



# Growth and morphology of Critically Endangered green sawfish *Pristis zijsron* in globally important nursery habitats

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## Abstract

Understanding growth rates and other basic life-history information of imperilled species is essential to assessing the extent of threats to a population, but often difficult due to limited access to study subjects. Here we used mark-recapture data to estimate growth rates of juvenile Critically Endangered green sawfish (*Pristis zijsron*) in a globally important nursery in the eastern Indian Ocean (Western Australia). Our results suggest that growth of juvenile sawfish in this part of the central Western Australian coast is significantly slower compared to populations on the north-eastern coast of Australia. Additionally, growth rates differed between nearby areas within the nursery region, potentially due to differential productivity or anthropogenic effects. Morphological relationships between total length, rostral length, mouth gape, and clasper length are presented, which will allow for greater accuracy in estimating biological parameters in this species, while updated information on size at maturity (> 3200 mm) and size at birth (approximately 750–900 mm) will help to clarify life-history parameters for this data-poor species. Furthermore, there were distinct differences in the number of rostral teeth of green sawfish between this eastern Indian Ocean population and other populations throughout their current distribution, indicating substantial genetic differentiation in this species globally. These results will help to accurately assess growth trajectories and potential impacts of fisheries and other threats to green sawfish. Additionally, results highlight the importance of assessing population-specific growth rates in threatened species and of considering potential long-term life-history impacts of anthropogenic developments and activities.

**Keywords** Pristidae · Age at maturity · Life-history · Threatened species

## Introduction

Understanding basic biological and life-history information such as growth rates and generation length in aquatic species is crucial to accurately assessing population productivity and forecasting responses or resilience to environmental and anthropogenic pressures (Hobday et al. 2011; Goldman et al. 2012; Maunder and Punt 2013). This is particularly true for threatened species, where accurate assessments of potential population recovery rates or sustainable levels of fisheries interactions are essential to promoting proper

management and recovery of declining populations (Dulvy et al. 2004; Cortés 2016). However, collecting basic biological information for threatened species is often difficult due to limited access to species that are naturally rare or have already undergone large population declines. Additionally, when working with threatened species there is limited potential for lethal sampling methods for assessing growth and reproductive parameters, which are often used in aquatic research. For example, growth curves for fishes are typically formed using length-at-age data calculated by measuring growth rings in calcified structures including otoliths or vertebrae (e.g. Campana 2001; Maceina et al. 2007), which often require lethal sampling of individuals.

Assessing growth rates through sequential recaptures of individuals offers a non-lethal method of measuring size development (e.g. Hamel et al. 2014; Meyer et al. 2014; Dureuil and Worm 2015). However, this technique requires access to individuals over extended time periods, which can be difficult when working with rare or migratory species,

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and requires animals to exhibit some level of site fidelity or residency to particular areas. Additionally, particularly in species which use different habitats during ontogeny, this can result in biased sampling of individuals, where, for example, juveniles using coastal nursery habitats are caught more often than adults using offshore habitats, or vice versa. Fortunately, recent advances in statistical modelling have shown that Bayesian methods for estimating growth, which can incorporate prior knowledge including lengths at birth and maximum lengths of a species, can still produce reasonably accurate growth models using age or size-biased data (Scherrer et al. 2021; Smart and Grammer 2021; Dureuil et al. 2022). Such techniques provide the opportunity to assess growth trajectories of a species or population from relatively sparse or biased recapture data, which is common in the case of threatened aquatic species.

The green sawfish (*Pristis zijsron*) is one such threatened species; currently considered Critically Endangered by the International Union for the Conservation of Nature (IUCN) and estimated to have undergone a more than 80% decline in global population size over the last 50 years (Harry et al. 2022). The species formerly ranged from South Africa across the western Indian Ocean to south-east Asia and Australia. While remnant populations exist throughout the Indo-Pacific, Australia is currently thought to host some of the last viable populations. Within Australia, green sawfish were historically found from the central Pacific east coast (New South Wales), around the northern continent to as far south-west as Shark Bay in the eastern Indian Ocean (Western Australia). However, populations in north-eastern Australia have declined substantially, with this species presumably extinct through much of its former east coast range (Wueringer 2017; Harry et al. 2022). In contrast, this species is still regularly found throughout most of its Western Australian range, with pupping reported along the expansive and sparsely populated coastline of northwest Australia (Stevens et al. 2008; Morgan et al. 2011, 2015). In particular, the Ashburton River region in the southern Pilbara, Western Australia, has been documented as a productive and consistent nursery habitat where pupping reliably occurs on an annual basis (Morgan et al. 2015), and where individuals remain throughout their juvenile phase until they reach a length of approximately 3 m (Morgan et al. 2017). A preliminary growth curve for this species has previously been estimated using length-at-age data from 18 specimens retrieved from fisheries interactions in north-eastern Australia (Peverell 2009), but there is genetic differentiation between green sawfish on the north-east and west coasts of Australia (Phillips et al. 2011), and growth rates have not been examined for this species in the south-western part of their Australian range. Growth rates for numerous taxa can vary widely between populations dependent on a number of factors, such as temperature and resource availability (Weatherley 1990;

Hewett and Kraft 1993; Jobling 1997). As such, it is important to examine growth rates for what is potentially one of the last remaining, relatively robust populations of green sawfish globally, to ensure that accurate growth rates can be incorporated into population assessments.

Here, we use mark-recapture data collected over a four-year period to estimate growth rates of green sawfish in a globally significant population in north-western Australia. Bayesian methods were used to construct a von Bertalanffy growth curve from mark-recapture data, which was then compared with growth rates estimated for green sawfish in north-eastern Australia. Additionally, body condition, size at birth, maturity, and morphometric and meristic characteristics of this population are reported and compared with other populations globally.

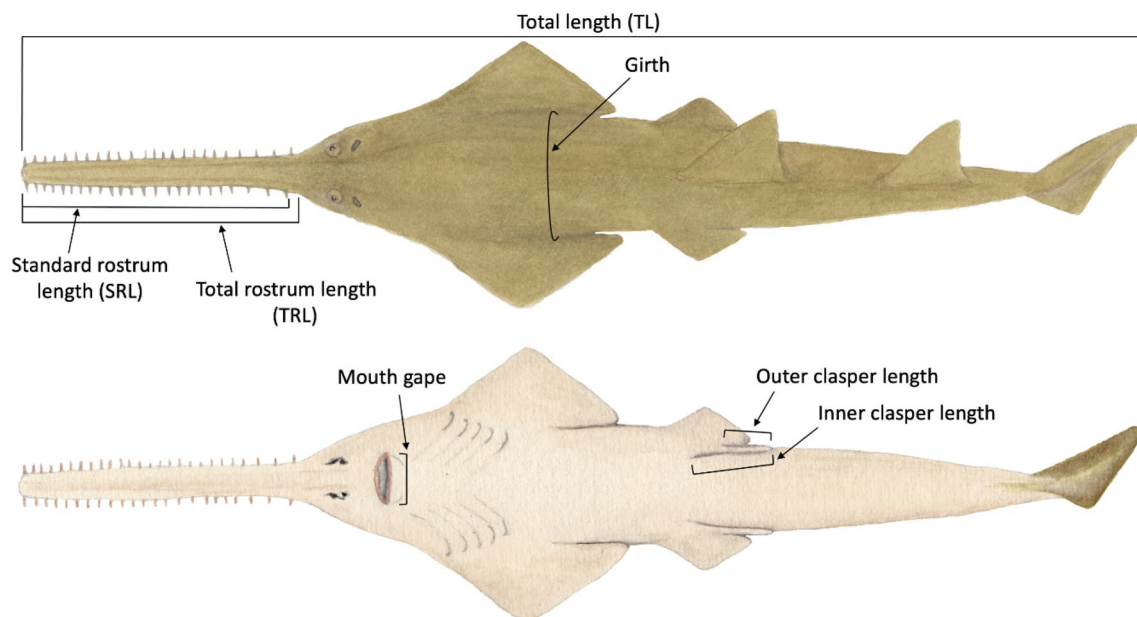
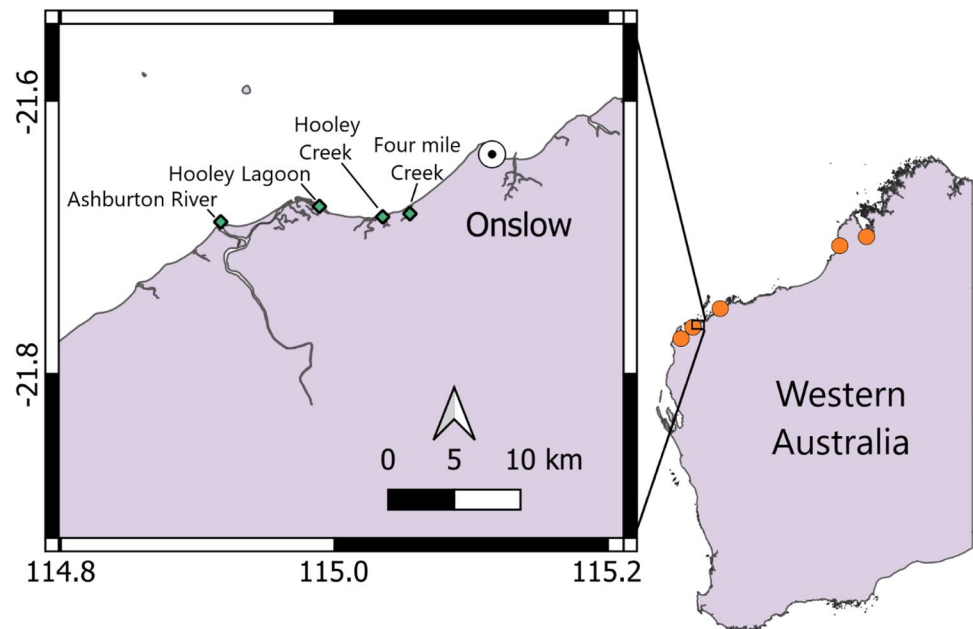
## Methods

### Sawfish capture and measurement

Green sawfish were captured in the Ashburton River and nearby lagoons and tidal mangrove creeks in the Pilbara region of Western Australia (Fig. 1). Surveys were conducted in mid-spring to early summer (Oct–Dec) and autumn (Apr–May) in 2011 and 2019–2022. Sawfish were captured using gillnets of 60 m length and 150 mm mesh size, set perpendicular to the bank. Nets were checked when activity was observed or at least once per hour. Upon capture, sawfish were removed from the net, sexed, and measured for total length (TL), total rostrum length (TRL), standard rostrum length (SRL), mouth gape (distance between corners of the mouth), inner and outer clasper length (in males; left clasper) and girth, which was measured immediately posterior to the pectoral fins and anterior to the first dorsal fin (Fig. 2). Additionally, the number of rostral teeth was counted, and sawfish were weighed to the nearest 100 g. Individuals were then externally tagged with either a small T-bar tag (4.5 cm length; model TBF, Hallprint Fish Tags, South Australia) or a larger dart tag (15 cm length; model PDAT, Hallprint Fish Tags, South Australia) depending on sawfish size. Alternatively, if the sawfish was a recapture, its tag number was noted. All sawfish were released at their site of capture.

For compilation of morphometric and meristic data, incidental captures of green sawfish in other areas of Western Australia (Exmouth Gulf, Fortescue River estuary, and Kimberley) during related work (2018–2022) were included (see Fig. 1).

**Fig. 1** Sampling locations for green sawfish *Pristis zijsron* in Western Australia. Green diamonds in inset map (left) show the four sampling locations within the main study area, while orange points on the larger map (right) show locations of incidental captures also included in morphological analyses



**Fig. 2** Locations of morphometric measurements taken from green sawfish *Pristis zijsron*. Illustrations: K. Lear

## Data analysis

Mark-recapture data were analysed in R (v. 4.0.3; R Foundation for Statistical Computing, Vienna, Austria). A von Bertalanffy growth curve was constructed out of the mark-recapture data using the R package ‘GrowthEstimation’ (Dureuil et al. 2022), which implements the Fabens method (Fabens 1965) of constructing a von Bertalanffy curve using Bayesian techniques. This requires the input of an estimated length at birth ( $L_0$ ) and maximum length

( $L_\infty$ ). We estimated  $L_0$  at 760 mm based on capture of a 760 mm individual in the Ashburton River that possessed a remnant rostral sheath and remnants of a yolk-sac, and the reported mean size at birth of 760 mm in the Gulf of Carpentaria (Peverell 2009). The mean  $L_\infty$  was estimated at 5500 mm, with the maximum  $L_\infty$  estimated at 6000 mm; while some literature suggests this species can attain lengths of over 7000 mm, verified records of individuals over 6000 mm are rare (Simpfendorfer 2013). Only recaptures with more than 90 days between captures were

used to assess growth rates. Differences in annual growth rates ( $\text{mm year}^{-1}$ ) between males and females were investigated using an Analyses of Variance (ANOVA); these were then further examined by running separate sets of Bayesian analyses to form von Bertalanffy curves for recaptured males and females, and examining overlaps in 95% confidence intervals (CIs) of estimated parameters. Additionally, we tested whether there were differences in growth rates and body condition between individuals inhabiting different areas within the main study region (the Ashburton River mouth vs Hooley Lagoon vs Four Mile Creek; no sawfish inhabiting Hooley Creek were recaptured more than 90 days apart). An individual was assigned to a specific location if both its initial capture and recapture were at that location, and if unpublished (and published; Morgan et al. 2017) acoustic tracking data indicated that the individual inhabited predominantly that location between captures. If an individual was recaptured at a different site to its initial capture, or if acoustic tracking data indicated that the individual moved amongst several sites, the individual was assigned to a 'mixed-location' group. Some young-of-year individuals were not acoustically tracked, but were assumed to remain within their initial capture location if recaptured at that same location, due to limited movement of individuals of this size (Morgan et al. 2017). As with inter-sex differences, differences in growth rates between locations were examined first through an ANOVA and subsequently through overlaps in 95% CIs of von Bertalanffy parameters calculated for recaptures from different sites.

To determine whether location, sex, or time of year influenced sawfish body condition, we built a set of linear models in R estimating girth using total length (both parameters natural log transformed), with capture location, season (autumn or spring/summer), and sex included as additional predictor variables. The Akaike's information criterion corrected for small sample size (AICc) was used to determine the model with the best fit combination of these predictor variables, with predictors that were included in the best-fit model deemed influential.

Additionally, morphometric data were tabulated and presented, including predictive relationships between total length and rostrum lengths (SRL and TRL), mass, girth, and mouth gape, as well as clasper length for males. To determine the best predictive equation for mass, again several potential linear models were built in R. This test set of models included those using either length, girth, or both length and girth as predictor variables, and every combination of untransformed or log-transformed predictors (length and girth) and response (mass). The best fit equation was determined using AICc. Similarly, to determine the best fit equation for describing the relationship between TL and various predictors (TRL, SRL, mouth gape, and clasper length),

a series of linear models were built with log transformed and untransformed predictors (TRL, SRL, mouth gape, or clasper length) and response (TL), and with sex included either as a fixed predictor, as an interactive factor with the fixed predictor, or not included. AICc was used to determine the best fit model for each of these predictive relationships. Linear model assumptions were checked using residual plots for all models.

## Results

A total of 143 unique green sawfish were captured within the Ashburton River region, with a further 9 individuals captured elsewhere in Western Australia included in morphometric analyses. The smallest individual caught was a female of 651 mm total length. However, this individual was substantially ( $> 100$  mm) smaller than any other individual caught, had notably lower rostral tooth counts (20 teeth per side), and appeared underweight and unhealthy, suggesting potential developmental defects or premature birth. This individual was therefore excluded from all morphometric analyses. The remaining individuals ranged from 751 to 3228 mm total length.

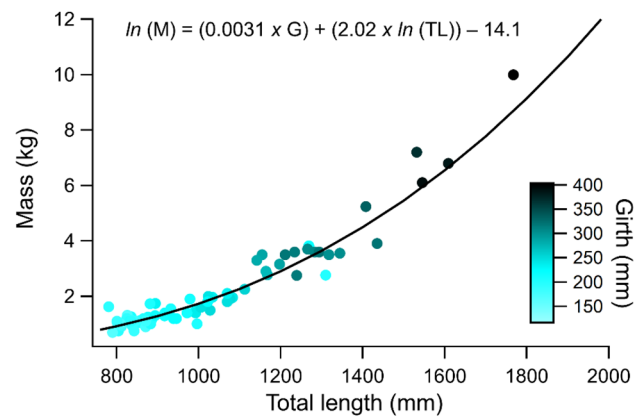
The sex ratio of captures was slightly biased towards females across juvenile age classes, including when considering all individuals caught (1.2:1 F:M juvenile ratio) and exclusively young-of-year (YOY) individuals (1.3:1 F:M YOY ratio). All males captured were immature based on uncalcified clasper morphology, with the largest of these measured at 3228 mm TL. The largest female caught was 3195 mm TL; it is likely that all females caught in the study were also immature based on the immaturity of similar sized males. Therefore, all results are based on analyses of strictly juvenile green sawfish.

Young-of-year pups with visible (open or partially healed) yolk-sac scars were caught in October, November, and December in the Ashburton River region. Excluding the 651 mm individual previously described with potential morphological defects, these young-of-year pups ranged in size from 751 to 972 mm. Of these, pups with fully or partially open yolk-sac scars ranged from 751–894 mm TL. Additionally, three newborn pups (with remnant rostral sheaths and partially open yolk-sac scars) were caught in the southwestern Exmouth Gulf in September 2021 (804–843 mm TL), and one pup with a visible yolk-sac scar was caught in the Fortescue River estuary in August 2022 (790 mm TL). Together, this information suggests an estimated pupping period of August–December in the southern Pilbara region of the eastern Indian Ocean, and an approximate size at birth of 750–900 mm TL.

### Recaptures and growth rates

A total of 19 individuals were recaptured during the study over periods of up to 734 days, with three individuals recaptured twice (22 recaptures total). The mean ( $\pm$ SD) duration of the time between captures was  $295 \pm 170$  days, and recaptured individuals ranged in size from 880 to 3228 mm.

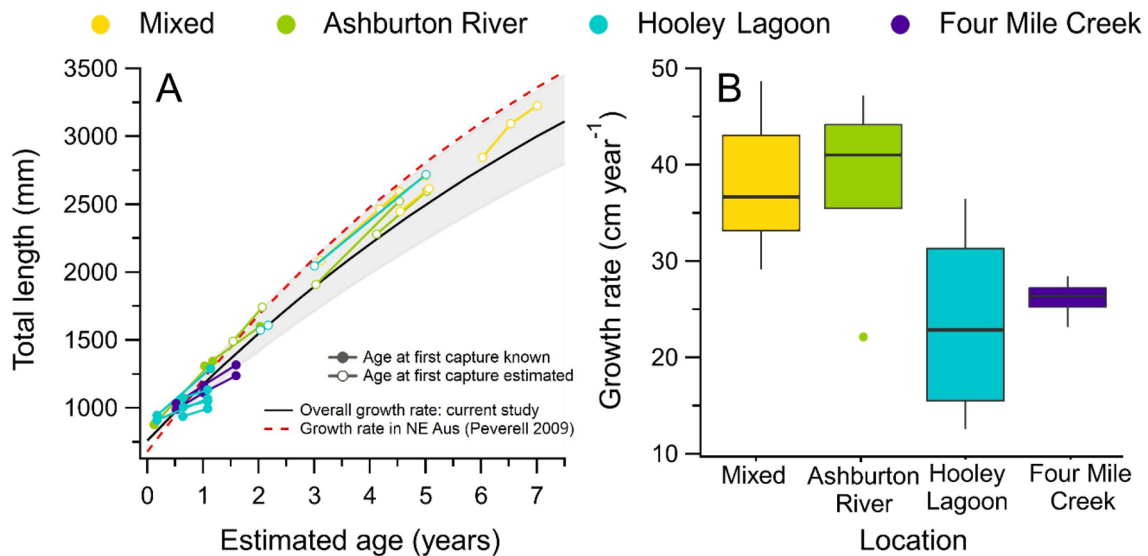
Bayesian analyses of all recaptures indicated von Bertalanffy growth parameters of  $k=0.090$  (95% CI: 0.074–0.11), and  $L_{\infty}=555$  (95% CI: 517–597) (Fig. 3). Growth rates did not differ between males and females (again noting that all individuals recaptured were immature; ANOVA  $p=0.4$ , 95% CIs fully overlap predicted values). However, growth rates were significantly different between locations within the main study area, with growth rates higher in the Ashburton River mouth and mixed location individuals compared to Hooley Lagoon or Four Mile Creek (ANOVA  $p < 0.05$ ; 95% CIs of predicted values in Bayesian analyses did not overlap means) (Fig. 3). There was no difference in sawfish body condition between sexes, capture locations, or seasons, with total length included as the only predictor of girth in the final body condition model (Supplemental Table S1).



**Fig. 4** Predictive equation for estimating mass (M; kg) using total length (TL) and girth (G) measurements (mm), based on morphometrics taken from 79 green sawfish *Pristis zijsron*

### Estimation of mass

Mass, length, and girth were measured for 79 individuals, which provided the data to assess estimation of mass from TL and girth measurements (Fig. 4). Sex was not maintained as a predictor in the best fit model, indicating that estimation of mass using length and girth measurements



**Fig. 3** Growth rates of juvenile green sawfish *Pristis zijsron* recaptured in the Ashburton River (green), Hooley Lagoon (blue), Four Mile Creek (purple), or in mixed locations (yellow). **A** Estimated von Bertalanffy growth rate (black line) for combined Ashburton River, Hooley Lagoon and Four Mile Creek captures, based on Bayesian analysis of recapture data; grey shaded region denotes 95% confidence intervals. Connected points show growth of recaptures, and are coloured according to capture location; solid points denote individuals first caught as young-of-year, where age could be estimated within

months (assuming an October 15<sup>th</sup> birth date), and open points show individuals where age was estimated based on probable growth patterns of cohorts (all assuming an October 15<sup>th</sup> birth date). The red dashed line shows the growth rate for green sawfish in north-eastern Australia estimated by Peverell (2009). **B** Median growth rates of juveniles inhabiting different locations within the study (black horizontal bar), with boxes showing the first and third quartiles of growth, whiskers showing growth limits within 1.5 inter-quartile ranges of the median, and any outlying values shown with points

did not differ between juvenile males and females (see Supplemental Table S1 for model selection results). The best fit equation (based on AICc) for estimation of mass (kg) using TL and girth (mm) was:

$$\ln(\text{mass}) = (0.0031 \times \text{girth}) + (2.02 \times \ln(\text{TL})) - 14.1 \quad (1)$$

In most cases, this equation predicted mass with relative accuracy, resulting in a mean standard error of the estimate of 11.7%. As many studies do not measure girth, we also report here the best fit equation for predicting mass solely with length measurements:

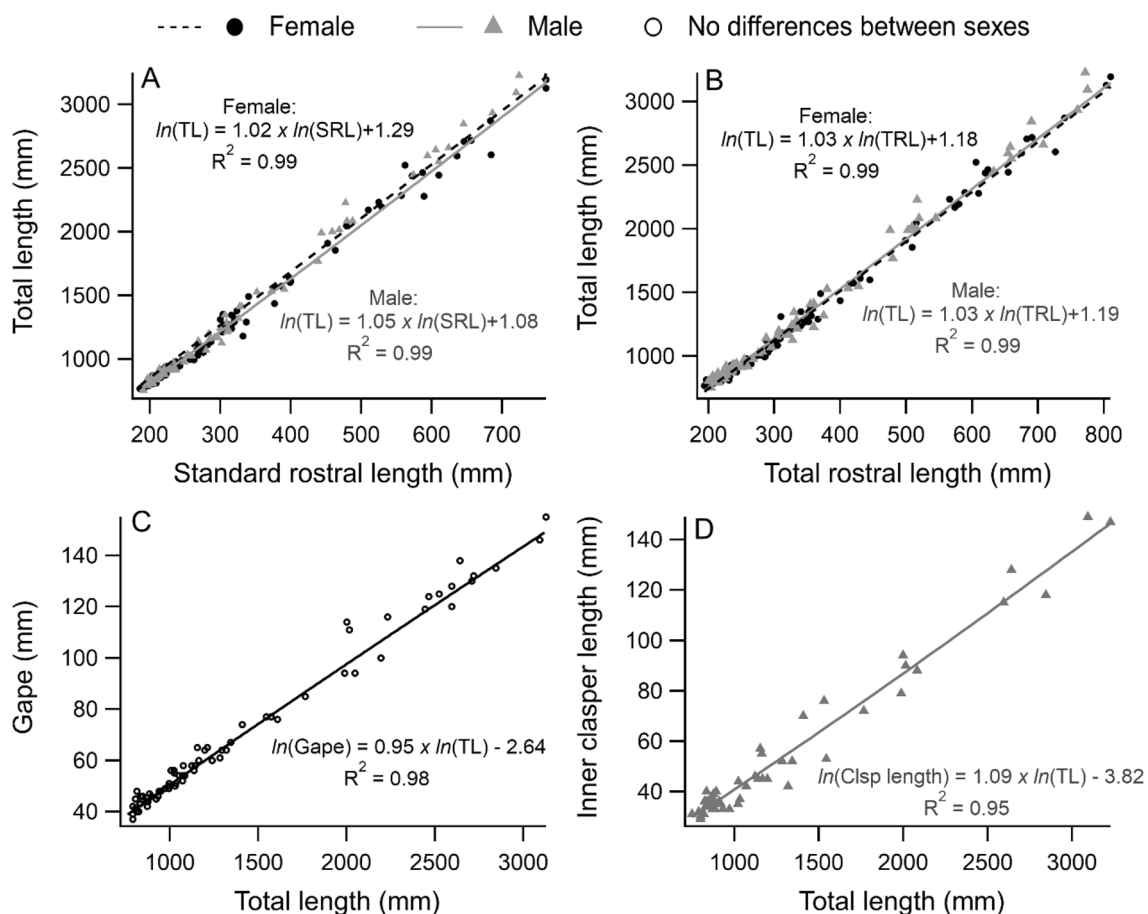
$$\ln(\text{Mass}) = 2.83 \times \ln(\text{TL}) - 19.0 \quad (2)$$

It is notable, however, that this method for estimating mass resulted in a slightly higher mean standard error of the estimate of 13.0%. Therefore, incorporating girth

measurements into estimation of mass likely yields more accurate results.

### Morphometric and meristic measurements

Measurements of TRL, SRL, and TL were collected from 170 sawfish (including recaptures). The ratio of TRL and SRL to TL were both size (regression  $p < 0.01$ ) and sex dependent (regression  $p < 0.05$ ), with the rostrum making up slightly but significantly less of the TL in males compared to females, and as fish grew larger (Fig. 5). An interaction between sex and size was also significant for SRL ( $p = 0.012$ ), indicating that the rate at which the ratio between SRL and TL changed with size was different between males and females. The best fit equations for predicting TL using TRL or SRL for both sexes are noted in Fig. 5 (see Supplemental Table S1 for model selection results).



**Fig. 5** Relationships between green sawfish *Pristis zijsron* total length (TL) and **A** standard rostral length (SRL); **B** total rostral length (TRL); **C** mouth gape; or **D** inner clasper length. Both sex and size had a slight but significant effect on the ratio of TRL and SRL to TL,

but the relationship between mouth gape and total length did not differ between sexes. Best fit equations and  $R^2$  values are noted on each plot

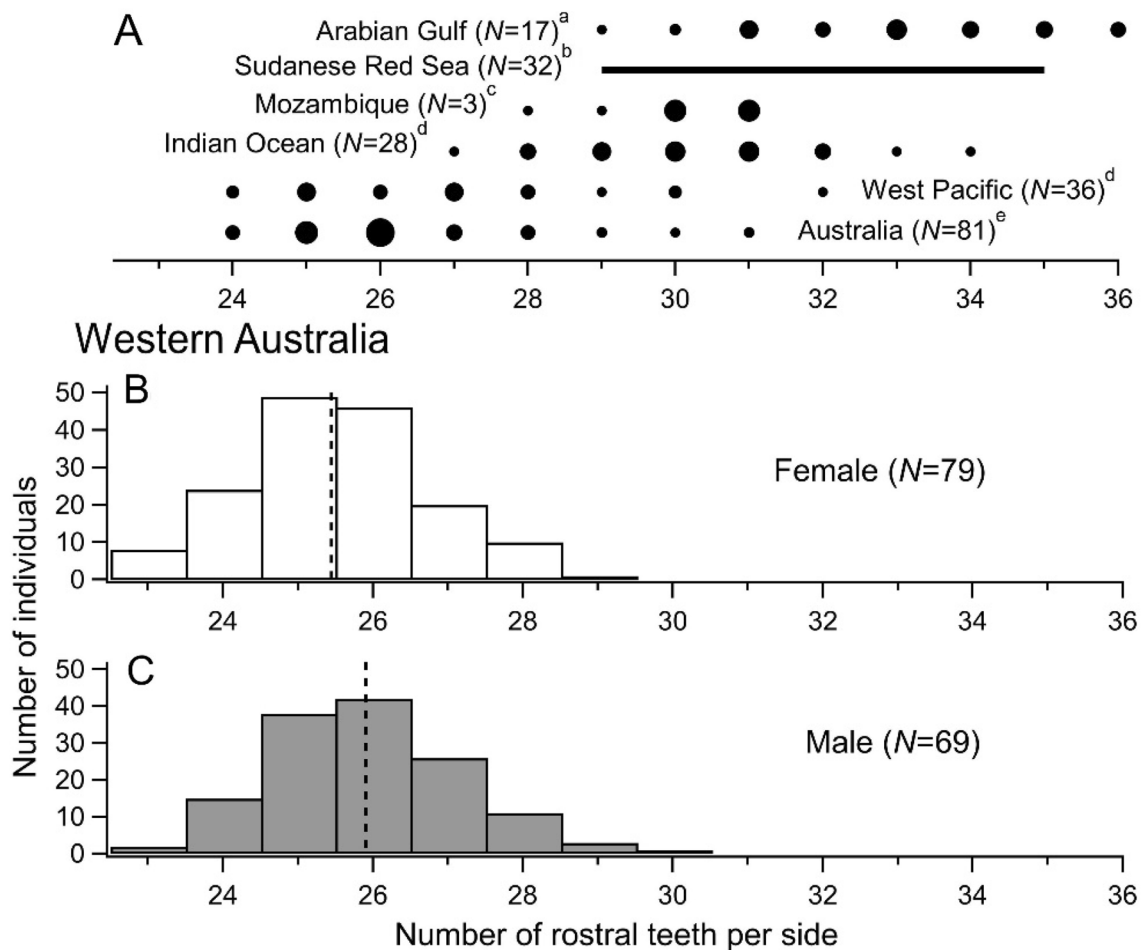
The predictive relationships for mouth gape and clasper length (inner) using TL were both improved by applying natural log transformed predictor and response variables (Supplemental Table S1). Sex did not affect the relationship between mouth gape and total length. Both mouth gape and clasper length had a high correlation with total length ( $R^2 > 0.95$ ; Fig. 5), with the best fit predictive equations shown in Fig. 5. Note that all clasper lengths included in this analysis were from immature individuals.

A total of 148 unique individuals were included in tooth count analyses. Sawfish possessed between 23 and 30 rostral teeth per side, with the exception of the previously noted female individual excluded due to potential developmental defects (which had 20 teeth on both sides of the rostrum). Otherwise, female tooth counts ranged

from 23–29 teeth per side, while males ranged from 23–30 teeth per side, noting that only a single male had 30 teeth on one side of the rostrum. Females had, on average, significantly fewer teeth than males (Wilcoxon rank sum  $p = 0.012$ ) (Fig. 6).

### Discussion

Western Australia currently supports the majority of the known robust populations of green sawfish remaining within their previous Indo-Pacific range (Harry et al. 2022), with the Ashburton River in the eastern Indian Ocean identified as an extremely important pupping and nursery area for this species (Morgan et al. 2015, 2017). While parts of



**Fig. 6** Number of rostral teeth per side in green sawfish *Pristis zijsron*. Tooth counts for green sawfish populations globally **A** were in some cases substantially higher than tooth counts measured for either females **B** or males **C** in Western Australian individuals. Vertical dashed lines (plots B & C) show the respective mean tooth count values for each sex. Size of points in (A) relates to the percentage of sawfish showing that number of teeth within the dataset; only a

range rather than distribution of rostral tooth counts is available for the Sudanese Red Sea (Elhassan 2018). Sources in (A) are as follows: <sup>a</sup>Jabado et al. (2017); <sup>b</sup>Elhassan (2018); <sup>c</sup>Leeney (2017); <sup>d</sup>Faria et al. (2013); <sup>e</sup>Whitty et al. (2014). Note that ‘Australia’ in (A) from Whitty et al. (2014) refers to all of northern Australia, including Western Australia, the Northern Territory, and Queensland, but does not necessarily include individuals from the current study area

the Pilbara region serve as important hubs for the Australian resource sector, this area also supports large sections of relatively pristine and undeveloped coastline. However, there is rapidly mounting pressure to further develop the region for salt, oil and gas, and iron ore mining, as well as several trawl and gillnet fisheries operating nearby. The growth rates and life-history information presented here will help to accurately assess the extent and mitigation of threats as well as the potential for population recovery and promotion of effective conservation measures. For example, the determination of a pupping period of approximately August – December for this species in the Pilbara region can inform scheduling for potential developments including times of year to limit construction or dredging around pupping habitats to avoid interference with female migrations and parturition behaviour.

### Size at birth and maturity

The size at birth of green sawfish observed here (approximately 750–900 mm TL) roughly agrees with most other accounts recorded for this species throughout its range, although there are a few reports of smaller neonates as well. For example, similarly to the current study, Peverell (2009) reports a size at birth of 760 mm in the Gulf of Carpentaria (south of the Arafura Sea, north-eastern Australia), and Elhassan (2018) reports full-term embryos from the Sudanese Red Sea measuring 600–800 mm TL and neonates measuring 810–890 mm TL. However, Faria (2007) reports specimens from Indonesia as small as 680 mm TL, although these were collected in the late 1800s, and therefore whether the individual was an embryo or neonate and the degree of shrinkage is unknown. Morgan et al. (2011) also reports the collection of a green sawfish rostrum from Western Australia (eastern Indian Ocean) measuring 160 mm, which would equate to a TL of approximately 606 mm based on the TRL-TL conversion established here; however, whether this rostrum was from a neonate or a premature birth cannot be determined. Additionally, a recent study within Australia's Northern Territory observed individuals estimated as small as 570 mm TL (Davies et al. 2022), but these measurements were approximated from drone footage rather than directly measured. Overall, these observations indicate that size at birth is similar for green sawfish across their extant distribution, and likely averages approximately 750–900 mm, with occasional smaller individuals recorded.

In compiling the data presented here with previous published records, we can also narrow the probable size at maturity for this species. Our capture of an immature male of 3228 mm (with short and fully uncalcified claspers) sets a lower limit to the size at maturity for males. Previous minimum size records of mature individuals include mature females at 3500 and 3800 mm TL in the Sudanese Red

Sea (Elhassan 2018) and north-eastern Australia (Peverell 2005), respectively, and a mature male at 3800 mm in the Sudanese Red Sea (Elhassan 2018). Together, this indicates a size at maturity for males between 3300 and 3800 mm TL, and likely a similar size range for females. While these ranges agree with the published lengths of mature individuals in primary literature, several reference volumes and articles list other sizes at maturity as rough estimates due to a lack of empirical data, including maturity for both sexes at 3000 mm (e.g. Last and Stevens 2009; Morgan et al. 2011) or 4300 mm (Last et al. 2016). Based on the sizes of immature and mature individuals in this study and recently published literature, these rougher estimates appear to be inaccurate.

### Growth rates

To our knowledge, the only previous estimate of growth rates in green sawfish was constructed using vertebral aging data from 18 individuals of 870–4490 mm caught in the Gulf of Carpentaria in north-eastern Australia (Peverell 2009). The estimated growth rate calculated here was significantly slower than this previous estimate (95% CIs of growth parameter  $k$  did not overlap  $k$  reported by Peverell (2009)), to the extent that time to maturity (assuming a size of 3500 mm at maturity) increases from 7–8 years as estimated by Peverell (2009) to 9–10 years estimated in the current study. Both the previous and current estimation of growth rates are based on somewhat small sample sizes, and can be interpreted as preliminary growth curves for this species. Therefore, the error in both these studies, inherent of small sample sizes, could partially account for the observed differences in growth rates, as well as the error incurred by using two different methods to form growth curves. However, there are also several biological explanations for the differences in growth between these two populations. For example, there is genetic differentiation between green sawfish populations in north-eastern Australia compared to the eastern Indian Ocean in Western Australia (Phillips et al. 2011), and therefore the different growth rates could stem from a genetic basis.

There are also several environmental parameters that could affect growth. Life history parameters including growth rates have been known to vary between fish populations dependent on many factors including resource availability and temperature (e.g. Lahti et al. 2001; Carlson et al. 2006; Gillanders et al. 2015; Uthe et al. 2016; Marchand et al. 2018; Chittaro et al. 2022). Since elevated temperatures increase vital rates in ectotherms (Gillooly et al. 2001; 2002), growth rates generally increase with temperature (up to a point) as long as there is sufficient food availability to sustain heightened metabolic requirements. Water temperatures in the Gulf of Carpentaria are on average approximately



2 °C warmer than the coastal Pilbara region, depending on time of year (seatemperatures.net). Therefore, these warmer temperatures could account for the faster growth estimated for green sawfish in north-eastern Australia compared to the Pilbara region. Additionally, while it is difficult to directly compare productivity or prey availability between the two systems given a lack of data, it is likely that there is higher productivity in the Gulf of Carpentaria compared to the Pilbara region. The Gulf of Carpentaria is located in the wet and dryland tropics of Australia and has several major rivers that consistently discharge into nearshore environments, bringing terrestrial nutrient input into these areas (and resulting in higher productivity; Gillanders and Kingsford 2002; Broadley et al. 2022). In comparison, the southern Pilbara region in the present study comprises an arid desert with limited terrestrial run-off; the few rivers in this region flow infrequently for only a few days at a time following sporadic rainfall events. Furthermore, coastal waters in Western Australia have been found to be generally less productive than those elsewhere in Australia due to limited terrestrial run-off as well as interactions of major currents and limited upwelling in Western Australia (Molony et al. 2011). Therefore, differential productivity and resource availability may also account for the differences observed in the growth of green sawfish between north-eastern and Western Australia.

Differential productivity between sites is also a likely explanation for the heightened growth observed in the Ashburton River compared to the two smaller tidal mangrove creeks in the present study. These sites are geographically close (within ~ 12 km of each other), with larger individuals known to transit between them, as observed from recapture data here as well as acoustic tracking data (Morgan et al. 2017). Therefore, a genetic basis for differences in growth rates between sites does not seem likely. Additionally, water temperatures between the sites are similar year-round and therefore not likely to drive major differences in growth rates. However, these sites are characterised by distinct environmental circumstances: the Ashburton River mouth has sporadic freshwater flows and dense mangroves; Hooley Lagoon is a shallow mudflat lagoon which is connected to small mangrove creeks; and Four Mile Creek is a mangrove creek system. The Ashburton River mouth is the only major input of terrestrial nutrients for several hundred kilometres of coastline, and therefore probably offers heightened productivity compared to the Hooley Lagoon and Four Mile Creek. This is likely to be the most influential driver of differences in growth rates between sites, and further research into how productivity rates and prey availability vary seasonally and between these systems would help to confirm this. Additionally, Hooley Lagoon and Four Mile Creek are both near to developments (a gas processing plant and boat ramp, respectively), and any heightened noise, light, or human activity associated with these areas

could have the potential to decrease growth rates if these factors increase refuging behaviour or affect foraging success (Becker et al. 2013; Davies et al. 2014; Voellmy et al. 2014). Comparatively, there is little human activity around the mouth of the Ashburton River due to lack of access (no paved roads or maintained boat launches; Authors, personal observation). In the case of Hooley Lagoon, a large offloading facility is situated adjacent to this site, with a rock wall extending ~ 250 m offshore that appears to limit movement of sawfish to the northeast (Lear and Morgan, unpublished data), and therefore could be artificially aggregating sawfish within the Hooley Lagoon area, with potential consequences for resource availability. However, it is difficult to determine whether any of these anthropogenic effects may be impacting growth, as no investigation of growth rates was conducted in this population before these boat ramps and developments were constructed. Whether anthropogenic noise, light, or artificial structures influence sawfish behaviour, feeding ecology, or growth is an important area for future research. Regardless of whether differences in resource availability, anthropogenic activities, or a combination thereof drive the differences in growth between nursery sites, the lack of significant difference in sawfish body condition between sites suggests that sawfish at all locations are obtaining sufficient energy to sustain condition and positive growth.

The similarities in growth rates between sexes found here is not unexpected, given that all animals examined were juveniles. Previous studies have found similar growth rates between sexes in a variety of fishes during early life stages, even when adult sizes differ (Simpfendorfer 2000; Curtis and Vincent 2006); sex-specific growth rates are more often found in larger animals reaching maturity (e.g. Simpfendorfer 1993; Simpfendorfer et al. 2000; Williams et al. 2012). However, it is notable that our sample sizes for growth in individual sexes were small ( $N=8$  or 14 recaptures) and could have obscured subtle differences in growth rates. Further investigation of sex specific growth rates and size at maturity in this species would help to clarify this point.

### Morphometric relationships

The morphological relationships determined here will be useful in estimating morphometric parameters in future studies when specific measurements are missing. For example, the relationships between TRL/SRL and TL are especially important, as many “sightings” of sawfish globally are from collected rostra rather than live animals (e.g. Morgan et al. 2011; Whitty et al. 2014; Wueringer et al. 2023), and these relationships help to estimate the size of these animals from collected rostra alone. Similarly, as the mass of sawfish is not often measured due to impracticality in the field, the ability to estimate mass from measurements of girth and TL can lend important biological information about these

animals, particularly regarding trophic interactions and energetics. Estimation of mouth gape from total length also provides biologically pertinent information as it enables an assessment of what prey size sawfish of different size classes are likely to target.

Although previous data describing morphological relationships in green sawfish are limited, the relationships determined here are relatively similar to the few previously reported. For example, in the current study (eastern Indian Ocean), TRL made up 23.1–29.4% of TL, and TRL similarly made up 24.0–30.6% of TL in nine individuals sampled from elsewhere in the Indian Ocean (Faria 2007), though Faria et al. (2013) measured TRL as 22.9–33.6% of TL including individuals from both the Indian and Pacific Oceans. This indicates that there could be slight distinctions in morphological ratios between ocean basins or populations, though most individuals appear to be within the same general range.

There were, however, large differences in rostral tooth counts for sawfish captured in the Ashburton River region compared to those in other parts of the world. The lowest tooth counts, globally, were found in the present study, with the tooth count range determined here, for example, barely overlapping tooth count ranges from the Middle East (Fig. 6). There were also distinct differences in tooth counts between green sawfish within Australia, where up to 31 teeth per side have been found previously for assemblages in north-eastern Australia (Queensland; Whitty et al. 2014), or up to 32 teeth for sawfish in the ‘West Pacific’ (exact location unspecified but likely north-eastern Australia and Indonesia; Faria et al. 2013), while only a (rarely displayed) maximum of 30 teeth were found here for Western Australia. Geographical delineations in rostral tooth counts have also been identified in other sawfish species, including the narrow sawfish *Anoxypristis cuspidata* (22–29 teeth per side in Indian Ocean vs 17–30 in the West Pacific; Faria et al. 2013) and smalltooth sawfish *Pristis pectinata* (22–29 teeth per side in the United States and 20–30 teeth per side in West Atlantic vs 20–27 teeth per side in East Atlantic; Wiley et al. 2008; Faria et al. 2013); however, for both these species, there is major overlap in tooth count ranges between locations.

Differences in morphological characteristics between populations are often (though not always) indicative of genetic separation (Barlow 1961), as has been supported in the case of green sawfish by genetic studies finding population structure between the West Pacific and Indian Ocean (Faria et al. 2013) as well as between western and eastern Australia (Phillips et al. 2011). Distinct and non-overlapping ranges in morphological characteristics such as those observed in green sawfish tooth counts could suggest potential past population bottlenecks or founder effects, where resulting populations are formed from genetic material

originating from a small pool of individuals (e.g. Spurgin et al. 2014). Considering the rapid and major population declines of sawfishes globally, the former may be more likely. Such a process is also supported by the low genetic diversity for this species found at least within parts of Australia (Phillips et al. 2011), and likely within other remnant populations throughout its range.

The sexual dimorphism in tooth counts for green sawfish found here, albeit minor, is mirrored in several other sawfishes. Similar to the present study, males of both large-tooth sawfish *Pristis pristis* (Thorson 1976; Ishihara et al. 1991; Thorburn et al. 2007; Whitty et al. 2014) and small-tooth sawfish (Simpfendorfer et al. 2008; Wiley et al. 2008) exhibit higher numbers of rostral teeth than females. Conversely, male narrow sawfish potentially average less rostral teeth than females (Compagno and Last 1999), though other studies have found no difference between sexes for this species (Whitty et al. 2014). No sexual dimorphism has been noted for dwarf sawfish *Pristis clavata* (Thorburn et al. 2008; Whitty et al. 2014). There is no clear evolutionary advantage to having higher rostral tooth counts in males or females (Simpfendorfer et al. 2008). Thus, the consistent sexual dimorphism in rostral tooth counts found in several sawfish species is not necessarily adaptive, and instead could potentially arise from genetic linkages to other sexually selected traits in this group.

## Conclusions and considerations for conservation

The life history information presented here for what is one of the least studied pristids will help to clarify several points about the basic biology and ecology of the highly imperilled green sawfish. Greater accuracy in the estimation of birth and maturation sizes of this species will help to inform our knowledge of population dynamics and occurrence of juveniles vs mature individuals across their current distribution. Furthermore, in combination with the updated growth rates provided here for juvenile green sawfish, this information will help to better inform our estimates of generation length for this species in Western Australia, one of the last global strongholds for this species. Such life-history information is highly relevant for fisheries management and assessing the vulnerability and recovery potential of this species.

The finding of varying growth rates based on fine-scale location differences within this study also raises several important considerations regarding conservation and threat assessments for this species. First, the higher growth rates of sawfish in the Ashburton River mouth (likely due, at least in part, to terrestrial nutrient input and resulting high productivity in this system) emphasizes the importance of preserving river mouths as highly productive habitats for estuarine and marine fishes. Further research determining relative productivity and prey

availability in the Ashburton River mouth compared to nearby mangrove creeks would be highly beneficial for assessing habitat value for a range of species. Second, the potential for human activities and developments to affect growth and behaviour of green sawfish, whether through noise or light pollution, the formation of barriers to dispersal, or direct disruption of behaviour within the habitat (e.g., boating activity or fishing), emphasizes the importance of considering long-term, sublethal effects of such developments and activities. This is particularly relevant as the potential consequences of human developments or disturbance are most often assessed based on the occurrence of lethal injury to a species or destruction of core habitats; more subtle long-term effects, such as slowing of growth rates, are not often considered as it is challenging to assess such parameters on the fast-track scale of many developments. In the present case, however, it is difficult to determine with certainty whether anthropogenic activities are affecting growth rates of green sawfish in the Pilbara region, as there is no direct comparison of growth in this population before and after the noted developments. More work is needed to determine how light, noise, development structures, and other human interactions affect this species on a long-term basis, in order to ensure that this globally important green sawfish nursery remains robust and functional.

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**Data availability** The datasets generated during the current study are not publicly available due to funder guidelines but are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors have no financial or non-financial competing interests to disclose.

**Ethical approval** All work with animals was conducted under Murdoch University Animal Ethics permit #RW3191-19, and Western Australia Department of Fisheries permits #3378 and #250922121.

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