Simpfendorfer, C.A., Chidlow, J., McAuley, R., & Unsworth, P. (2000). Age and growth of the whiskery shark, *Furgaleus macki*, from southwestern Australia. *Environmental Biology of Fishes*. **58**, 335–343. <https://doi.org/10.1023/A:1007624828001>.
- Smart, J.J. (2020). BayesGrowth: Estimate fish growth using MCMC analysis. R package version 0.3.0. <https://github.com/jonathansmart/BayesGrowth>.
- Smart, J.J. & Grammer, G.L. (2021). Modernising fish and shark growth curves with Bayesian length-at-age models. *PLOS ONE*. **16**(2), e0246734. <https://doi.org/10.1371/journal.pone.0246734>.
- Stan Development Team. (2020). RStan: the R interface to Stan, Version R package version 2.21.2.
- Vehtari, A., Gabry, J., Magnusson, M., Yao, Y., Bürkner, P.-C., Paananen, T., & Gelman, A. (2020). loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models, Version R package version 2.4.1.
- Vivekanandan, E. (1991). Spawning and growth of three species of threadfin breams off Madras. *Indian Journal of Fisheries*. **38**(1), 9–12.
- Wang, N., Courtney, A.J., Campbell, M.J., & Yang, W-H. (2020). Quantifying long-term discards from Queensland's (Australia) east Coast otter trawl fishery. *ICES Journal of Marine Science*. **77**(2), 680–691. <https://doi.org/10.1093/icesjms/fsz205>.

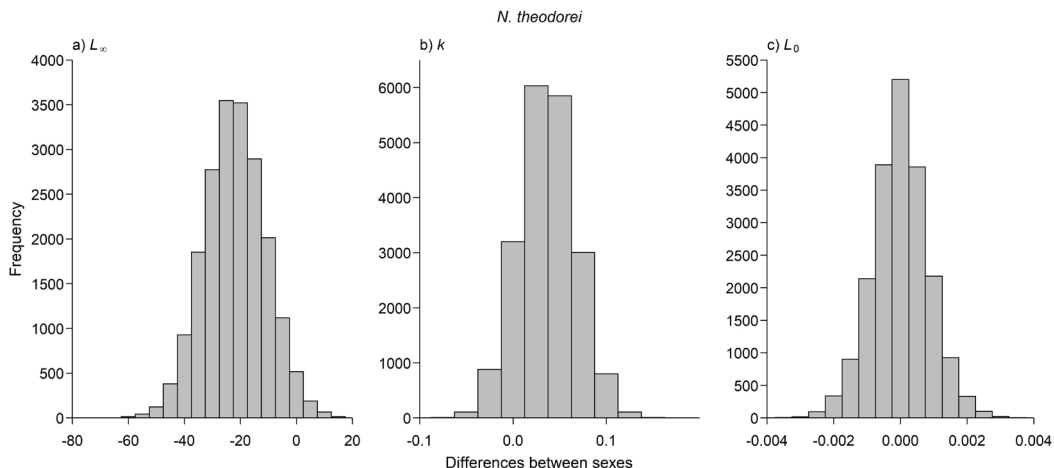
APPENDIX: SUPPLEMENTARY MATERIAL



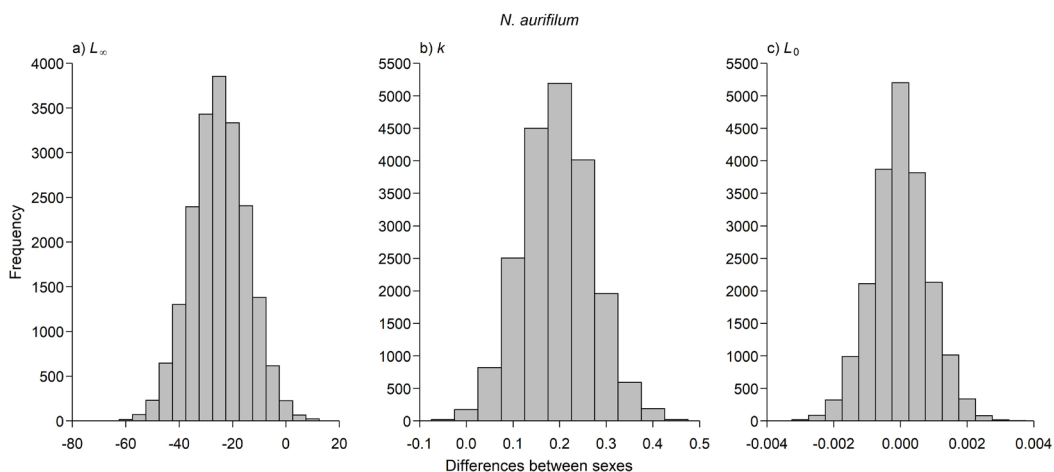
Supplementary Figure 1. Age bias plot for two distinct reads by the same reader for **A** *Nemipterus theodorei* and **B** *Nemipterus aurifilum* otolith samples. The 1:1 line of equivalence is represented by the grey line for both species. The number of each species assigned to each nominal age is displayed above each point. The relevant parameters of agreement between each read are also shown.



Supplementary Figure 2. Variation in mean marginal increment ratio (MIR, \pm SE) as a function of month for **A** *Nemipterus theodorei* and **B** *Nemipterus aurifilum* caught in south-east Queensland, Australia.



Supplementary Figure 3. Differences in values of L_{∞} , k and L_0 between sexes for *Nemipterus theodorei* caught in south-east Queensland, Australia. **Note:** L_{∞} is the asymptotic length (mm), k (year^{-1}) is the growth coefficient of the von Bertalanffy function (see Table 2) and L_0 is the length (mm) at $t = 0$.



Supplementary Figure 4. Differences in values of L_{∞} , k and L_0 between sexes for *Nemipterus aurifilum* caught in south-east Queensland, Australia. **Note:** L_{∞} is the asymptotic length (mm), k (year^{-1}) is the growth coefficient of the von Bertalanffy function (see Table 2) and L_0 is the length (mm) at $t = 0$.

Supplementary Table 1. Confidence intervals (95%) and median value of parameter differences between sexes for both *Nemipterus theodorei* and *Nemipterus aurifilum*. **Note:** L_{∞} is the asymptotic length (mm); L_0 is the length (mm) at $t = 0$; k (year^{-1}) is the growth coefficient of the von Bertalanffy function (see Table 2).

Parameter	Median	95% confidence intervals
<i>N. theodorei</i>		
L_{∞} (mm)	-22.07	(-43.01 – -0.19)
k (year^{-1})	0.04	(-0.02 – 0.10)
L_0 (mm)	0.00	(0.00 – 0.00)
<i>N. aurifilum</i>		
L_{∞} (mm)	-25.04	(-45.36 – -4.63)
k (year^{-1})	0.19	(0.05 – 0.34)
L_0 (mm)	0.00	(0.00 – 0.00)