

Variations in life history characteristics of the deep-water giant ruby snapper (*Etelis* sp.)
between the Indian and Pacific Oceans and application of a data-poor assessment

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Abstract

The giant ruby snapper, *Etelis* sp., attains the largest size of any lutjanid in the Indo-Pacific and is one of the most valuable species harvested from deep-water fisheries along the continental and insular shelf margins throughout its broad geographic distribution.

5 Despite this species supporting important commercial, artisanal and subsistence fisheries, quantitative assessments of the status of stocks have been limited by an absence of biological information, unreliable catch and effort statistics, and until recently, misidentification with a cryptic congener. This study aimed, firstly, to describe and compare the age, growth and reproductive characteristics of *Etelis* sp. between the eastern
10 Indian and western central Pacific Oceans; and secondly, to provide an age-based assessment of the stock in north-western Australia, the only stock for which available data were sufficient to quantify stock status. Although the growth of *Etelis* sp. differed significantly between sexes and oceans, longevity was similar with a maximum age of 56 years recorded in the Pacific Ocean. Spawning of this species occurred over five months
15 during the austral summer to mid-autumn (i.e. December to April) in the Indian Ocean, but was not well defined in the Pacific Ocean. The estimated ages at 50% maturity for females and males in the Indian Ocean were similar (i.e. 4-5 years), whereas lengths at 50% maturity differed ($L_{50}^{\text{mat}} = 527$ and 456 mm fork length, FL, respectively), but were consistent with corresponding differences in growth between sexes. Estimates of the
20 relative female spawning potential ratio for *Etelis* sp. in north-western Australia suggest the status of this stock remained relatively unchanged from 1997 to 2011, at around 60% of the unfished level. This assessment provides an example of the relative sustainable exploitation levels for this stock, and potentially other Eteline snappers that exhibit similar life history characteristics, particularly in locations where monitoring and
25 assessments may be data and/or resource limited.

Keywords: Stock status; Etelinae; Age and growth; Reproduction; Maturity

1. Introduction

There is insufficient information available on the life history characteristics and stock
30 status of most species of Etelinae in the Indo-Pacific region to inform management
(Newman et al., 2016; 2017). In fact, some genera in this sub-family, such as the
monotypic *Randallichthys*, are so rarely encountered that even their distribution is still
relatively undefined (Newman, 2009; Wakefield et al., 2016). For some more heavily
35 exploited species in this group, such as *Etelis coruscans*, despite being considered
overfished in some locations (Hill et al., 2016; 2018), its life-history characteristics
remain relatively unknown. Only recently the taxonomic revision of the highly valued
nominal *E. carbunculus* identified a cryptic species pair that are morphologically similar,
and now recognised as *Etelis* sp. (giant ruby snapper) and *E. carbunculus* (pygmy ruby
40 snapper, Wakefield et al., 2014; Andrews et al., 2016). These two cryptic species are
sympatric and typically co-occur in catches with varying abundances throughout their
distribution. Thus, their previous misidentification has inevitably resulted in significant
historical biases for key data inputs required for monitoring and assessment of their
status.

45 The giant ruby snapper, *Etelis* sp., attains the largest size for its genus (> 100 cm, > 20
kg, Williams et al., 2013; Wakefield et al., 2014) and, like most *Etelis* species, its life
history is poorly understood. Regional and/or location-specific assessments of stock
status for this species have not been undertaken or have mistakenly included data for its
cryptic congener (Williams et al., 2013; 2015; Newman et al., 2016). Given the
50 importance of this species to fisheries (Newman et al., 2016), there is a need to describe

its life history and ascertain whether this species shares the typical characteristics associated with similar deep-water lutjanids. For example, the closely related *E. carbunculus* exhibits a modest age at maturity (i.e. ~5 years) and longevity (i.e. 32 years), similar to many shallower water Lutjanidae, inferring a relatively similar population productivity (Newman and Dunk, 2003; Williams et al., 2017). Williams et al. (2017) examined the age-specific demography of *E. carbunculus* across 90° of longitude and 20° of latitude in the western central Pacific and eastern Indian Oceans and reported that growth differs significantly between oceans and sexes and in relation to latitude. Thus, stock assessments of *Etelis* species may need to consider regional variations in life history characteristics.

Deepwater Eteline snappers constitute important deep-water fisheries resources throughout their distribution, particularly around islands throughout the tropical and subtropical Indo-Pacific region (Williams and Nicol, 2012; Newman et al., 2016). These deep-water resources typically sustain small-scale fisheries offering economic and/or cultural value to many Indo-Pacific countries (Dalzell et al., 1996). Catches from these small-scale fisheries are biodiverse, with over 200 species from 93 genera reported in the western central Pacific Ocean (Dalzell and Preston, 1992). Only a small number of deep-water commercial fisheries targeting *Etelis* species exist, mostly in developed countries (Newman et al., 2016). Unfortunately, however, catch statistics for *Etelis* sp. from even these developed countries are unreliable due to misidentification with its cryptic congener. The proportion of *E. sp.* to *E. carbunculus* within catches varies markedly throughout their geographic distribution, for example, *E. sp.* is not represented in the

catches in Hawaii (Andrews et al., 2016), but comprises ~99% of their combined catches
75 in Indonesia (Mous et al., 2020). In north-western Australia, combined annual catches of
Etelis sp. and *E. carbunculus* from both Commonwealth and State-managed commercial
fisheries were first recorded in *ca* 1993, with catches increasing to a peak of 70 t in the
Commonwealth-managed fisheries in 2001 and 115 t in the State-managed fisheries in
2004. Since 2007, the combined annual catches for these two cryptic species have
80 averaged ~10 t and 32 t in the Commonwealth and State-managed fisheries, respectively.
To date, however, the life history characteristics and stock status of *Etelis* sp. in this
region of the eastern Indian Ocean have not been determined.

This study examined the age-specific life history characteristics of *Etelis* sp. in the
85 eastern Indian Ocean and compared it to those for this species in the western central
Pacific Ocean to investigate the extent to which they differed across its broad geographic
distribution. Specifically, we compared sex-specific age and length distributions, growth
and mortality, annual spawning periodicity, and the lengths and ages at which females
and males of this species mature between these oceanic regions. Recognising that
90 opportunities to collect sufficient and representative samples for an age-based stock
assessment are limited in most locations throughout this species range, this study also
provides estimates of the relative female spawning potential ratio (SPR, based on female
spawning-biomass-per-recruit), calculated using life history information and mortality
derived from age-composition data to determine the stock status in north-western
95 Australia. Unlike dynamic integrated assessment models, SPR can be estimated without a
time series of catch and an index of abundance, which are not available for *Etelis* sp. The

results from this assessment provide useful information on sustainable exploitation levels for this and potentially other *Etelis* snappers that exhibit similar life history characteristics in other locations for which monitoring and assessment may be data and/or resource limited.

2. Methods

2.1 Sampling

In the eastern Indian Ocean, *Etelis* sp. were sampled from the upper continental slope along the north and west coasts of Western Australia, and from the island slopes of Christmas and Cocos (Keeling) Islands from a depth range of 150 to 480 m from 1996 to 2014 (Fig. 1). These samples were collected predominantly from commercial catches (85%), with samples from recreational fishers and research surveys providing minor contributions (2% and 13%, respectively). In the late 1990s these commercial catches were taken using demersal trawls, with more recent commercial fishing involving hook and line (since ca 2000). Samples collected onboard research surveys from the eastern Indian Ocean were caught using traps and lines. In the western central Pacific Ocean, samples of this species were collected from seamounts and island reef slopes in the Exclusive Economic Zones (EEZs) of New Caledonia, Vanuatu, Wallis and Futuna, Tonga, and Samoa (Fig. 1, Pacific Islands Fisheries Science Center, 2020). Samples from this region were collected from commercial catches (80%) or research surveys (20%) from 2012 to 2016 and were all obtained using hook and line.

For each *Etelis* sp. the fork length (FL) was measured to the nearest 1 mm (and
120 occasionally to the nearest 5 mm during sampling in the western central Pacific Ocean)
and the two sagittal otoliths were removed, washed and stored in envelopes or plastic
vials. When possible, the wet weight (W) of each fish was recorded to the nearest 0.1 g.
For each region, an allometric relationship between length (L , in mm FL) and weight (W ,
in g) was derived by fitting a linear function using least-squares to the log-transformed
125 data: $W = \alpha_W L^{\beta_W}$, where α_W and β_W are parameters of this allometric relationship
(Quinn and Deriso, 1999). This equation was used to estimate the weights of *Etelis* sp.
donated by fishers as frames (skeletons). The back-transformed estimates of weight were
adjusted for the bias associated with the log transformation (Quinn and Deriso, 1999).
The relationships between length and weight for *Etelis* sp. from the Indian and Pacific
130 Oceans were tested for significant differences using a likelihood-ratio test (Cerrato,
1990).

2.2 Ageing and growth

Thin otolith sections were prepared using the methods recently described for *Etelis* sp. by
135 Wakefield et al. (2017a). This involved embedding the sagittal otolith in epoxy resin and
sectioning transversely through the primordium, perpendicular to the sulcus acusticus,
using a low speed saw (IsometTM Buehler Ltd) with a diamond tipped blade. Prior to
sectioning, the micrometer on each saw was calibrated to improve the consistency in the
thickness of otolith sections. Otolith sections were cut thinly at ~180-200 μm , rinsed in
140 2% hydrochloric acid for 15-30 seconds (Gauldie et al., 1990), and mounted on a glass
slide with a cover slip using casting resin. Opaque zone counts from each otolith section

were derived using a dissecting microscope (fitted with 20x stereoscopic oculars) under reflected light at 40-60x magnification, and without any knowledge of fish size. Bomb radiocarbon dating has previously confirmed that a single opaque and translucent zone is deposited annually in the otoliths of *Etelis* sp. (Andrews et al., 2011). Otolith sections from these absolute aged fish ($n = 3$) provided a useful reference for the formation of growth zones in otolith sections of this species. Precision in opaque zone counts was deemed acceptable (i.e., Index Average Percent Error, IAPE < 5.5%, Campana, 2001; Wakefield et al., 2017a) among readers ($n = 100$, CBW, BMT, SJN, AJW) with experience interpreting growth zones from thin otolith sections (Wakefield et al., 2010; 2015; 2017a; Williams et al., 2017). The ages of *Etelis* sp. were calculated using a combination of the date that they were captured, an assumed birth date corresponding to the peak in spawning (i.e., 1 January), the time of year when opaque zones in the majority of otoliths become delineated (i.e. 1 October), and the number of opaque zones.

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The growth of female and male *Etelis* sp. from both the Indian and Pacific Oceans was described separately using the von Bertalanffy growth equation fitted to the length-at-age data. The form of the equation was:

$$L_a = L_\infty(1 - \exp[-k(a - t_0)]),$$

160 where L_a is the predicted fork length (mm) of fish at age a (years), L_∞ is the asymptotic length (mm) at an infinite age, k is the growth coefficient, a constant that determines the rate (year^{-1}) at which L_a approaches L_∞ , and t_0 is the hypothetical age (years) at which fish would have zero length. Growth curves were fitted using least squares regression, and estimates of L_∞ , k , and t_0 ($\pm 95\%$ confidence limits, CLs) were determined by

165 bootstrapping, where 1,000 sets of parameters were obtained from the analysis of data
produced by random resampling with replacement. The von Bertalanffy growth
parameters and their lower and upper 95% CLs were calculated as the median, 2.5, and
97.5 percentiles, respectively, of the 1,000 bootstrap estimates. Growth curves were
compared between sexes and oceanic regions using a likelihood-ratio test (Cerrato, 1990).

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2.3 Spawning period and maturity analyses

When possible, the gonads from each fish were weighed (GW) to the nearest 0.01 g,
sexed and macroscopically allocated to a maturational stage using the criteria in
Wakefield et al. (2010), i.e., stage I (immature/resting), stage II (developing), stage III
175 (developed), stage IV (ripe), and stage V (spent). A subsample of freshly dissected
gonads from fish caught in the Indian ($n = 56$ females and 27 males) and Pacific Oceans
($n = 270$ females and 269 males) were preserved in pH neutral 10% buffered formalin for
investigating histological characteristics. Medial transverse sections of the preserved
gonads were embedded in paraffin wax, sectioned at 5 μm , mounted on glass slides, and
180 stained with Mayer's haematoxylin and eosin. Gonad histology was used to confirm that
the reproductive mode of *Etelis* sp. is gonochoristic. The gonadosomatic index (GSI) for
each fish was determined using the equation, $GSI = 100 GW / W$, where GW and W are
the wet weight of the gonad and whole fish in g, respectively. The data for gonadal stages
and GSIs for fish of each sex were pooled for each calendar month for the Indian and
185 Pacific Ocean regions separately. The spawning periods of *Etelis* sp. for the Indian and
Pacific Oceans were determined on the basis of annual trends in mean monthly GSIs and

the monthly prevalences of females and males (\geq the length at 50% maturity) with developed (stage III) and/or spawning (stage IV) gonads.

190 The lengths by which 50% of female and male *Etelis* sp. have attained sexual maturity
(L_{50}^{mat}) during the spawning period were estimated for the Indian Ocean separately, using
logistic regression to determine the relationships with length of the probability that a
female or male during the spawning period possessed gonads at stages II–V. It is
therefore assumed that during the spawning period, fish with gonads of these stages
195 would have the potential to spawn, were spawning, or had recently spawned and were
thus regarded as mature, and that fish with gonads at stage I would have remained
immature. The maturity ogive used was a re-parameterised form of the logistic equation
(e.g., Punt and Kennedy, 1997; Hesp et al., 2004; Wakefield et al., 2007):

$$\psi_L = \left\{ 1 + \exp \left[-\log_e (19) \frac{(L - L_{50}^{\text{mat}})}{(L_{95}^{\text{mat}} - L_{50}^{\text{mat}})} \right] \right\}^{-1},$$

200 where ψ_L is the proportion of mature *Etelis* sp. at a particular fork length L , and L_{50}^{mat} and
 L_{95}^{mat} are the estimated lengths by which 50 and 95% of *Etelis* sp. have attained sexual
maturity, respectively. The L_{50}^{mat} and L_{95}^{mat} for the females and males in this oceanic
region, and their 95% CLs, were determined by bootstrapping, where 2,000 sets of
estimates of the logistic equation parameters were obtained from the analysis of data
205 produced by random resampling, with replacement. The point estimates and 95% CLs of
the proportions of mature fish in each length class were calculated as the median, 2.5 and
97.5 percentiles, respectively, of the 2,000 bootstrap estimates. The same approach was
employed to determine the relationship between the proportion mature with respect to
age, a , i.e.:

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$$\psi_a = \left\{ 1 + \exp \left[-\log_e (19) \frac{(a - A_{50}^{\text{mat}})}{(A_{95}^{\text{mat}} - A_{50}^{\text{mat}})} \right] \right\}^{-1},$$

where A_{50}^{mat} and A_{95}^{mat} are the ages by which 50 and 95% of individuals were mature.

In contrast to data for the Indian Ocean, and noting that sample sizes for the species was much lower for data from the Pacific Ocean, trends for the lengths and ages at which
 215 female and male *Etelis* sp. attained sexual maturity in the Pacific Ocean did not exhibit a typical logistic relationship and thus no such relationship was fitted. Instead, the L_{50}^{mat} for female and male *Etelis* sp. from this oceanic region were derived from the average life history invariant ratio of $L_{50}^{\text{mat}}/L_{\infty}$ for females and males from the Indian Ocean (i.e. $L_{50}^{\text{mat}}/L_{\infty} = 0.67$). Note this value of $L_{50}^{\text{mat}}/L_{\infty}$ for *Etelis* sp. is consistent with those
 220 typically exhibited for most teleosts (Prince et al., 2015; Thorson et al., 2017).

2.4 Stock assessment for north-western Australia

In the absence of a reliable time series of catch and an abundance index required to construct a dynamic integrated model for assessing *Etelis* sp. in north-western Australia,
 225 the status of the stock was examined using catch curve and per-recruit analyses based on age composition data. Common to these methods is the assumption of the population being in an equilibrium state, with recruitment and total mortality remaining constant over the lifespan of fully-recruited fish (Ricker, 1975; Goodyear, 1993). Although simulations have shown that departures from these assumptions can result in biased catch
 230 curve outputs (Dunn et al., 2002), the age-composition data collected for *Etelis* sp. in north-western Australia provided no indication of significant inter-annual recruitment variability or change in total mortality among the year classes represented by each sample

(see results). Stock status for this species in the Pacific Ocean was not assessed as sample sizes were relatively small.

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The instantaneous rate of fishing mortality (F) for *Etelis* sp. in north-western Australia was estimated by fitting a catch curve model separately to each of the two age composition samples, collected by trawling in 1997 ($n = 471$) and by line fishing in 2011 ($n = 418$). The fitted catch curve was essentially the same as that described by Thorson and Prager (2011), which allows for estimation of logistic selectivity at age but assumes a constant natural mortality (M). Simulation testing of multiple catch curve methods by Thorson and Prager (2011) demonstrated that a catch curve model with logistic selectivity performs better than one that assumes knife-edge selectivity, markedly improving the accuracy of F estimates.

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The catch curve model applied to the *Etelis* sp. assessment for north-western Australia describes the logistic selectivity of fish at age a , S_a , as:

$$S_a = \{1 + \exp[-s(a - A_{50}^{\text{sel}})]\}^{-1},$$

where A_{50}^{sel} is the age by which 50% of individuals are selected by the fishery and s is the slope of the logistic curve at A_{50}^{sel} . The fishing mortality at age, F_a , was calculated as:

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$$F_a = S_a F,$$

and total mortality at age, Z_a , was determined from natural mortality, M , as:

$$Z_a = F_a + M.$$

255 Recognising the difficulty of reliably estimating M using indirect methods, several
alternative values of this parameter for *Etelis* sp. in north-western Australia were
considered. Natural mortality was first calculated as:

$$M = -\log_e(0.01)/A_{\max},$$

based on the theoretical assumption that 1% of individuals survive to the maximum
260 observed age A_{\max} in this region (Quinn and Deriso, 1999). To test the sensitivity of
results to this assumption, values of M were also calculated from empirical mortality
equations for fish described by Hoenig (1983) and Then et al. (2015) as:

$$M = \exp(1.46 - (1.01 \log_e(A_{\max}))) \text{ and}$$

$$M = 4.899 A_{\max}^{-0.916},$$

265 where these estimates relate to approximately 1.5% and 0.12% of fish surviving to the
maximum age, respectively. Another estimate of M was calculated from the empirical
equation of Pauly (1980), which relates mortality to von Bertalanffy growth parameters
and water temperature, i.e.:

$$M = \exp\left(-0.0066 - (0.279 \log_e(L_{\infty})) + (0.6543 \log_e(k)) + (0.4634 \log_e(T))\right),$$

270 where L_{∞} (in cm) and k are the growth parameters estimated for *Etelis* sp. in this study
and T is the mean water temperature (~ 15 °C) at the depths at which this species occurs in
north-western Australia.

Setting survival at age zero, $\hat{N}_{a=0}$, to 1, the expected number of survivors per recruit for
275 all ages above zero were calculated as:

$$\hat{N}_a = \hat{N}_{a-1} \exp[-Z_{a-1}].$$

The estimated catch per recruit at age, \hat{C}_a , was derived from the Baranov catch equation, i.e.:

$$\hat{C}_a = \hat{N}_a(F_a/Z_a)(1 - \exp[-Z_a]),$$

280 while the expected catch proportion at age, \hat{P}_a , assuming constant annual recruitment, was calculated as:

$$\hat{P}_a = \hat{C}_a / \sum_{a=0}^A \hat{C}_a.$$

The maximum age assumed for the analysis, A , was set well above the observed maximum recorded age in the samples, A_{\max} . Assuming that observed frequencies of fish
285 at age, f_a , represent samples from a multinomial distribution of the expected proportions of fish at age, the multinomial log-likelihood λ was calculated as:

$$\lambda = \sum_{a=0}^A f_a \log_e \hat{P}_a.$$

The model was fitted to data by maximizing λ using Solver in Microsoft Excel.

290 Bootstrap resampling methods (Efron, 1982; Efron and Tibshirani, 1986) were applied to estimate uncertainty around catch curve estimates of F , A_{50}^{sel} and s , with separate analyses undertaken for each sampling period. From each observed age composition with sample size n , 1,000 data sets were generated by randomly drawing n values with replacement from that sample. The catch curve model was then fitted separately to the 1,000
295 resampled age compositions generated for each sampling year (1997 and 2011) to determine the point estimate and the lower and upper 95% CLs for each parameter.

The bootstrapped catch curve estimates of fishing mortality and age-based logistic selectivity from each sampling period were next applied to calculate the ratio of

300 equilibrium spawning potential of *Etelis* sp., relative to that of an unfished stock. The
analyses applied two alternative equilibrium models, both which assumed an annual time
step and incorporated information about the growth and maturity of *Etelis* sp. from north-
western Australia as estimated in this study. Firstly, the female spawning potential ratio
(SPR, based on female spawning biomass per recruit, i.e. SBPR) was estimated using a
305 traditional per-recruit model assuming constant recruitment (Goodyear, 1993). For a
given level of fishing mortality F , female spawning biomass-per-recruit was calculated
according to the per-recruit model as:

$$SBPR_F = \sum_{a=0}^A \rho W_a \psi_a \exp(-Z_a),$$

where ρ is the proportion of recruits that are female (set to 0.5, assuming a 1:1 sex ratio),
310 W_a is the weight of fish at age a (based on the estimated length-weight relationship and
von Bertalanffy growth curve for females), and ψ_a is the proportion of females that have
attained maturity at age a . Female SPR was then calculated as:

$$SPR = SBPR_F / SBPR_{F=0},$$

where $SBPR_{F=0}$ is the unfished female spawning biomass-per-recruit.

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Considering the assumption of constant recruitment in the traditional per-recruit analysis
can be difficult to satisfy (Punt et al., 1993; Horbowy and Luzeńczyk, 2012), a second
age-structured model that incorporates a stock-recruitment relationship was used to
account for the potential effect of fishing on recruitment of *Etelis* sp. when estimating the
320 equilibrium level of relative spawning biomass (Horbowy and Luzeńczyk, 2012). It was
assumed that this stock-recruitment curve is of the form described by Beverton and Holt

(1957), where the expected recruitment, R , may be calculated from spawning stock biomass of females, B , as:

$$R = B/(\alpha + \beta B),$$

325 where α and β are parameters that determine the shape of the relationship. This equation may be reparametrised into an alternative form that employs a steepness parameter, h , i.e., the proportion of the unexploited equilibrium recruitment expected to recruit when spawning biomass is reduced to 20% of its unfished equilibrium level (Mace and Doonan, 1988). If the stock-recruitment relationship is of the Beverton and Holt form and 330 the population of fish is at equilibrium for a given value of F , the proportion to which spawning female biomass is reduced from its unfished equilibrium level, i.e. the relative spawning biomass, RSB, of females, may be calculated as:

$$RSB = (4h SPR + h - 1)/(5h - 1).$$

The steepness parameter h was set to 0.75, as recommended by Francis (1993).

335 Sensitivity analysis was undertaken to test the sensitivity of model outputs to uncertainty around this parameter, recognising that h varies among species with differing life history characteristics (e.g., Myers et al., 2002).

In the absence of a direct estimate of B_{MSY} for the stock, the estimates of SPR and RSB 340 for females in 1997 and 2011 were compared to a proxy reference level based on a proportion of the unfished spawning biomass, B_0 . Although several studies have shown that the relationship between B_{MSY} and B_0 is sensitive to the steepness of the stock-recruitment relationship, the current use of $0.3B_0$ as a proxy threshold level for State-managed Western Australian fisheries (and in this study) is consistent with B_{MSY}

345 estimates for species where $h \sim 0.7-0.8$ (e.g., Mangel et al., 2013; Punt et al., 2014). For
Etelis sp., this threshold value also corresponded well to the estimated relative stock
biomass at which fishing mortality generated the maximum long-term equilibrium yield
(Horbowy and Luzeńczyk, 2012).

350 3. Results

3.1 Length and age compositions, and length-weight relationship

A total of 2,230 *Etelis* sp. were sampled from the eastern Indian Ocean, ranging in length
from 157 to 1,127 mm FL. The length frequency distributions of females and males of
Etelis sp. from the Indian Ocean differed markedly (Fig. 2). The distribution of lengths
355 for both sexes were essentially unimodal. However, females comprised a greater
proportion of larger individuals with a broad mode of 575-725 mm FL compared to a
narrow mode of 525-625 mm FL for males. In this region, no sampled males were larger
than 770 mm FL, whereas 20% of sampled females exceeded this length ($n = 271 > 770$
mm FL).

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In comparison, although fewer *Etelis* sp. ($n = 733$) were sampled from the western central
Pacific Ocean, they had a very similar range in lengths to that of samples from the Indian
Ocean (i.e. 140 to 1,150 mm FL, Fig. 2). Unlike the Indian Ocean, the length
compositions of females and males from the Pacific Ocean were very similar, with a
365 relatively even distribution in frequencies across their length range and a broad mode at
~650 mm FL for both sexes (Fig. 2). There was a less conspicuous higher abundance of

larger females sampled from the Pacific Ocean, with 33 females compared to only two males greater than 900 mm FL (Fig. 2).

370 Despite the length-frequency compositions of *Etelis* sp. being markedly different between females and males in the Indian Ocean, the age-frequency distributions were similar (Fig. 2). The distributions in ages for both sexes exhibited a mode at ~ 10 years and ranged from 1-42 years for females and 1-36 years for males. The age-frequencies for this species from the Pacific Ocean had a unimodal distribution with a mode at ~5 years for
375 both females and males and, with the exception of two old males (i.e. 48 and 56 years), the age ranges were similar at 3-43 years for females and 1-44 years for males (Fig. 2).

The range in whole weights obtained for *Etelis* sp. were similar between the Indian (46 to 31,000 g, $n = 709$) and Pacific Oceans (60 to 26,000 g, $n = 692$). There was no significant
380 difference in the length-weight relationships between sexes or oceans (all $p > 0.05$), resulting in a combined equation for all samples of $W = 0.00001884 L^{2.997}$ ($r^2 = 0.99$).

3.2 Ageing precision, longevity and growth trajectories

The precision of opaque zone counts from thin transverse sections of otoliths was
385 acceptable, with an IAPE of 5.1% ($n = 100$, range = 1 to 38 opaque zones) for counts by the two readers (CBW and AJW). Opaque zone counts between readers concurred or differed by one for 79% of fish and no counts differed by more than three. The longevity of female *Etelis* sp. was very similar between the Indian and Pacific Oceans (female $A_{\max} = 42$ vs 43 years, respectively, Table 1), but varied markedly for males (male $A_{\max} = 36$

390 vs 56 years, respectively, Table 1), with the ages of eight males in the Pacific Ocean
exceeding that recorded for the oldest male in the Indian Ocean by ≥ 20 years.

The von Bertalanffy growth curves provided good fits to the lengths at age for female and
male *Etelis* sp. in each oceanic region, and t_0 values did not differ from zero by more
395 than 2 years (Table 1, Fig. 3). The growth curves differed significantly between females
and males within each oceanic region and between sexes from the different regions (all p
< 0.05, Figs 3 and 4). In both oceanic regions, growth was sexually dimorphic with
females attaining an asymptotic length (L_∞) of 190 mm larger than males, and their
respective corresponding k values were much lower for females than males (Table 1). For
400 both sexes, *Etelis* sp. attained a larger L_∞ in the Pacific than in the Indian Ocean (Table 1,
Fig. 4).

3.3 Spawning period, and length and age at maturity

In the eastern Indian Ocean, the mean monthly GSIs for females increased sharply from
405 1.0 in December to 5.4 in January before gradually declining over the four ensuing
months to 0.7 in May (Fig. 5). The prevalence of *Etelis* sp. with developed or ripe staged
ovaries (i.e., stages III and IV) exceeded 20% in each month from January to April, with
a peak of 98% in January (Fig. 5). Similarly, the mean monthly GSIs for males increased
from 0.7 in October to a peak of 2.8 in January before declining to 0.6 in April (Fig. 5).
410 Hence, the spawning period for *Etelis* sp. in this region predominantly occurs over five
months from December to April with a conspicuous peak in January. In contrast, the
trends in mean monthly GSIs and prevalence of ovaries in spawning condition (i.e.,

stages III and IV) in the western central Pacific Ocean did not exhibit a similar clearly defined annual spawning period. In this region, although the months with the highest
415 GSIs occurred at a similar time to the Indian Ocean (i.e., January and February), the mean monthly GSIs never exceeded 2.0 for either sex (Fig. 5). Further, the months when the prevalence of developed or ripe staged ovaries (i.e., stages III and IV) exceeded 20% occurred over a longer period of approximately seven months from October to April, but were highest from January to April which corresponded with the peak spawning period in
420 the Indian Ocean (Fig. 5). It should be noted that the number of samples collected in each month in this region were lower than those from the Indian Ocean.

The smallest mature *Etelis* sp. recorded from the Indian Ocean was 517 mm FL for females and 422 mm FL for males (Fig. 6), and the youngest mature individual was 4
425 years of age for both sexes (Fig. 7). Although the fork length of 527 mm by which 50% of females of *Etelis* sp. collected from the Indian Ocean during the main spawning months of January and February had attained sexual maturity is larger than the 456 mm of the males (Table 2; Fig. 6), the ages by which 50% of females and males had attained maturity were similar (Table 2; Figs 6 & 7). Considering the lengths at 50% maturity for
430 females and males occurred at similar proportions of their corresponding asymptotic lengths (63% and 70%, respectively), these differences in the length at maturity likely correspond to an invariant relationship with growth (i.e. $L_{50}^{\text{mat}}/L_{\infty}$).

The smallest mature *Etelis* sp. recorded from the Pacific Ocean was 530 mm FL for
435 females and 390 mm FL for males, and the youngest mature individual was 4 years of age

for males and 5 years for females (Figs 6 & 7). The trends in the proportion of mature *Etelis* sp. did not exhibit a typical logistic relationship with increasing length and age for either sex from samples collected across the western central Pacific Ocean during the main spawning months of January to April (Figs 6 & 7). Thus, the lengths and ages by which this species have attained sexual maturity were not estimated for this region.

3.4 Stock status in north-western Australia

The catch curve models, which assumed age-based logistic selectivity, provided good visual fits to age composition samples of *Etelis* sp. from 1997 and 2011, with expected values closely reflecting the observed data (Figs 8a, b). Point estimates of fishing mortality ($F = 0.038$ and 0.052 year^{-1} in 1997 and 2011, respectively) and associated upper 95% CLs (Table 3) were well below the value for natural mortality (M) of 0.11 year^{-1} , corresponding to the assumption that 1% of individuals survive to the maximum observed age of 42 years for *Etelis* sp. in north-western Australia. This suggests that, on average over the life span of the fish in the samples, exploitation has been relatively low. The application of a slightly lower estimate of M (0.10 year^{-1}) based on Hoenig's (1983) empirical mortality equation for fish did not markedly affect estimates of F , whilst using higher M estimates resulting from the equations of Then et al. (2015; $M = 0.16 \text{ year}^{-1}$) and Pauly (1980; $M = 0.31 \text{ year}^{-1}$) yielded values of F which were below zero, and therefore, were not considered biologically plausible for *Etelis* sp in north-western Australia. Estimates of selectivity at age differed markedly between the two sampling years, with individuals selected at an earlier age by trawling compared to line fishing (Table 3). The results indicate that 50% of *Etelis* sp. were selected by the

commercial trawl fishery at around 5 years, compared to 7 years by the commercial line
460 fishery.

Based on catch curve estimates of mortality and selectivity from 1997 and 2011, the
analyses of female relative spawning potential suggest the *Etelis* sp. stock in north-
western Australia has remained at around 60% of the unfished level over the years
465 represented by the age composition samples (Figs 8c, d). As expected, the relationships
between F and the two alternative measures of spawning potential (SPR and equilibrium
relative spawning biomass, RSB) were relatively similar at low levels of mortality ($F <$
 0.05 year^{-1}), but with the model accounting for the effect of fishing on recruitment
providing less optimistic results than the traditional per-recruit analysis when exploitation
470 increases (Fig. 8c). Selectivity had a marked impact on model outputs, with the spawning
potential based on the earlier selectivity at age of fish in the trawl fishery rapidly reducing
to a substantially lower level as F increased than estimates based on the line fishery
selectivity (Fig. 8c). A sensitivity analysis using different values to describe the steepness
of the stock-recruitment relationship (h , ranging from 0.6 to 0.9) showed that estimates of
475 equilibrium RSB did not change more than 0.02 for any increase or decrease in h by 0.05
(results not shown).

4.0 Discussion

This study provides the first estimates of age-based life history characteristics of the
480 deep-water giant ruby snapper, *Etelis* sp., since its recent taxonomic separation from a
cryptic congener, i.e. the pygmy ruby snapper, *E. carbunculus* (Wakefield et al., 2014;

Andrews et al., 2016). Thus, previous studies investigating the life history of *Etelis* sp. offer limited comparisons as samples used in those studies are highly likely to also include *E. carbunculus*. The life history parameters determined for *Etelis* sp. in this study
485 were combined with mortality estimates derived from representative age structure data in equilibrium-based per-recruit models to assess the stock status of this highly valued species in north-western Australia. Where the strong equilibrium assumptions of these methods can be satisfied, assessments based on age-composition data may be useful for several deep-water fisheries across the Indo-Pacific region, particularly those in
490 developing countries where complexities associated with subsistence and artisanal fisheries typically result in poor reporting of catch statistics (Newman et al., 2015; Newman et al., 2017; Hill et al., 2018), or even in developed countries where catch statistics may be pooled among a complex of species with disparate life histories (DeMartini, 2019). However, when applying such stock assessment approaches, there is a
495 need to consider that the required life history parameter inputs may vary considerably across a species geographic range (e.g. Wakefield et al., 2017b; Williams et al., 2017).

The *Etelis* sp. attains the largest size of any lutjanid in the Indo-Pacific region and this, along with an excellent palatability, affords it a high value among deep-water fishers. The
500 largest individuals sampled during this study were 1,150 mm FL and 21 kg from New Caledonia in the Pacific Ocean and 1,218 mm FL and 24 kg from Exmouth in north-western Australia. The growth of *Etelis* sp. varies significantly between sexes and oceans, with females attaining a length at age up to ~20% greater than that of males and both sexes attaining a length at age of up to ~15% larger in the Pacific than in the Indian

505 Ocean. These differences in growth between sexes and oceans identified for *Etelis* sp. follow the same trends as those determined by a recent study for the congener *E. carbunculus* (Williams et al., 2017). The longevities of female *Etelis* sp. are essentially the same between oceans (i.e., 42 years), and similar to that for males from the Pacific Ocean with the exception of the two oldest males (i.e. 48 and 56 years, sampled from
510 Papua New Guinea and Fiji, respectively). Thus, despite the oldest male sampled from the Indian Ocean being only 36 years and considering sample sizes and fishing exploitation can influence estimates of maximum age, it appears the longevity of this species is similar across the Indo-Pacific region and can be up to 56 years of age. This is the oldest recorded age for any *Etelis* species and the second oldest record for the
515 Etelinae, with the oldest being *Pristipomoides filamentosus* from the western central Pacific Ocean at ~64 years of age (Williams et al., 2015; Newman et al., 2016).

The annual spawning period of *Etelis* sp in the eastern Indian Ocean occurred over five months from the austral summer to mid-autumn (i.e., December to April), and exhibited a
520 conspicuous peak in January. The spawning period for this species in the western central Pacific Ocean did not exhibit a clear annual trend, but spawning was recorded in most months from September to June. The poorly defined estimates of annual spawning period in the Pacific Ocean may have resulted from either relatively small samples sizes per month and/or annual variations in the timing of spawning among the numerous
525 seamounts and island reef slopes sampled throughout this region. Additional evidence for the latter was exhibited by the higher proportions of immature (i.e., possessing gonads in a resting developmental stage) larger and older females and males sampled during

potential spawning months. The presence of these immature larger and older individuals in the samples also resulted in a poorly defined relationship between the proportion of
530 mature females and males with increasing length and age in this region, and thus estimates of maturity using a typical logistic function were not estimated. Nonetheless, an approximate length at 50% maturity for *Etelis* sp in the Pacific Ocean can be inferred using a life history invariant relationship with growth (i.e., $L_{50}^{\text{mat}}/L_{\infty}$) (Prince et al., 2014; Thorson et al., 2017). In the eastern Indian Ocean, the estimated length at 50% maturity
535 for females and males occurred at similar proportions of their corresponding asymptotic lengths (i.e., 63% and 70%, respectively). If these proportions are consistent for *Etelis* sp in the Pacific Ocean, then it is anticipated that the corresponding lengths at 50% maturity would be approximately 600 and 537 mm FL for females and males, respectively. If stock assessments for this species are to be performed in seamount and/or island slope
540 locations throughout the western central Pacific Ocean, and require reproductive life history inputs, then future studies should consider investigating these parameters specifically for each location.

The results of the catch curve assessment of *Etelis* sp. in north-western Australia suggest
545 that, over the periods represented by the age composition samples, the stock has experienced a relatively low level of exploitation, with the relative spawning potential of females estimated at around 60% of an unfished state. Currently, this stock is harvested from waters > 180 m deep by recreational-based fishers and both State (via line and trap fishing) and Commonwealth (via trawl fishing) managed commercial fisheries, creating
550 overlapping jurisdictional boundaries. Although commercial catches of *Etelis* sp. and *E.*

carbunculus cannot be separated to species, the former is far more abundant in these catches (accounting for ~97% of samples, see also Williams et al., 2017) and catches have remained relatively stable, ranging between 10 and 45 t per year across Commonwealth and State-managed fisheries since 2011. Thus, it is likely that the stock is
555 currently at a similar level to that in 2011 when the most recent sample was collected. Unless exploitation by either fishery increases substantially, the risk of unacceptable stock depletion is low.

Despite the strong equilibrium assumptions of catch curve and per-recruit analyses, these
560 methods are frequently used to assess the exploitation of stocks for which an index of abundance allowing application of more complex stock assessment models is not available (Punt et al., 1993; Thorson and Prager, 2011). For stocks that are not in steady states, a common situation for species where recruitment varies markedly between years and/or there have been recent changes to exploitation, catch curve estimates of fishing
565 mortality are often negatively biased (e.g. Dunn et al., 2002) and result in overly optimistic assessments of stock status. The assumptions of the method thus need to be assessed carefully, and implications of the findings considered when drawing inferences from the results of such analyses. In this assessment the similarity of fishing mortality estimates for fully-selected fish, derived from age composition data collected 14 years
570 apart by two very different fishing methods, indicates that exploitation of *Etelis* sp. has not changed markedly over this period. The lack of marked peaks and troughs in the age composition samples, which are often evident in species exhibiting substantial inter-

annual variability in recruitment, provides further support that these assumptions have been adequately satisfied in this assessment.

575

The importance of accounting for selectivity in stock assessments has been well recognised in the scientific literature (Thorson and Prager, 2011; Punt et al., 2014).

Simple catch curve analyses that assume knife-edge selectivity can be very sensitive to the assumed age at which fish are considered fully recruited to the fishery (Smith et al., 580 2012). Moreover, for species where fish are not vulnerable to fishing gear until an older age (and larger size), as was demonstrated for *Etelis* sp. in the line fishery, an assessment of fishing mortality alone may not provide an accurate measure of overall exploitation.

This is because the estimated fully-selected mortality may not be experienced by a large proportion of the stock that is not yet fully vulnerable to capture. Where some 585 information on growth and maturity is available, or can be inferred from other studies, it is important to extend such assessments to estimate the relative spawning potential of the stock for comparison against biomass-based reference points (Goodyear, 1993; Mace and Sissenwine, 1993). Ultimately, an acceptable level of exploitation estimated for a stock will depend on a range of factors, including the age at which fish are vulnerable to fishing

590 relative to that at which they mature. For *Etelis* sp., which attain maturity prior to becoming fully vulnerable to the line fishery, the stock can tolerate a higher level of fully-selected fishing mortality than it could if fished by the trawl fishery, which selects this species at a younger age. As exploitation increases, however, it becomes increasingly important to ensure that the effect of fishing on recruitment is adequately accounted for in 595 the assessment.

Applying a dynamic population model, such as an integrated, statistical catch-at-age model, or a surplus-production model, to assess the status of *Etelis* sp. would overcome several of the strong assumptions inherent in equilibrium-based catch curve and per-
600 recruit models. Integrated models are typically informed by an accurate time series of total catches combined with a reliable, long-term index of population abundance and representative age structure data, sampled over many years. Unfortunately, such data are not currently available for *Etelis* sp. in north-western Australia. This is, in part, due to *Etelis* sp. and *E. carbunculus* not being able to be reported separately by commercial
605 fishers, due to their very similar appearance. Although many of these limitations could be overcome with a well-structured, long-term fishery-independent monitoring program, maintaining such a program would be challenging due to the very remote locations of fisheries for this species, and limited resources for undertaking such research. Future collections of periodic age samples and data on the contributions of this species to annual
610 catches provides a basis for helping to improve future assessments of this species with limited sampling resources. With time, such data, together with the biological information collected for *Etelis* sp. in this study, could enable assessments to be undertaken using dynamic fish population models.

615 Recognising the difficulty of selecting appropriate reference points corresponding to B_{MSY} , current default proxies used in harvest strategies for Australian fisheries resources vary among jurisdictions (e.g. Smith et al., 2013; Fletcher et al., 2016). The results of several simulation studies (Mangel et al., 2013; Punt et al., 2014) provide support that

0.3 B_0 represents a reasonable proxy for a species with an assumed high steepness of the
620 stock-recruitment relationship of 0.7-0.8, particularly when used as a threshold below
which exploitation will be reduced. For *Etelis* sp. a threshold value of 0.3 B_0 also
corresponded well to the estimated relative stock biomass at which fishing mortality
generated the maximum long-term equilibrium yield. Considering the estimates of
relative stock size for *Etelis* sp. from north-western Australia were well above these
625 levels (~0.6 B_0), the stock in this region is highly likely to have experienced a sustainable
level of exploitation.

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825 **Table 1.** von Bertalanffy growth parameters (estimates and associated 95% lower and
 upper confidence limits) for curves fitted to the fork lengths (FL) at age of female and
 male *Etelis* sp. from the eastern Indian and western central Pacific Oceans. L_{∞} ,
 hypothetical asymptotic length at an infinite age; k , growth coefficient; t_0 , hypothetical
 age at zero length; A_{\max} , maximum age; L_{\max} , maximum length; n , sample size.
 830

	L_{∞} (mm)	k (yr ⁻¹)	t_0 (yr)	A_{\max} (yr)	L_{\max} (mm)	n
Eastern Indian Ocean						
Female						
Estimate	842	0.16	-0.40	42	1127	982
(Low, Upp)	(821, 878)	(0.13, 0.18)	(-1.29, 0.00)			
Male						
Estimate	648	0.23	-0.25	36	899	605
(Low, Upp)	(637, 661)	(0.20, 0.26)	(-0.90, 0.08)			
Western central Pacific Ocean						
Female						
Estimate	952	0.11	-1.84	42	1150	253
(Low, Upp)	(909, 1010)	(0.08, 0.14)	(-3.40, -0.31)			
Male						
Estimate	767	0.18	-0.09	56	1000	242
(Low, Upp)	(747, 799)	(0.14, 0.22)	(-1.31, 0.80)			

835 **Table 2.** Fork lengths (mm, FL) and ages (years) by which 50% and 95% (L_{50}^{mat} , L_{95}^{mat} ,
 A_{50}^{mat} and A_{95}^{mat} , respectively) of female and male *Etelis* sp. have attained sexual maturity
 in the eastern Indian Ocean, together with 95% lower and upper confidence limits for
 these parameters and the minimum fork length and age of mature fish (L_{\min} and A_{\min}) in
 that region.

	L_{50}^{mat}	L_{95}^{mat}	L_{\min}	n	A_{50}^{mat}	A_{95}^{mat}	A_{\min}	n
Female								
Estimate	527	635	517	344	5.4	9.3	4	334
(Low, Upp)	(510, 540)	(603, 666)			(4.9, 5.8)	(8.2, 10.6)		
Male								
Estimate	456	502	422	235	4.4	5.6	4	226
(Low, Upp)	(436, 472)	(470, 520)			(4.2, 4.7)	(5.3, 6.1)		

840

845 **Table 3.** Catch curve estimates of fishing mortality (F , based on estimates of natural
mortality, M , derived using the equation described by Quinn and Deriso, 1999) of fully-
selected fish and age-based selectivity parameters (A_{50}^{sel} and s) with associated 95% lower
and upper confidence limits for *Etelis* sp. sampled from north-western Australia in 1997
and 2011. n , sample size.

850

	F (year ⁻¹)	A_{50}^{sel} (years)	s (year ⁻¹)	n
1997 - Trawl				
Estimate	0.038	4.7	1.6	471
(Low, Upp)	(0.025, 0.054)	(4.2, 5.3)	(1.1, 2.3)	
2011 - Line				
Estimate	0.052	7.1	1.2	418
(Low, Upp)	(0.036, 0.071)	(6.5, 7.8)	(0.9, 1.6)	

Figure captions

855 **Figure 1.** Locations in the eastern Indian Ocean ($n = 26$ sites) and western central Pacific
Ocean ($n = 114$ sites) where *Etelis* sp. were collected (circles).

860 **Figure 2.** Length (above) and age (below) frequency compositions for female (white
bars, above x-axis) and male (grey bars, below x-axis) *Etelis* sp. from the eastern Indian
Ocean (left) and western central Pacific Ocean (right). Dashed lines represent
corresponding lengths and ages at 50% maturity (L_{50} and A_{50} , respectively) for females
and males from the eastern Indian Ocean. Sample sizes shown (n).

865 **Figure 3.** Length-at-age data for female (above) and male (below) *Etelis* sp. from the
eastern Indian (left) and western central Pacific (right) Oceans, with fitted von
Bertalanffy growth curves (lines) and $\pm 95\%$ confidence limits (dashed lines). Sample
sizes shown (n).

870 **Figure 4.** von Bertalanffy growth curves ($\pm 95\%$ confidence limits) for females (above)
and males (below) of *Etelis* sp. from the eastern Indian (IO) and western central Pacific
Oceans (PO).

875 **Figure 5.** Mean monthly gonadosomatic indices (± 1 SE, lines) of female (above) and
male (below) *Etelis* sp. and percentage of females with developed or ripe ovaries (grey
bars, stage III or IV) for fish $\geq L_{50}$ at maturity from the eastern Indian (left) and western
central Pacific (right) Oceans. On the x-axis the open rectangles represent austral winter
and summer months and closed rectangles spring and autumn months. Numbers above
curves are monthly sample sizes.

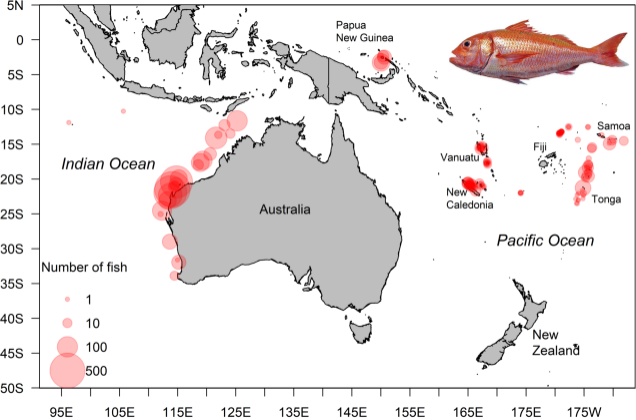
880 **Figure 6.** Percentage frequency of female (top) and male (bottom) *Etelis* sp. with
immature (stage I, white bars) and mature gonads (stages II – V, grey bars) in sequential
50 mm FL classes (sample sizes above) collected during the main spawning months from
the eastern Indian (i.e. January and February) and western central Pacific (i.e. January to
April) Oceans. Logistic curves and their 95% confidence limits (dashed lines) for the
Indian Ocean were derived from the probability that a fish of a given FL is mature.

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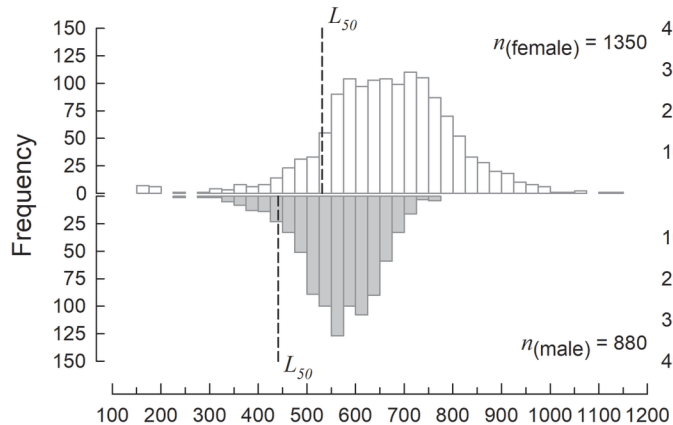
Figure 7. Percentage frequency of female (top) and male (bottom) *Etelis* sp. with
immature (stage I, white bars) and mature gonads (stages II – V, grey bars) in sequential
age cohorts (sample sizes above) collected during the main spawning months from the
eastern Indian (i.e. January and February) and western central Pacific (i.e. January to
April) Oceans. Logistic curves and their 95% confidence limits (dashed lines) for the
Indian Ocean were derived from the probability that a fish of a given age is mature.

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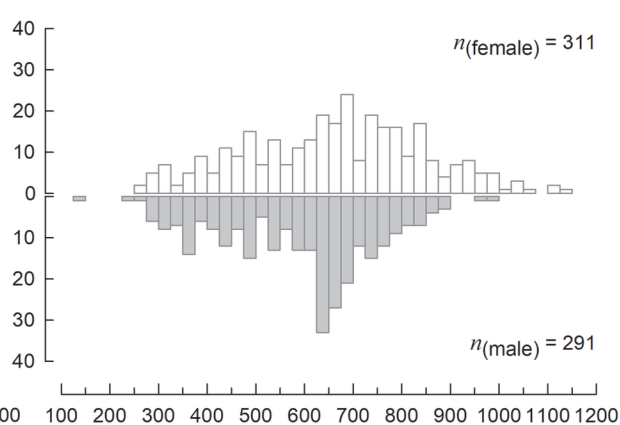
Figure 8. Catch curves assuming logistic selectivity ($\pm 95\%$ CLs) fitted to age
compositions for *Etelis* sp. collected from north-western Australia by (a) commercial
trawling in 1997 and (b) commercial line fishing in 2011 (sample sizes shown).
895 (c) Relationships between fishing mortality and relative spawning biomass of females
based on estimated trawl selectivity (1997, dark grey) and line selectivity (2011, light
grey), where the upper lines of these relationships represent the female spawning
potential ratio (SPR) and the lower lines represent the equilibrium relative spawning
900 biomass (RSB). (d) SPR and RSB estimates ($\pm 95\%$ CLs) of females for 1997 and 2011
relative to a proxy threshold reference level for B_{MSY} based on a proportion of unfished
spawning biomass (i.e. $0.3B_0$).



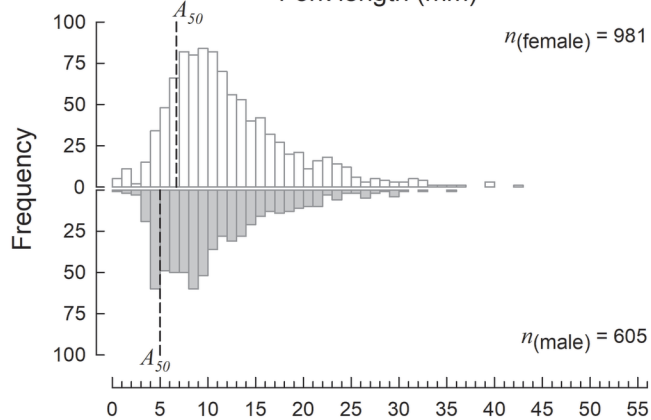
Indian Ocean



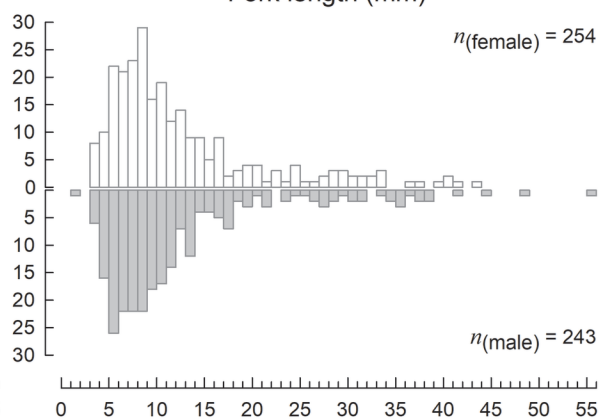
Pacific Ocean



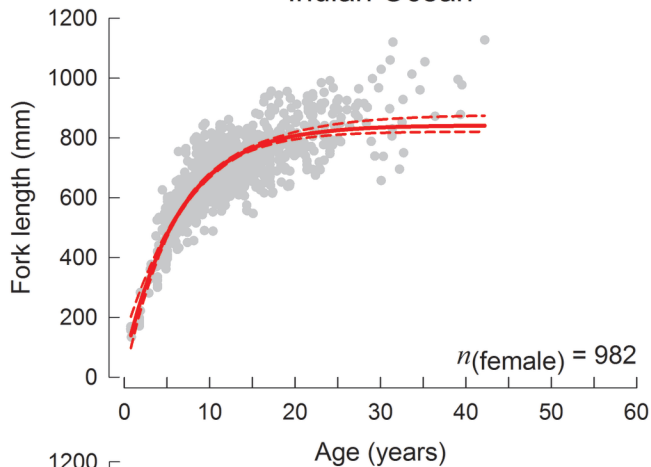
Fork length (mm)



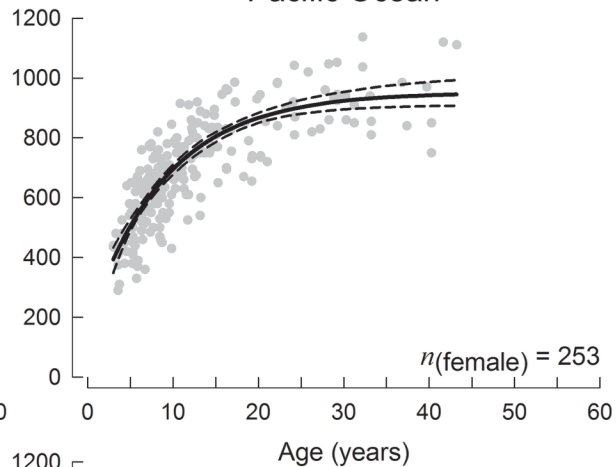
Fork length (mm)



Indian Ocean

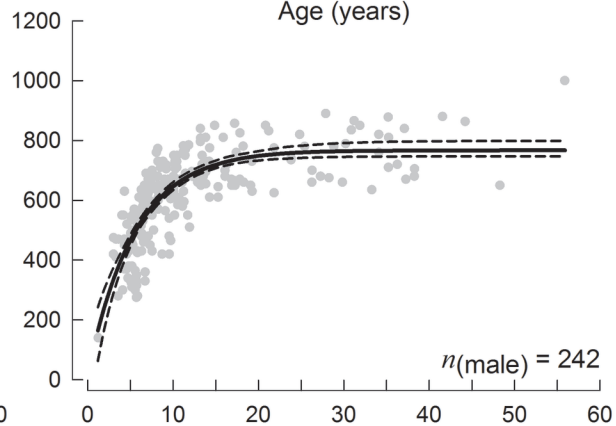
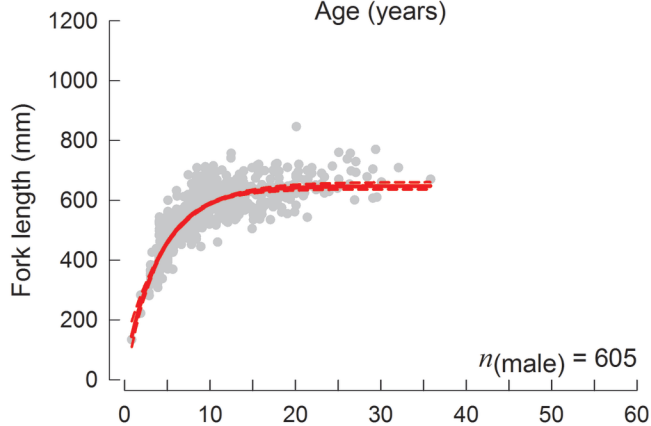


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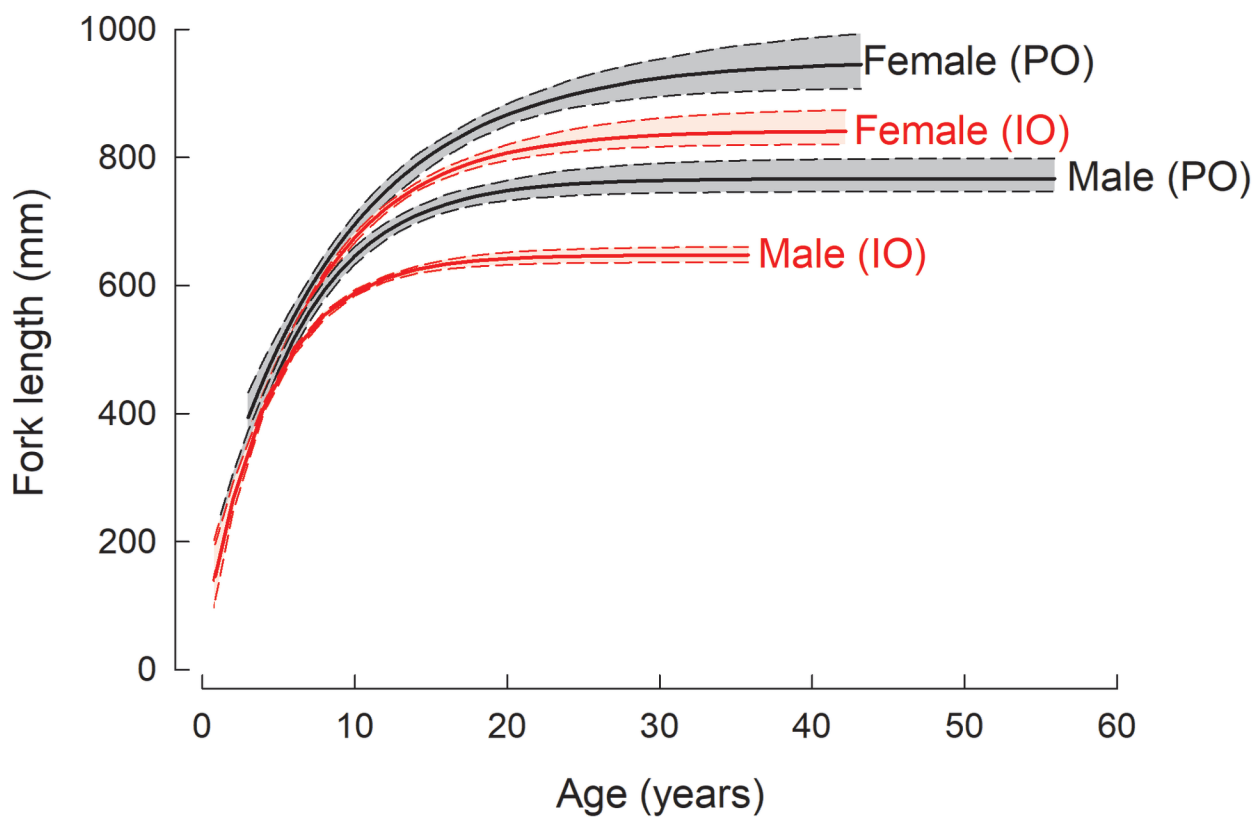
Age (years)

Age (years)

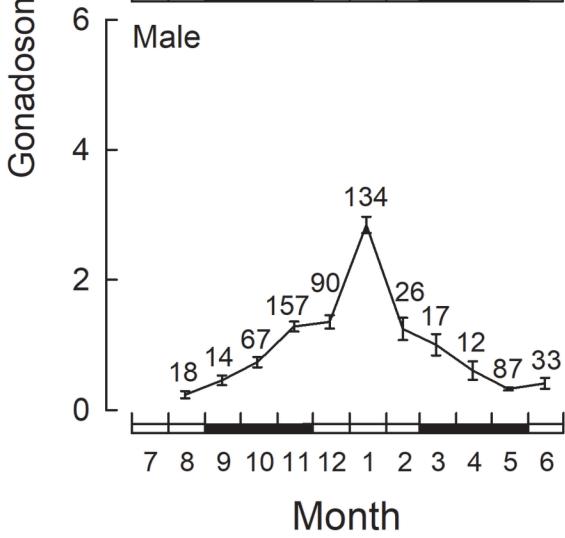
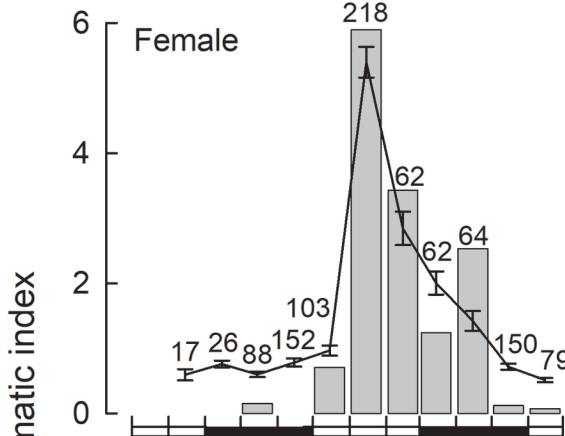


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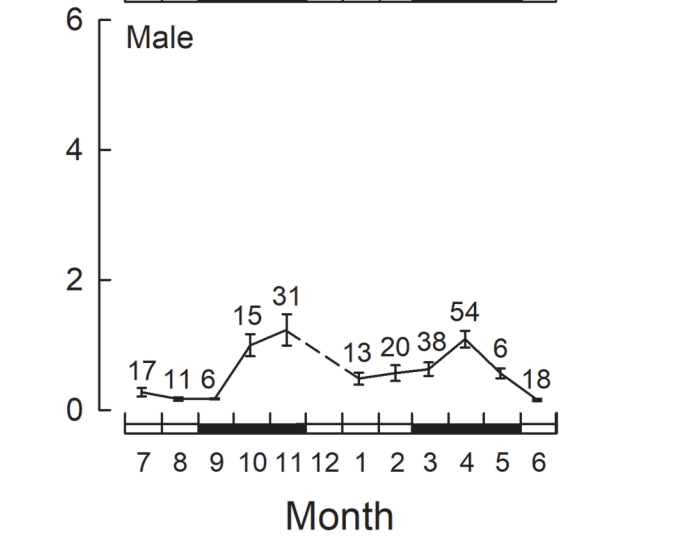
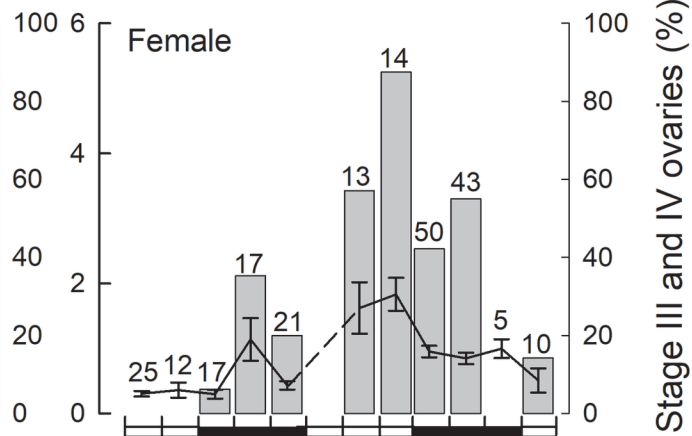
Age (years)



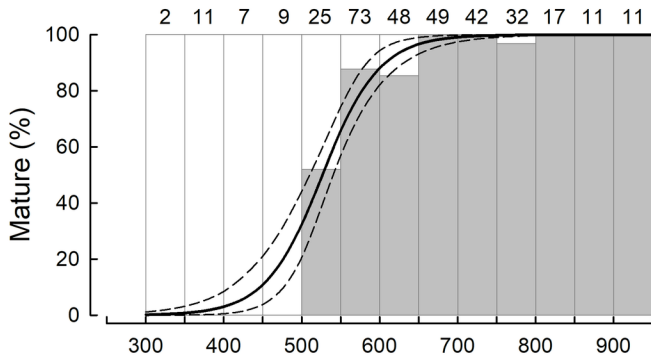
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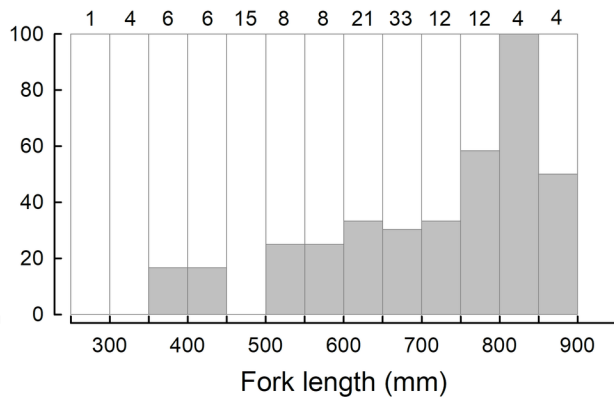
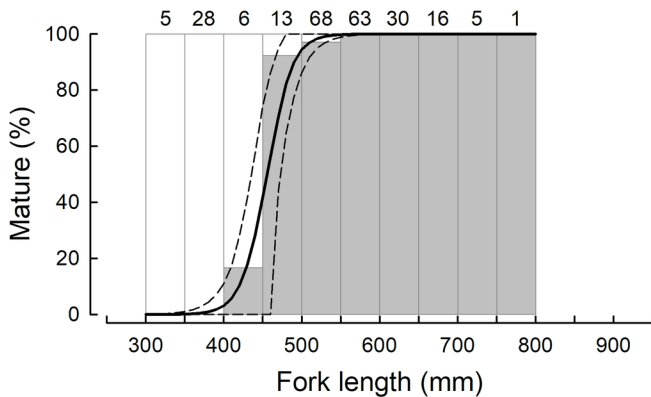
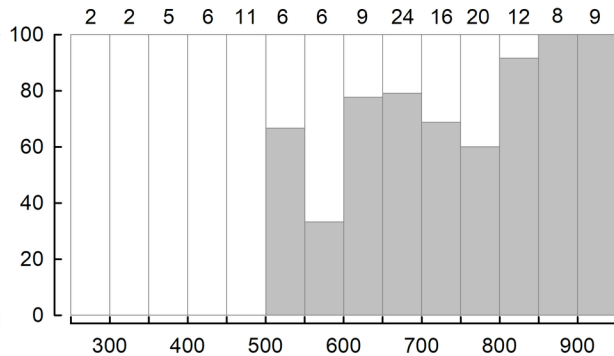
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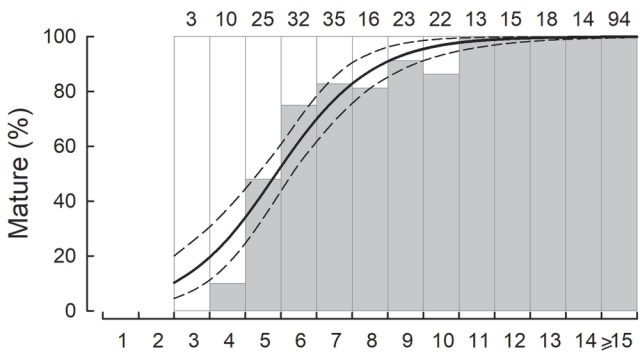
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