Received: 20 November 2022 | Accepted: 1 May 2023
DOI: 10.1111/jfb.15425

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

Nonlethally assessing elasmobranch ontogenetic shifts in energetics

Carolyn R. Wheeler[1,2] | **Duncan J. Irschick**[3] | **John W. Mandelman**[2,4] | **Jodie L. Rummer**[1,5]

[1]ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, Queensland, Australia

[2]School for the Environment, The University of Massachusetts Boston, Boston, Massachusetts, USA

[3]Department of Biology, The University of Massachusetts Amherst, Amherst, Massachusetts, USA

[4]Anderson Cabot Center for Ocean Life, New England Aquarium, Boston, Massachusetts, USA

[5]College of Science and Engineering, James Cook University, Townsville, Queensland, Australia

Correspondence
Carolyn R. Wheeler, ARC Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD, Australia.
Email: carolyn.wheeler23@gmail.com

Funding information
American Australian Association; Australian Society for Fish Biology; Centre of Excellence for Coral Reef Studies, Australian Research Council; Save Our Seas Foundation; The Australian Wildlife Society

Abstract

Body condition is an important proxy for the overall health and energetic status of fishes. The classically used Fulton's condition factor requires length and mass measurements, but mass can be difficult to obtain in large species. Girth measurements can replace mass for wild pelagic sharks. However, girth-calculated condition has not been validated against Fulton's condition factor intraspecifically, across ontogeny or reproduction, or in a controlled setting. We used the epaulette shark (*Hemiscyllium ocellatum*), because they are amenable to captive reproduction, to track fine-scale body condition changes across life stages, oviparous reproduction and between condition indices. We measured four girths, total length and mass of 16 captive epaulette sharks across 1 year and tracked female reproduction daily. We also collected length and mass data from an additional 72 wild-caught sharks and 155 sharks from five previous studies and two public aquaria to examine the relationship between length and mass for this species. Even though data were derived from a variety of sources, a predictable length–mass relationship ($R^2 = 0.990$) was achievable, indicating that combining data from a variety of sources could help overcome knowledge gaps regarding basic life history characteristics. We also found that condition factor decreased during early life stages, then increased again into adulthood, with predictable changes across the female reproductive cycle. Finally, we determined that both Fulton's and girth condition analyses were comparable. Outcomes from this study uniquely provide body condition changes across the complete life history, including fine-scale female reproductive stages, and validate the use of girths as a nonlethal whole-organism energetic assessment for fishes.

KEYWORDS
chondrichthyes, condition factor, isometric scaling, life history, morphometrics, reproduction

1 | INTRODUCTION

Body condition is a common metric used to assess the overall energetic status of fishes, where changes can indicate energetic or health shifts across ontogeny in relation to growth, development, reproduction and illness (Cone, 1989; Lambert & Dutil, 1997; Murphy *et al*., 1991; Stevenson & Woods, 2006). Long-term energetic patterns can help discern population-level reproductive cycles as well as indicate large-scale environmental patterns that impact body condition (e.g., Abujanra *et al*., 2009; Brosset *et al*., 2017; Lyons *et al*., 2020).

Indeed, habitat loss or climate change effects that cause ecosystem imbalances can reduce food sources and therefore shift the energetics of individuals (Stevenson & Woods, 2006). Broadly, improving our understanding of individual and population-level fish conditions ultimately provides an indication of overall ecosystem health.

Given the generally imperilled state of many fish species globally, nonlethal research methodologies have become increasingly popular (Hammerschlag & Sulikowski, 2011). Indeed, nonlethal methods for estimating condition for these fishes may improve our understanding of the energetics of current-day populations and allow for better nonlethal monitoring of these fishes under anthropogenic stressors now and in the future (Hammerschlag & Sulikowski, 2011). Amongst the fishes, body condition is classically assessed using whole animal length and mass, and the simplest form of Fulton's seminal equation [$K = (\text{mass}/\text{length}^3) \times 100$], in which the cubed exponent is a scaling estimate (Fulton, 1904). Intraspecifically, if length and mass data are available across a wide range of life-history stages and both sexes, sex-specific log–log linear regression coefficients can be estimated, where the *y* intercept (*b*) replaces the cube exponent when determining body condition [*i.e.*, relative condition factor, $K_n = ((\text{mass}/\text{length}^n) \times 100)$; Le Cren, 1951]. However, even when body condition can be estimated by length and mass, there can be large interspecific variations due to differences in body plan (*i.e.*, fusiform verses depressiform) as well as intraspecific variability between life stages, seasons and populations (Froese, 2006; Le Cren, 1951). However, despite this, *K* has endured in fish research for more than a century, partially because of its simplicity and familiarity (Stevenson & Woods, 2006). In other organisms, a variety of methods using mainly length and mass to calculate body condition have been assessed, but these alternative approaches beyond *K* are not yet common in fish research (Hayes & Shonkwiler, 2001; Krebs & Singleton, 1993; Labocha *et al.*, 2014; Peig & Green, 2009; Viblanc *et al.*, 2012).

Two other measurements, gonadosomatic and hepatosomatic indices (GSI and HSI respectively), in which the proportion between reproductive tissues or liver mass is assessed as proportion of somatic mass (Rizzo & Bazzoli, 2019), have also been used to assess fish energetic status. The gonads are a known energy sink, given that gamete production is an energetically costly process (e.g., Hayward & Gillooly, 2011; Martin *et al.*, 2017). Fishes are known to store substantial energy in the liver, which can be used during juvenile growth (*e.g.*, Stallings *et al.*, 2010) or can be mobilized through processes like vitellogenesis to ultimately create yolk in the ovaries during female reproduction (Awruch, 2015; Lambert & Dutil, 1997). Therefore, both GSI and HSI are good indicators of short-term and seasonal changes in condition related to energy stores, reproduction and even the influence of environmental factors such as temperature or environmental contaminants (Hoffmayer *et al.*, 2006: Hussey *et al.*, 2009; Lyons *et al.*, 2017; Rizzo & Bazzoli, 2019; Weideli *et al.*, 2019). However, sampling to obtain GSI or HSI is lethal and therefore not feasible for many species (Hammerschlag & Sulikowski, 2011), and in many large-bodied fishes such as pelagic sharks, obtaining body mass can be logistically challenging, if possible at all (Irschick & Hammerschlag, 2014). Alternatively, a body condition metric using the sum of spans and length has been developed (Irschick & Hammerschlag, 2014). This method aims to reflect changes in body condition without weighing the animal and has been implemented on various large-bodied shark species such as bull (*Carcharhinus leucas*), blacktip (*C. limbatus*), blacktip reef (*C. melanopterus*), nurse (*Ginglymostoma cirratum*), tiger (*Galeocerdo cuvier*) and white sharks (*Carcharodon carcharias*) (Gallagher *et al.*, 2014; Irschick & Hammerschlag, 2014; Merly *et al.*, 2019; Moorhead *et al.*, 2021; Weideli *et al.*, 2019). However, to date, no comparison between this metric and Fulton's condition factor has been conducted for a species across all life-history stages.

The epaulette shark (*Hemiscyllium ocellatum*) is an oviparous long-tailed carpet shark that is docile, capable of reproduction in captivity and an ideal candidate for tracking body condition changes across life-history stages. We examined newly hatched neonates up to reproducing adults, and we also used fine-scale semiweekly tracking to quantify body condition changes across the female reproductive cycle. Additionally, we compared K_n and girth condition analysis (GCA, A_{gc}; adapted from Irschick & Hammerschlag, 2014) by compiling data on total length, mass and environmental variables from five other studies and two public aquaria to improve our assessment of the epaulette shark length–mass relationship. Overall, we aim to use epaulette sharks to validate an alternative body condition metric and for this species to serve as a proxy for nonlethal energetic assessment for other elasmobranchs with similar reproductive strategies and similar morphological and ecological changes through ontogeny.

2 | MATERIALS AND METHODS

2.1 | Ethics

All experimental protocols in this study were assessed and approved by the James Cook University Animal Ethics Committee (protocols A2655 and A2739). Collections and sampling were conducted under the appropriate Great Barrier Reef Marine Park Authority (GBRMPA G19/43380.1 and G21/44922.1) and Queensland Fisheries (#200891 and #255136) permits.

2.2 | Animal collection and husbandry

Six female epaulette sharks that were at least 61 cm total length (TL) to ensure maturity [Heupel *et al.* (1999) reports female maturity above 55 cm TL] were hand-collected with dip nets in shallow water from Magnetic Island ($n = 1$, −19.129041, 146.877586) and Balgal Beach, Queensland (QLD), Australia ($n = 4$, −19.021387, 146.418124) in February and March 2020, respectively. Sharks were transported back to the Marine and Aquaculture Research Facility Unit at James Cook University (JCU) (Douglas, QLD, AUS) within 2 h of capture in 50 l of fresh seawater with aeration packs to provide oxygen. Furthermore, six mature adults (one female, five males) and five juveniles (three females, two males) were obtained from Cairns Marine in September 2020 and June 2021, respectively (Cairns, QLD, Australia). In total, five juveniles, six mature females and five mature males were held at JCU for the 1 year length of the study.

Sharks were maintained in five 1000 l oblong tanks connected to a 5500 l reservoir fitted with a heater, protein skimmer, bio-filtration and UV sterilization. Adult males and females were segregated into separate tanks, and the five juveniles were maintained in one tank together. The system was maintained at 25°C with a 0.5°C diel temperature change (24.5–25.5°C over a 24 h period) to mimic diel changes in water temperature. This water temperature was chosen to promote year-round reproduction, as this species typically follows a seasonal cycle in the wild (Heupel *et al*., 1999), but will reproduce year-round when maintained at water temperatures experienced during the wild reproductive season (Heupel *et al*., 1999). Temperature was monitored within the external reservoir by a sensor that controlled the heaters and chillers as well as individual HOBO pendant loggers (Onset, Bourne, MA, USA) attached to the standpipe inside each tank. Water quality parameters (pH, nitrites, nitrates and ammonia) were monitored daily for the first month that the sharks were introduced to the system and subsequently checked weekly (Table S0). Additionally, each tank had one large air stone, a lid constructed of 30% light blocking shade cloth and two PVC pipes provided as shelter. All sharks in the study were fed 2% of their body mass three times weekly (6% body mass per week) of prawn, squid and pilchard as recommended for small benthic sharks (Janse *et al*., 2004). Any pieces not consumed were removed and the amount consumed was recorded. Sharks were supplemented with ElasmoTabs (The Aquarium Vet, Melbourne, Australia) to ensure no deficiencies occurred during captivity. Wet mass (g) and total length (cm) were measured for each shark every 2–4 weeks throughout the study after 72 h of fasting.

2.3 | Captive female reproductive monitoring

Female reproductive monitoring occurred from March 2020 to March 2021, with egg deposition and quality [*i.e*., wind (empty egg case) *vs*. viable yolk sac] monitored daily. Adult female sharks were measured two or three times per week for four girths: (1) posterior of the pectoral fins, (2) anterior of the pelvic fins, (3) anterior of the first-dorsal fin and (4) anterior of the second-dorsal fin (see Figure 3). The first two girths were chosen to represent potential changes in liver and reproductive tissue volumes (and thereby energy stores), and the two tail girths were chosen to represent changes in nonhepatic skeletal muscle tissue energy stores. Sharks were freely resting in the aquaria during these measurements to ensure minimal stress, and girth measurements were accurate to 0.1 cm. Sharks were measured just prior to a feeding event so that all measurements were postabsorptive and standardized to 48 h after the previous feeding. Next, female sharks were palpated between the pectoral and pelvic fins to determine if egg cases were within the oviducts/uteri. The reproductive cycle was divided into four distinct phases by combining egg deposition timing and palpation information, where a female was classified as resting (*i.e*., had been reproductively inactive for at least 1 month), pre-encapsulating, encapsulating an egg case(s) or within 48 h postoviposition following Koob and Callard (1999) (see Table 1 and Supporting Information Figure S1 for details).

2.4 | Field sampling

In addition to the captive epaulette sharks, data were also collected from wild sharks during catch and release sampling. Epaulette sharks were sampled at Balgal Beach, QLD ($n = 12$; −19.021387, 146.418124) from May to June in 2021 and 2022 and on the Heron Island reef flat, QLD ($n = 60$; −23.444622, 151.914889) from October to November 2021 (Wheeler *et al*., 2022). Sharks were caught and measured in the same manner as described above. Sharks were photographed for spot identification, and a passive integrated

TABLE 1 Life-history stage classification of epaulette shark based on age in days (neonates) or sex-specific total lengths at maturity reported in Heupel *et al*. (1999) and Wheeler *et al*. (2022)

Life stage	Reproductive stage	Determination criteria	Age or total length (TL)
Neonates			Up to 30 days posthatch
Juveniles			From 30 days posthatch to subadult lengths
Sub-adult			Males: 53–61 cm TL
			Females: 55–61 cm TL
Mature female	Resting	Above TL of maturity (Heupel *et al*., 1999) but not producing egg cases	>61 cm TL
	Egg case encapsulation and retention	Egg case present in one or both oviduct/uteri, confirmed with postabsorptive palpation	
	Post-oviposition	Within 48 h of depositing the last egg case of the cycle	
	Pre-encapsulation	The period after the postoviposition stage and prior to detection of any forming egg cases	
Mature male			>61 cm TL

Note: Female reproductive stages were subdivided based on elasmobranch oviparous reproduction reported in Koob and Callard (1999) (see Supporting Information Figure S1 for female reproductive cycle details).

TABLE 2 Slope *a* and *y* intercept *b* coefficients of the length–weight relationship of epaulette shark

$\log_{10}(a)$ ± 95% CI	*a*	*b* ± 95% CI	$a_{3.0}$ (form factor)	R^2	*N*
−2.3263 ± 0.225	0.098	2.860 ± 0.135	0.00423	0.990	318

Note: The form factor $a_{3.0}$ was estimated from Froese (2006) assuming an elongated body shape.
Abbreviation: CI, confidence interval.

transponder (PIT) tag (Hallprint, Hindmarsh, SA, AU) was implanted into the dorsal musculature to ensure they could be identified if recaptured. Sharks were all released in excellent condition at the location of capture.

2.5 | Literature data compilation

To further inform the length–mass relationship and body condition across life-history stages, individual total length and mass data were sourced from six epaulette shark studies (Gervais *et al*., 2018; Heinrich *et al*., 2014; Nay *et al*., 2021; Payne & Rufo, 2012; Schwieterman *et al*., 2021 and Wheeler *et al*., 2021), the New England Aquarium and the New York Aquarium, where sex, location (captivity *vs*. wild) and maturity (*i.e*., if females were producing egg cases or if males had calcified claspers) were obtained when available. Sharks were categorized into life-history stages based on days posthatch for neonates or total length from sex-specific total length at maturity data reported in Heupel *et al*. (1999) (Table 1).

2.6 | Isometry assessment

Top-down images of epaulette shark neonates reared in Wheeler *et al*. (2021) and in the current study that were all at JCU were used to assess whether body proportions changed across life-history stages. From each photograph, we measured head (from the tip of the rostrum to fifth gill slit), abdomen (from fifth gill slit to the most anterior part of the pelvic fin) and tail (from anterior pelvic fin to end of caudal fin; Figure 2) lengths down the midline using a scale bar in the photo and ImageJ (Schneider *et al*., 2012). Each body measurement was then standardized as a proportion of TL.

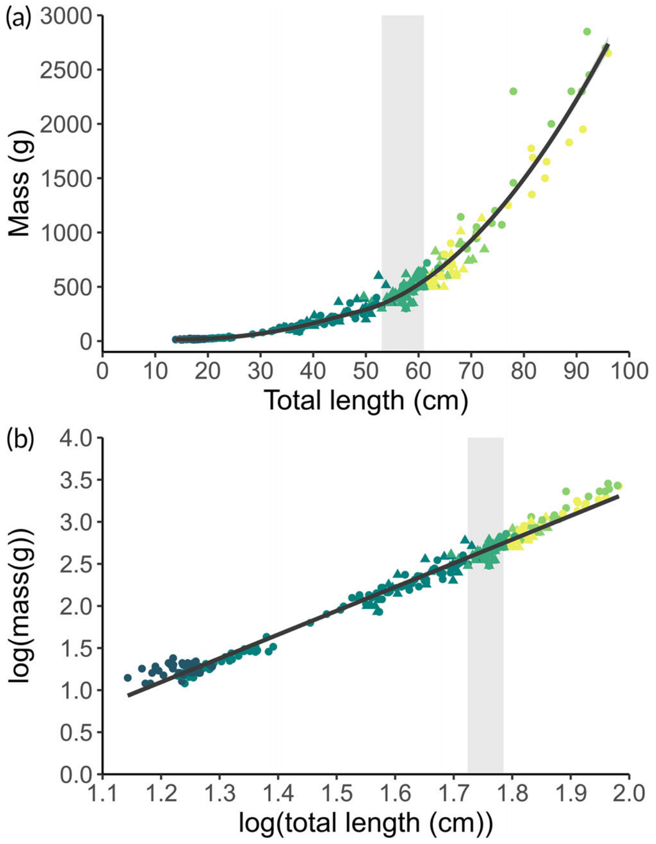

FIGURE 1 (a) The relationship between total length (cm) and mass (g) observations from 245 individual epaulette sharks, 318 data points and eight sources (current study, five previous studies and two public aquaria). (b) The log–log relationship between total length and mass ($R^2 = 0.990$). The grey vertical regions represent the range of length at maturity from Heupel *et al*. (1999), data point colours represent the life-history stage and the point shape represents the location of the shark at the time of the measurements. Location: ●, captivity; ▲, wild; life-history stage: ●, neonate; ●, juvenile; ●, subadult; ●, mature female; ●, mature male

2.7 | Statistical analyses

Compiled length and mass data from this study, previous research and public aquaria contributions were log transformed and fit with a full mixed-effects model (*lme4*, Bates *et al*., 2015) testing a three-way interaction between log(length), sex and location (*i.e*., wild *vs*. captive sharks) as well as the individual shark as a random effect to account for repeated measurements of captive individuals over time (Supporting Information Table S1A). Next, the step function of the *lmerTest* package (Kuznetsova *et al*., 2017) was used for backwards elimination of the model terms, where the final model included location as a fixed term, an interaction between log(length) and sex, and individual shark as a random effect (Supporting Information Table S1A). We did not explore sex-specific length–mass relationships beyond inclusion of sex in the model due to sparse data for animals larger than 70 cm TL, where growth differences are most likely to occur (*e.g*., Sen *et al*., 2018). The slope of this linear model was derived (Table 2) and the *y* intercept (*b* value) was used to calculate a species-specific condition factor (K_n; Froese, 2006) where:

$$K_n = \text{mass}/\text{total length}^{2.860} \qquad (1)$$

Given that *b* for the log–log length–mass relationship was less than 3, this may indicate that epaulette sharks elongate with growth (*i.e*., they grow longer without significant increases in mass) (Froese, 2006), therefore we analysed for differences in body proportions across life-history stages to assess potential allometric shifts using a log-ratio linear regression (Supporting Information Table S2).

Next, the four girth morphometrics were standardized for TL (girth/total length × 100) given that all males in the captive portion of the study had longer TLs and therefore proportionally larger girths. Next, a modified version of span condition analysis, first reported in Irschick and Hammerschlag (2014), was calculated. Given epaulette sharks are a small-bodied docile species, we used standardized girths instead of span measurements in the following modified function to conduct girth condition analysis (GCA):

$$A_{\mathrm{gc}} = (\mathrm{PPG} + \mathrm{APG} + \mathrm{AFG} + \mathrm{ASG}) \times \mathrm{TL}^{-1} \qquad (2)$$

where PPG is posterior pectoral girth, APG is anterior pelvic girth, FDG is anterior first dorsal girth and SDG is anterior second dorsal girth (see Figure 3). The four standardized girths (girth × TL^{-1}) were assessed across reproductive and life-history stages using linear mixed-effects models (*lme4*, Bates *et al.*, 2015), accounting for repeated sampling of captive sharks with each individual shark treated as a random effect (Supporting Information Table S3A–D). Finally, the linear relationship between K_n and A_{gc} was assessed using a linear mixed-effects model with an interaction between K_n and life-history stage and the individual sharks as a random effect (Supporting Information Table S4).

For all linear mixed-effects models, pairwise *post hoc* comparisons were conducted between estimated marginal means (EMMs) of the life-history stages using the *emmeans* package (Lenth, 2022). All data met the assumptions of normality, nonmulticollinearity and homoscedasticity, noting that the mixed-effects models used here are fairly robust for minor violations of these assumptions (Schielzeth *et al*., 2020). All statistical analyses were conducted in R (version 4.2.2; R Core Development Team, 2022), where results were considered significant at $\alpha = 0.05$.

3 | RESULTS

3.1 | Length–mass relationship and scaling

There was an exponential relationship between length and mass, which was highly linear after log transformations of both variables (Figure 1, Table 2 and Supporting Information Table S1; conditional $R^2 = 0.99$). Overall, the body proportions assessed were fairly constant across life history; there was a slight elongation of the tail after the neonate stage (Figure 2 and Supporting Information Table S2). Furthermore, the *b* coefficient of the length–mass linear model was less than 3 ($b = 2.78$; Table 2), also indicating a small elongation and/or decreasing body condition with increasing length (Froese, 2006).

3.2 | Life history stages and girth changes

For pectoral and pelvic standardized girths (PPG and APG), neonates and reproducing females had the highest values (Figure 3a,b). Indeed, these girths were high after hatching, decreasing into the juvenile life stage and increasing into adulthood. Resting female pectoral and

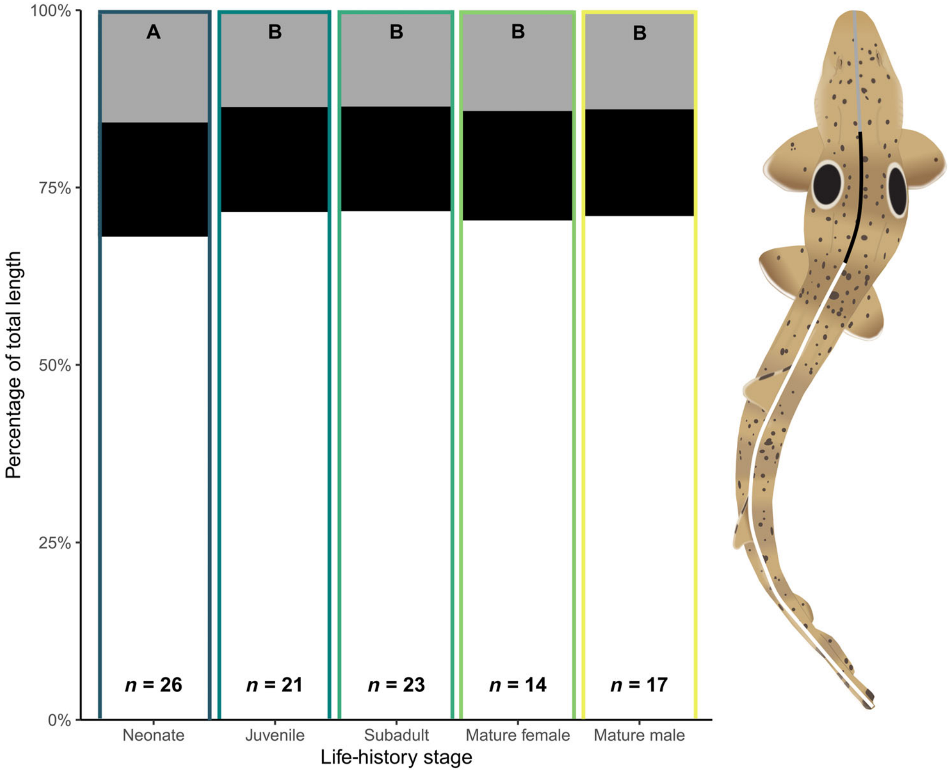

FIGURE 2 The head (grey), abdomen (black) and tail (white) proportion of total length across epaulette shark life-history stages. Outlining colours correspond to life-history stages. Differing letters in each category represent statistically significant differences in proportions between life stages at $\alpha = 0.05$

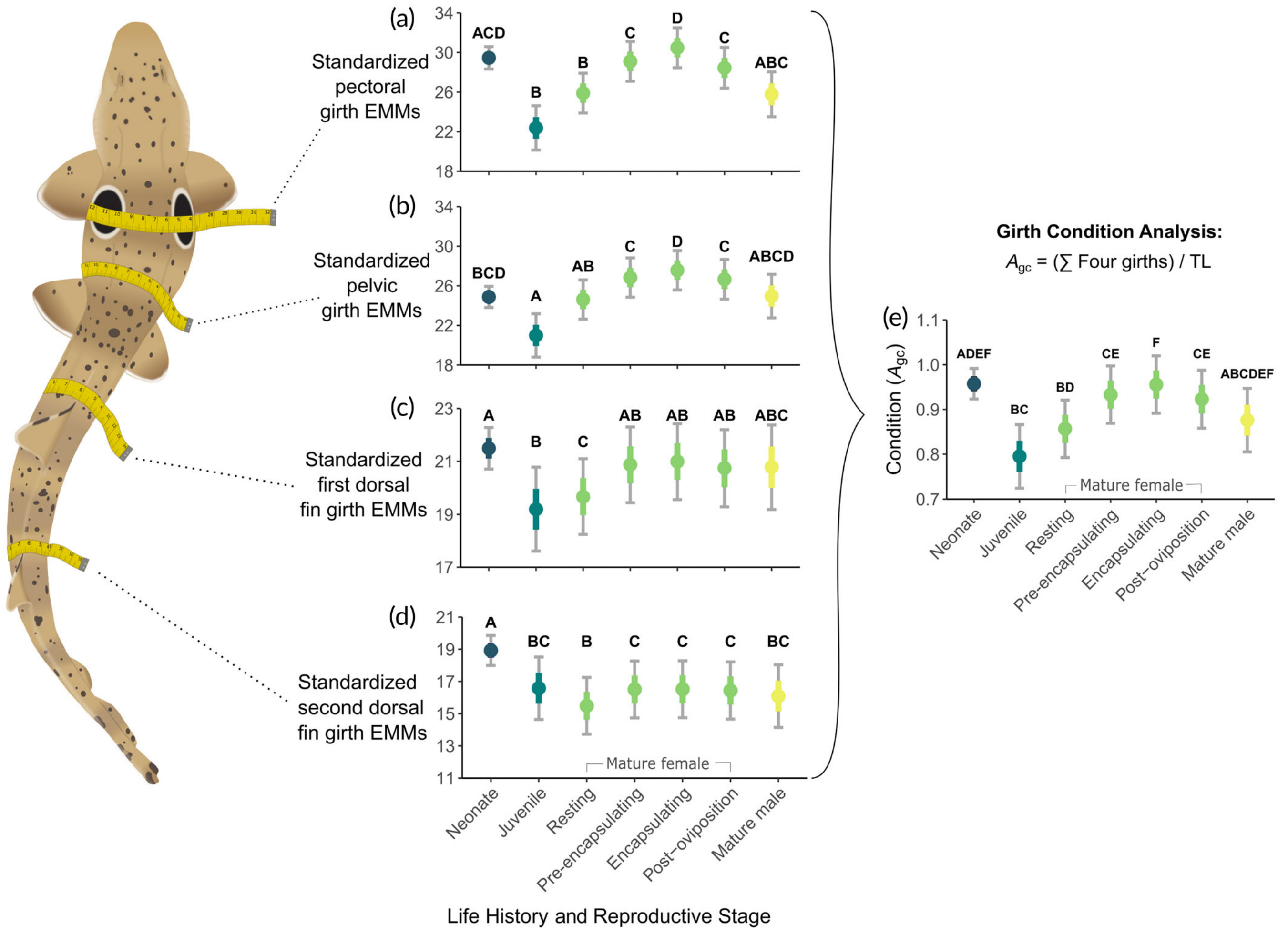

FIGURE 3 The changes in the estimated marginal means (EMMs) of four standardized girths (a–d) and condition [A_{gc}, (e)] across life-history and female reproductive stages of 16 laboratory-maintained epaulette sharks. The coloured points and bars represent the EMMs and standard error, and the grey error bars represent the 95% confidence intervals. Different letters represent significant differences at $\alpha = 0.05$ and NS represents no significance between any groupings

pelvic girths increased through folliculogenesis, peaking during egg encapsulation, then decreased after both egg cases were deposited (Figure 3a,b and Supporting Information Table S3A,B). Mean male pectoral and pelvic girths were comparable to juveniles and resting female girths (Supporting Information Table S3A,B and Figure 3a,b). Both tail girths (AFG and ASG) were high in neonates, then decreased into the juvenile stage, and then for the first dorsal fin girth increased into adulthood (Figure 3c,d and Supporting Information Table S3C,D). Overall, from summing these girths and calculating A_{gc}, this condition metric was highest in neonates and reproducing females, highlighting that small body condition changes occur across the egg production cycle (Figure 3e and Supporting Information Table S3E). Male A_{gc} did not differ from neonates, juveniles or any phase of female reproduction (Figure 3e and Supporting Information Table S3E).

3.3 | Condition factor indices

The residuals of the log–log length–mass relationship, K_n and A_{gc} were high in neonates, decreased into the juvenile stage and then increased after subadult ranges into adulthood (Figure 4). This trend was more prominent in the model residuals and K_n, as these datasets were more robust, but a similar pattern was still evident in A_{gc} (Figure 4). Finally, there was a moderately positive linear relationship between K_n and A_{gc} (conditional $R^2 = 0.68$), where the slope of the relationship only differed between juveniles and adult males (Figure 5 and Supporting Information Table S4).

4 | DISCUSSION

4.1 | Length–mass relationship and scaling

Body condition is a common metric for assessing energetics and overall health in fishes, and relates to the energy content and stores of an individual (Lambert & Dutil, 1997). Here we established a length–mass relationship for a model oviparous shark and then assessed two body condition metrics across a complete range of life-history and reproductive stages. Data compiled from the current study, five previously conducted studies and animals from two public aquaria produced a

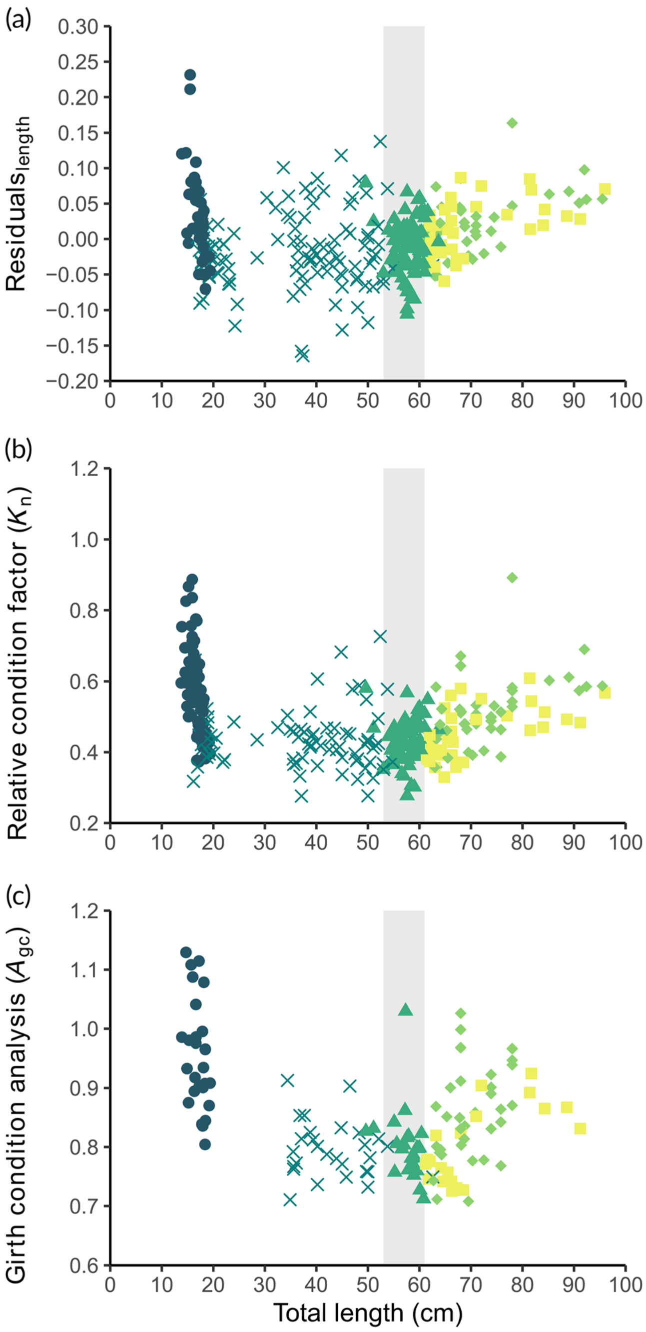

FIGURE 4 (a) The residuals from the log–log linear mixed-effects model regression of length and mass in Figure 1b, (b) the relative condition factor (K_n) (c) and girth condition analysis (A_{gc}) across epaulette shark total length (cm). The grey vertical regions represent the range of length at maturity reported in Heupel *et al.* (1999), and the data point colours and shapes represent the life-history stage. Life-history stage: ●, neonate; ×, juvenile; ▲, subadult; ◆, mature female; ■, mature male

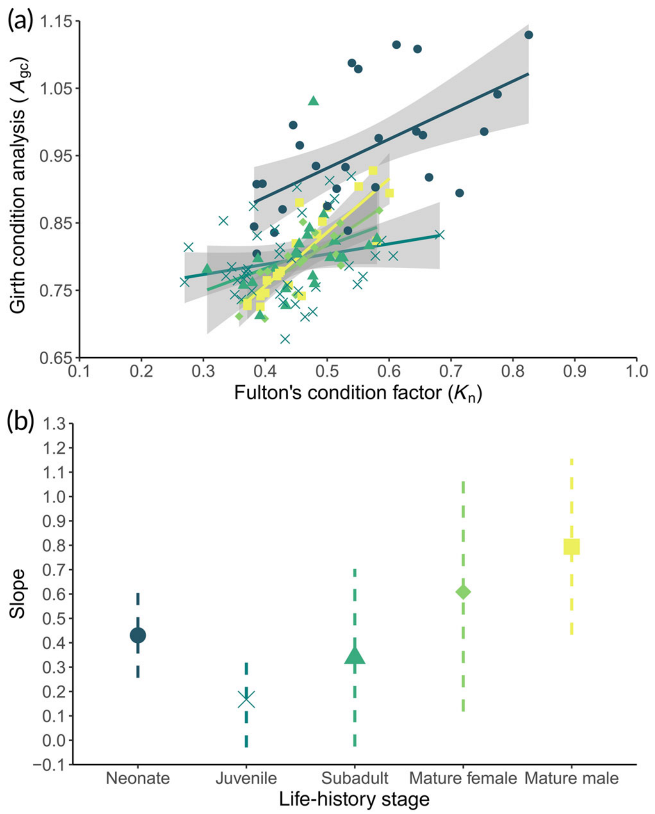

FIGURE 5 (a) The linear relationship (and 95% confidence interval) between relative condition factor (K_n) and girth condition analysis (A_{gc}), and (b) the slopes of the model fits (and 95% confidence interval) across life-history stages. Data point colours and shapes represent the life-history stages. Life-history stage: ●, neonate; ×, juvenile; ▲, subadult; ◆, mature female; ■, mature male

well-correlated exponential length–mass relationship from 245 individuals (Figure 1). The log–log length–mass model fit coefficients reported herein indicate that epaulette sharks have slight negative allometry across ontogeny (Table 2: $b = 2.860 \pm 0.135$, where $b = 2.5–3.5$ indicates isometry; Froese, 2006) and that this species has an 'elongated' body plan (Table 2, $a_{3.0} = 0.00423$; Froese, 2006). The epaulette shark *b* coefficient is similar to reports from another Orectobliformes, such as the nurse shark ($b = 2.911$; Castro, 2000), and more closely related Hemiscylliid sharks, such as the Arabian carpet shark (*Chiloscyllium arabium*, $b = 2.372–2.588$; Alhajji *et al.*, 2022), grey bamboo shark (*C. griseum*, $b = 2.56–2.83$; Kishore Kumar *et al.*, 2021), whitspotted bamboo shark (*C. plagiosum*, $b = 2.51–2.93$; Kishore Kumar *et al.*, 2021), brownbanded bamboo shark (*C. punctatum*, $b = 2.81–3.21$; Pattarapongpan *et al.*, 2021) and Cenderawasih epaulette shark (*H. galei*, $b = 1.3–2.3$; Insani *et al.*, 2022). Our estimates of epaulette shark body proportions were different in neonates compared to every other life-history grouping, where neonates had disproportionally larger heads and abdomens, indicating some elongation occurs during the transition to the juvenile stage (Figure 2). Additionally, we also noted a decrease in body condition from neonates to juveniles (Figures 3 and 4), which could also be a factor influencing estimates of *b* that were less than 3 (Froese, 2006). Whole-body isometry is likely the rule and allometry the exception in elasmobranchs, where most length–mass relationships for elasmobranchs report *b* values between 2.5 and 3.5 (Irschick *et al.*, 2017; Kishore Kumar *et al.*, 2021; Motta *et al.*, 2014). However, morphological features such as fin proportions do show allometric growth in some species (*e.g.*, Ahnelt *et al.*, 2020; Fu *et al.*, 2016; Irschick & Hammerschlag, 2015). These ontogenetic shifts are potentially linked to changes in swimming kinematics and/or feeding behaviour (Ahnelt *et al.*, 2020), but more research in this area is required.

4.2 | Girths and body condition across ontogeny

Of the four girths assessed, the pectoral and pelvic girths should exhibit the largest changes across ontogeny. The high pectoral and pelvic girths in neonates reported herein therefore reflect posthatch endogenous yolk reserves and large liver size (Figure 3a,b; Lechenault *et al.*, 1993). These girths then decreased as sharks expended energy growing into juveniles (Figure 3a,b). Both tail girths also decreased from neonate to juvenile stages, indicating that growth is a costly process during which time energy stores from both the liver and skeletal muscle may be mobilized as fuel (Figure 3c,d). The smaller changes observed within the two tail girths could reflect changes in skeletal muscle energy stores (*e.g.*, glycogen) and the subsequently affected water content (Spargo *et al.*, 1979). Another explanation for changes in tail girths during the early stages could be the transition from very limited body movement in the final stages of development *in ovo* and furthermore reduced activity after hatching when endogenous yolk stores may inhibit foraging and thereby activity. Then, as late-stage neonates/juveniles begin foraging, activity increases, decreasing tail girths *via* exercise. Overall, during neonatal and juvenile stages, length increased disproportionally to mass (Figure 3a), which is reflected in decreasing body condition (Figure 3e). In other fishes, HSI also decreases when neonates transition to juveniles (Corsso *et al.*, 2018; Hussey *et al.*, 2009, 2010; Lyons *et al.*, 2020). In the Brazilian sharpnose shark (*Rhizoprionodon lalandii*), but not the dusky shark, condition factor decreased as HSI decreased during this early life stage transition (Corsso *et al.*, 2018; Hussey *et al.*, 2009). Perhaps the differences in body plans between Carcharhinid sharks and the epaulette shark explains why the condition factors assessed here are likely good tools for detecting early life stage HSI shifts when this is not the case in dusky sharks (Hussey *et al.*, 2009).

4.3 | Girths and body condition across maturation and reproduction

Within female reproduction, both pectoral and pelvic abdominal girths increased when females transitioned from resting to reproducing stages (Figure 3a,b), reflecting an increase in abdomen volume caused by changes in the reproductive tract (*i.e.*, increase in ovarian and oviducal gland volumes). Indeed, the increase in pectoral girth during the 2–3 week-long reproductive cycle is well explained by the presence of large ova in the ovaries and the 2–4-fold increase in oviducal gland volume reported in Heupel *et al.* (1999), both located in the same region as these girth measurements. In adult elasmobranchs, females generally have larger livers and consequently HSI when compared to males, which is because of vitellogenesis, the process by which the liver creates lipoproteins that are used for oocyte formation in the ovaries (Awruch *et al.*, 2008; Capapé *et al.*, 2014; Chen & Liu, 2006; Craik, 1978; Estalles *et al.*, 2009; Kousteni & Megalofonou, 2020; Rossouw, 1987). Prior to the reproductive season, HSI increases, then decreases when reproduction ensues, as stored hepatic energy is mobilized, mainly vitellogenesis (Awruch *et al.*, 2008; Craik, 1978; Estalles *et al.*, 2009; Koob & Callard, 1999). It is likely that for the reproducing females in this study, the increase in abdominal girths and overall body condition reflects an increase in GSI, masking expected decreases in HSI (Awruch *et al.*, 2008). In several other oviparous shark species, immature females had high HSI values that then decreased on maturing into reproducing females (Awruch *et al.*, 2008; Craik, 1978). For example, in both the oviparous whitespotted bamboo shark (*C. plagiosum*) and the Arabian carpet shark (*C. arabicum*), close relatives of the epaulette shark, female GSI increases during the reproductive season while HSI concurrently decreases, showing a clear reproductive energetic shift (Alhajji *et al.*, 2022; Chen & Liu, 2006). Indeed, it is difficult to discern from our data whether HSI is changing, as the reproductive tract is generally increasing body condition. So, although body condition is increasing, the energetic status in these individuals in relation to hepatic stores may be reduced, as energy is allocated to reproduction.

Both tail girths increased as females transitioned from resting to active reproduction stages (Figure 3c,d). However, within the reproductive cycle, the tail girths were consistent, indicating that nonhepatic energy use from tail skeletal muscle tissue may be consistent across the cycle or that energy may be stored and unused (Figure 3c,d). More research assessing the seasonality of various girths in this species or in an elasmobranch with prolonged viviparous gestation may indicate how hepatic verses nonhepatic stores contribute to reproductive costs. Furthermore, research where energetic stores (*e.g.*, amino acids, fatty acids, glycogen) are directly measured across ontogeny may help further elucidate these findings.

In oviparous sharks, mature males generally have lower HSI values compared to mature females (Awruch *et al.*, 2008; Chen & Liu, 2006; Craik, 1978). In epaulette sharks, we found that mature male girths and body condition did not differ from most other life-history or female reproductive stages. Indeed, only the male pectoral girth differed from females that were actively encapsulating egg cases (Figure 3a). Seasonally, male sharks do show small changes in GSI and HSI (Hoffmayer *et al.*, 2006), although usually less so than females (Awruch *et al.*, 2008; Chen & Liu, 2006; Craik, 1978). However, because sharks in this study were maintained at water temperatures that promote year-round reproduction, male condition was consistent. Furthermore, a seasonal analysis of condition in wild sharks was not possible here, as we were only able to sample during 3 months of the year. In the future, more research assessing wild shark conditions across a full range of months would better inform cyclical changes in condition related to both male and female reproductive seasonality in this species.

Traditionally, when compared to body condition, GSI and HSI have been the best metrics to reflect short- and long-term energetic shifts, but incorporating targeted girths/spans in key areas (*i.e.*, the body cavity and the tail) may provide an alternative, nonlethal option with excellent short-term resolution. We were unable to compare our condition data directly to GSI or HSI given the nonlethal nature of the study. Yet we saw similarities in our condition data with HSI reported over ontogeny and reproduction for dusky sharks in Hussey *et al.* (2009), which is promising. We hypothesise that the decrease in body condition that occurs when neonates transition to juveniles is due to decreasing HSI, whereas the increase in body condition that occurs when juveniles transition into adulthood reflects increasing GSI related to reproduction (Figure 4). It is highly likely that HSI decreases during reproduction in the epaulette shark but was potentially masked in body condition metrics by increasing GSI. More research using nonlethal energetic markers (*i.e.*, fatty acids) and reproductive hormones involved in energy transfer (*i.e.*, vitellogenin and estradiol) in a controlled laboratory setting may help to further elucidate the relationship between HSI and GSI during reproduction for this species.

4.4 | Body condition metrics comparison

Overall, the residuals of the log–log relationship, K_n and A_{gc}, showed similar patterns across ontogeny, and whilst model residuals and K_n seemed to better reflect condition changes, this is likely due to having more data than A_{gc} (Figure 4). In neonatal blacktip reef sharks (*Carcarhinus melanopterus*), the relationship between Fulton's condition factor and a girth condition factor, like the one used in this study, also produced a weak linear correlation (Weideli *et al.*, 2019; Supporting Information Data S1). We found these two metrics also had weak to moderate linear correlations across life stages, where adults and neonates had stronger correlations than neonates, juveniles and subadults (Figure 5). However, given the overall similarity of the condition trends reflected by both K_n and A_{gc} (Figure 4b,c), both metrics highlight body condition changes across ontogeny, but perhaps are not directly comparable (Figure 5). The incorporation of other measurements beyond length and mass into whole-animal condition scoring is not common in fishes. However, in milkfish (*Chanos chanos*), a body condition metric incorporating mass, length and body height performed better than K_n (Ritcher *et al.*, 2000), indicating that in elasmobranchs, improving condition calculations with additional measurements that reflect body shape may be useful.

4.5 | Applications and future directions

Length–mass relationships and body condition in fishes can vary between populations and under different environmental factors (*e.g.*, water temperature, food availability; Hussey *et al.*, 2009; Lear *et al.*, 2021). Herein, despite sourcing data from a variety of captive and wild epaulette sharks with differing thermal histories and feeding regimes, mass and length were well correlated, and body condition changes across ontogeny were similar across data sources (Supporting Information Figure S2). So, in the case of rare or critically endangered species where data are lacking, compilation from various sources can still provide useful length–mass relationships pertinent to conservation of imperilled species. Furthermore, defining length–mass relationships provides more accurate species-specific scaling coefficients for condition factor analyses (Froese, 2006).

For tracking short- and long-term changes in growth, reproduction and overall health in large-bodied sharks where obtaining mass is not possible, we recommend A_{gc}. This metric is also a useful tool for identifying the reproductive status of adult females, as the body condition of resting females was lower than that of reproducing females (Figure 3e). In application, it is important to note that we observed significant abdominal swelling postfeeding, therefore it is imperative that measurements are postabsorptive for repeatability and accuracy. This factor, of course, causes issues with wild sharks, where feeding status is unknown at the time of capture. For larger sharks that are not as easily measured for girth or spans (*e.g.*, species that are monitored through aerial surveys or without capture), we recommend investigating extensions of laser photogrammetry techniques (*e.g.*, Leurs *et al.*, 2015; Rohner *et al.*, 2015) and stereo-photogrammetry (*e.g.*, Lewis *et al.*, 2021) to estimate spans for condition analysis, but validation would be needed against specimens. In public aquaria settings, long-term tracking of length, mass and body condition can help quantify growth rates that are difficult to determine from wild sharks, as well as identify potential health issues or insufficient food rationing. Furthermore, batoids are typically assessed with disc width and total length, but given their flat body plan are not conducive to girths. Therefore, other methods, such as a combination of disk spans and abdominal thickness, should be investigated for this superorder of Chondrichthyans.

Validation of girth/span condition analysis to HSI may help to clarify how hepatic and nonhepatic energy stores are used throughout reproduction, where GSI changes here likely masked HSI differences in adults. However, from this research, we provide strong evidence that the A_{gc} condition metric can reflect changes across life history and between sexes; however, large sampling efforts may be required for desired resolution. Overall, the incorporation of standardized and repeatable (*i.e.*, easily and quickly measured in an exact body location in a field setting) span, girth, width and/or height measurements in condition factor may improve nonlethal estimates of whole-fish energetics. General improvement in estimations and better detectability of small differences of body condition can aid scientists in understanding the life history and reproductive timing of fishes, a key understanding for conservation and management strategies.

ACKNOWLEDGEMENTS

Support for this work came from a Save Our Seas Foundation small grant, an American Australian Association graduate scholarship, a JCU Postgraduate Research Scholarship, the Australian Research Council Centre of Excellence for Coral Reef Studies, the Save Our Seas Foundation, The Australian Wildlife Society and the Australian Society for Fish Biology. The authors would like to thank past and present Rummer Lab members for their assistance with husbandry and data collection during this project. Furthermore, we thank the staff of the Marine Aquaculture Research Facilities Unit at JCU and the Heron

Island Research Station at the University of Queensland for their technical support. We thank D. Heinrich, C. Gervais, T. Nay, G. Schwieterman, S. Tempesta, N. Ethier, the New England Aquarium and the New York Aquarium for their invaluable data contributions. Finally, we thank J. Kneebone and two anonymous examiners of C. Wheeler's Ph.D. thesis for their feedback on this manuscript. Open access publishing facilitated by James Cook University, as part of the Wiley - James Cook University agreement via the Council of Australian University Librarians.

FUNDING INFORMATION

Save Our Seas Foundation; American Australian Association, Australian Research Council (ARC) Centre of Excellence for Coral Reef Studies; The Australian Wildlife Society; Australian Society for Fish Biology.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing or financial interests.

DATA AVAILABILITY STATEMENT

Data are openly available from Research Data JCU at James Cook University at https://doi.org/10.25903/pdze-bw08.

ORCID

Carolyn R. Wheeler https://orcid.org/0000-0001-9976-8420
Duncan J. Irschick https://orcid.org/0000-0003-3433-6576
John W. Mandelman https://orcid.org/0000-0002-4679-2694
Jodie L. Rummer https://orcid.org/0000-0001-6067-5892

REFERENCES

Abujanra, F., Agostinho, A. A., & Hahn, N. S. (2009). Effects of the flood regime on the body condition of fish of different trophic guilds in the Upper Paraná River floodplain, Brazil. *Brazilian Journal of Biology*, *69*, 469–479.

Ahnelt, H., Sauberer, M., Ramler, D., Koch, L., & Pogoreutz, C. (2020). Negative allometric growth during ontogeny in the large pelagic filter-feeding basking shark. *Zoomorphology*, *139*, 71–83.

Alhajji, A. H., Hsu, H. H., Alkhamis, Y. A., Alsaqufi, A. S., Ajmal Khan, S., & Nazeer, Z. (2022). Maturity and reproduction in the Arabian carpet shark, *Chiloscyllium arabicum* from the Saudi Arabian waters of the Arabian Gulf. *Marine Biology Research*, *18*, 1–11.

Awruch, C. (2015). Reproduction strategies. In R. Shadwick, A. Farrell, & C. Brauner (Eds.), *Physiology of elasmobranch fishes: Structure and interaction with environment, Vol. 34A* (pp. 255–297). London: Academic Press.

Awruch, C. A., Pankhurst, N. W., Frusher, S. D., & Stevens, J. D. (2008). Endocrine and morphological correlates of reproduction in the draughtboard shark *Cephaloscyllium laticeps* (Elasmobranchii: Scyliorhinidae). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, *309*, 184–197.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Brosset, P., Fromentin, J.-M., Beveren, E. V., Lloret, J., Marques, V., Basilone, G., … Saraux, C. (2017). Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Progress in Oceanography*, *151*, 149–162.

Capapé, C., Mnasri-Sioudi, N., El Kamel-Moutalibi, O., Boumaïza, M., Ben Amor, M. M., & Reynaud, C. (2014). Food and feeding habits of the small-spotted catshark, *Scyliorhinus canicula* (Chondrichthyes: Scyliorhinidae) from the northern coast of Tunisia (Central Mediterranean). *Journal of Ichthyology*, *54*(1), 111–126.

Castro, J. I. (2000). The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida East Coast and the Bahama Islands. *Environmental Biology of Fishes*, *58*(1), 1–22.

Chen, W. K., & Liu, K. M. (2006). Reproductive biology of whitespotted bamboo shark *Chiloscyllium plagiosum* in northern waters off Taiwan. *Fisheries Science*, *72*(6), 1215–1224.

Cone, R. S. (1989). The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society (1900)*, *118*(5), 510–514.

Corsso, J. T., Gadig, O. B. F., Barreto, R. R. P., & Motta, F. S. (2018). Condition analysis of the Brazilian sharpnose shark *Rhizoprionodon lalandii*: Evidence of maternal investment for initial post-natal life. *Journal of Fish Biology*, *93*(6), 1038–1045.

Craik, J. C. A. (1978). An annual cycle of vitellogenesis in the elasmobranch *Scyliorhinus canicula*. *Journal of the Marine Biological Association of the United Kingdom*, *58*, 719–726.

Estalles, M., Perez Comesaña, J. E., Tamini, L. L., & Chiaramonte, G. E. (2009). Reproductive biology of the skate, *Rioraja agassizii* (Müller and Henle, 1841), off Puerto Quequén, Argentina. *Journal of Applied Ichthyology*, *25*, 60–65.

Froese, R. (2006). Cube law, condition factor and weight–length relationships: History, meta-analysis and recommendations. *Journal of Applied Ichthyology*, *22*(4), 241–253.

Fu, A. L., Hammerschlag, N., Lauder, G. V., Wilga, C. D., Kuo, C. Y., & Irschick, D. J. (2016). Ontogeny of head and caudal fin shape of an apex marine predator: The tiger shark (*Galeocerdo cuvier*). *Journal of Morphology*, *277*(5), 556–564.

Fulton, T. W. (1904). The rate of growth of fishes. In *Twenty-second annual report, part III* (pp. 141–241). Edinburgh: Fisheries Board of Scotland.

Gallagher, A. J., Wagner, D. N., Irschick, D. J., & Hammerschlag, N. (2014). Body condition predicts energy stores in apex predatory sharks. *Conservation Physiology*, *2*(1), 1–8.

Gervais, C. R., Nay, T. J., Renshaw, G., Johansen, J. L., Steffensen, J. F., & Rummer, J. L. (2018). Too hot to handle? Using movement to alleviate effects of elevated temperatures in a benthic elasmobranch, *Hemiscyllium ocellatum*. *Marine Biology*, *165*(11), 162.

Hammerschlag, N., & Sulikowski, J. (2011). Killing for conservation: The need for alternatives to lethal sampling of apex predatory sharks. *Endangered Species Research*, *14*(2), 135–140.

Hayes, J. P., & Shonkwiler, S. J. (2001). Morphometric indicators of body condition: Worthwhile or wishful thinking? In J. R. Speakman (Ed.), *Body composition analysis of animals: A handbook of non-destructive methods*. Cambridge: Cambridge University Press.

Hayward, A., & Gillooly, J. F. (2011). The cost of sex: Quantifying energetic investment in gamete production by males and females. *PLoS One*, *6*(1), e16557.

Heinrich, D. D. U., Rummer, J. L., Morash, A. J., Watson, S., Simpfendorfer, C. A., Heupel, M. R., & Munday, P. L. (2014). A product of its environment: The epaulette shark (*Hemiscyllium ocellatum*) exhibits physiological tolerance to elevated environmental CO_2. *Conservation Physiology*, *2*, 1–12.

Heupel, M. R., Whittier, J. M., & Bennett, M. B. (1999). Plasma steroid hormone profiles and reproductive biology of the epaulette shark, *Hemiscyllium ocellatum*. *Journal of Experimental Zoology*, *284*, 586–594.

Hoffmayer, E. R., Parsons, G. R., & Horton, J. (2006). Seasonal and interannual variation in the energetic condition of adult male Atlantic sharpnose shark *Rhizoprionodon terraenovae* in the northern Gulf of Mexico. *Journal of Fish Biology*, *68*(2), 645–653.

Hussey, N. E., Cocks, D. T., Dudley, S. F. J., McCarthy, I. D., & Wintner, S. P. (2009). The condition conundrum: Application of multiple condition indices to the dusky shark *Carcharhinus obscurus*. *Marine Ecology Progress Series*, *380*, 199–212.

Hussey, N. E., Wintner, S. P., Dudley, S. F. J., Cliff, G., Cocks, D. T., & Aaron MacNeil, M. (2010). Maternal investment and size-specific reproductive output in carcharhinid sharks. *Journal of Animal Ecology*, *79*(1), 184–193.

Insani, M., Sala, R., & Kolibongso, D. (2022). Some aspects of bio-ecology of walking shark (*Hemiscyllium galei*) in Doreri Bay, Manokwari, Indonesia. *Indonesian Journal of Marine Sciences*, *27*, 279–284.

Irschick, D. J., Fu, A., Lauder, G., Wilga, C., Kuo, C. Y., & Hammerschlag, N. (2017). A comparative morphological analysis of body and fin shape for eight shark species. *Biological Journal of the Linnean Society*, *122*(3), 589–604.

Irschick, D. J., & Hammerschlag, N. (2014). A new metric for measuring condition in large predatory sharks. *Journal of Fish Biology*, *85*(3), 917–926.

Irschick, D. J., & Hammerschlag, N. (2015). Morphological scaling of body form in four shark species differing in ecology and life history. *Biological Journal of the Linnean Society*, *114*(1), 126–135.

Janse, M., Firchau, B., & Mohan, P. J. (2004). Elasmobranch nutrition, food handling, and feeding techniques. In M. Smith, D. Warmolts, D. Thoney, & R. Hueter (Eds.), *Elasmobranch husbandry manual* (pp. 183–200). Columbus, OH, USA: Ohio Biological Survey, Inc.

Kishore Kumar, M., Jayakumar, N., Karuppasamy, K., Manikandavelu, D., Uma, A., & Kavipriya, M. (2021). Length–weight relationships of eight elasmobranch species captured along the Coromandel coast of Tamil Nadu, Eastern Indian Ocean. *Journal of Applied Ichthyology*, *37*(3), 487–491.

Koob, T. J., & Callard, I. A. N. P. (1999). Reproductive endocrinology of female elasmobranchs: Lessons from the little skate (*Raja erinacea*) and spiny dogfish (*Squalus acanthias*). *Journal of Experimental Zoology*, *284*, 557–574.

Kousteni, V., & Megalofonou, P. (2020). Reproductive strategy of *Scyliorhinus canicula* (L., 1758): A holistic approach based on macroscopic measurements and microscopic observations of the reproductive organs. *Marine and Freshwater Research*, *71*(6), 596–616.

Krebs, C. J., & Singleton, G. R. (1993). Indices of condition for small mammals. *Australian Journal of Zoology*, *41*(4), 317–323.

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*, 1–26.

Labocha, M. K., Schutz, H., & Hayes, J. P. (2014). Which body condition index is best? *Oikos*, *123*(1), 111–119.

Lambert, Y., & Dutil, J.-D. (1997). Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)? *Canadian Journal of Fisheries and Aquatic Sciences*, *54*, 104–112.

Le Cren, E. D. (1951). The length–weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). *Journal of Animal Ecology*, *20*(2), 201–219.

Lear, K. O., Morgan, D. L., Whitty, J. M., Beatty, S. J., & Gleiss, A. C. (2021). Wet season flood magnitude drives resilience to dry season drought of a euryhaline elasmobranch in a dry-land river. *Science of the Total Environment*, *750*, 142234.

Lechenault, H., Wrisez, F., & Mellinger, J. (1993). Yolk utilization in *Scyliorhinus canicula*, an oviparous dogfish. *Environmental Biology of Fishes*, *38*(1–3), 241–252.

Lenth, R. V. (2022). Emmeans: Estimated marginal means, aka least-squares means. R Package Version 1.7.2. https://CRAN.R-project.org/package=emmeans.

Leurs, G., O'Connell, C. P., Andreotti, S., Rutzen, M., & Vonk Noordegraaf, H. (2015). Risks and advantages of using surface laser photogrammetry on free-ranging marine organisms: a case study on white sharks *Carcharodon carcharias*. *Journal of Fish Biology*, *86*(6), 1713–1728.

Lewis, R., Dawson, S., & Rayment, W. (2021). Size structure of broadnose sevengill sharks (*Notorynchus cepedianus*) in Sawdust Bay, Rakiura/Stewart Island, estimated using underwater stereo-photogrammetry. *New Zealand Journal of Marine and Freshwater Research*, *57*(1), 104–118.

Lyons, K., Carlisle, A. B., & Lowe, C. G. (2017). Influence of ontogeny and environmental exposure on mercury accumulation in muscle and liver of male round stingrays. *Marine Environmental Research*, *130*, 30–37.

Lyons, K., Galloway, A. S., Adams, D. H., Reyier, E. A., Barker, A. M., Portnoy, D. S., & Frazier, B. S. (2020). Maternal provisioning gives young-of-the-year hammerheads a head start in early life. *Marine Biology*, *167*(11), 1–13.

Martin, B. T., Heintz, R., Danner, E. M., Nisbet, R. M., & Dussutour, A. (2017). Integrating lipid storage into general representations of fish energetics. *The Journal of Animal Ecology*, *86*(4), 812–825.

Merly, L., Lange, L., Meÿer, M., Hewitt, A. M., Koen, P., Fischer, C., … Hammerschlag, N. (2019). Blood plasma levels of heavy metals and trace elements in white sharks (*Carcharodon carcharias*) and potential health consequences. *Marine Pollution Bulletin*, *142*(March), 85–92.

Moorhead, S. G., Gallagher, A. J., Merly, L., & Hammerschlag, N. (2021). Variation of body condition and plasma energy substrates with life stage, sex, and season in wild-sampled nurse sharks *Ginglymostoma cirratum*. *Journal of Fish Biology*, *98*(3), 680-693.

Motta, F. S., Caltabellotta, F. P., Namora, R. C., & Gadig, O. B. F. (2014). Length-weight relationships of sharks caught by artisanal fisheries from southeastern Brazil. *Journal of Applied Ichthyology*, *30*(1), 239–240.

Murphy, B. R., Willis, D. W., & Springer, T. A. (1991). The relative weight index in fisheries management: Status and needs. *Fisheries*, *16*(2), 30–38.

Nay, T. J., Longbottom, R. J., Gervais, C. R., Johansen, J. L., Steffensen, J. F., Rummer, J. L., & Hoey, A. S. (2021). Regulate or tolerate: Thermal strategy of a coral reef flat resident, the epaulette shark, *Hemiscyllium ocellatum*. *Journal of Fish Biology*, *98*(3), 723–732.

Pattarapongpan, S., Arnupapboon, S., Ali, A., & Takashi Fritz, M. (2021). Yield per recruit and spawning per recruit of brownbanded bamboo shark, *Chiloscyllium punctatum* in Southeast Asia. *Journal of Fisheries and Environment*, *45*(3), 14–27.

Payne, E. J., & Rufo, K. S. (2012). Husbandry and growth rates of neonate epaulette sharks, *Hemiscyllium Ocellatum* in Captivity. *Zoo Biology*, *31*(6), 718–724.

Peig, J., & Green, A. J. (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. *Oikos*, *118*(12), 1883–1891.

R Core Team. (2022). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing https://www.R-project.org/.

Ritcher, H., Lückstädt, C., Focken, U., & Becker, K. (2000). An improved procedure to assess fish condition on the basis of length-weight relationships. *Archive of Fishery and Marine Research*, *48*(3), 255–264.

Rizzo, E., & Bazzoli, N. (2019). Reproduction and embryogenesis. In B. Baldisserotto, E. Urbinati, & J. Cyrino (Eds.), *Biology and physiology of freshwater neotropical fish* (pp. 287–313). San Diego: Elsevier Science & Technology.

Rohner, C. A., Richardson, A. J., Prebble, C. E. M., Marshall, A. D., Bennett, M. B., Weeks, S. J., … Pierce, S. J. (2015). Laser photogrammetry improves size and demographic estimates for whale sharks. *PeerJ*, *2015*(4), 1–20.

Rossouw, G. J. (1987). Function of the liver and hepatic lipids of the lesser sand shark, *Rhinobatos annulatus* (Müller & Henle). *Comparative Biochemistry and Physiology B: Biochemistry & Molecular Biology*, *86*(4), 785–790.

Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Allegue, H., Teplitsky, C., … Araya-Ajoy, Y. G. (2020). Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods in Ecology and Evolution*, *11*(9), 1141–1152.

Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675.

Schwieterman, G. D., Rummer, J. L., Bouyoucos, I. A., Bushnell, P. G., & Brill, R. W. (2021). A lack of red blood cell swelling in five elasmobranch fishes following air exposure and exhaustive exercise. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, *258*, 110978.

Sen, S., Chakraborty, S. K., Zacharia, P. U., Dash, G., Joe Kizhakudan, S., Bharadiya, S. A., & Gohel, J. K. (2018). Reproductive strategy of spadenose shark, *Scoliodon laticaudus* Muller and Henle, 1839 along northeastern Arabian Sea. *Journal of Applied Ichthyology*, *34*(6), 1304–1313.

Spargo, E., Pratt, O. E., & Daniel, P. M. (1979). Metabolic functions of skeletal muscles of man, mammals, birds and fishes: a review. *Journal of the Royal Society of Medicine*, *72*(12), 921–925.

Stallings, C. D., Coleman, F. C., Koenig, C. C., & Markiewicz, D. A. (2010). Energy allocation in juveniles of a warm-temperate reef fish. *Environmental Biology of Fishes*, *88*(4), 389–398.

Stevenson, R. D., & Woods, W. A. (2006). Condition indices for conservation: New uses for evolving tools. *Integrative and Comparative Biology*, *46*(6), 1169–1190.

Viblanc, V. A., Bize, P., Criscuolo, F., Le Vaillant, M., Saraux, C., Pardonnet, S., … Robin, J.-P. (2012). Body girth as an alternative to body mass for establishing condition indexes in field studies: A validation in the king penguin. *Physiological and Biochemical Zoology*, *85*(5), 533–542.

Weideli, O. C., Bouyoucos, I. A., Papastamatiou, Y. P., Mescam, G., Rummer, J. L., & Planes, S. (2019). Same species, different prerequisites: Investigating body condition and foraging success in young reef sharks between an atoll and an Island system. *Scientific Reports*, *9*(1), 1–11.

Wheeler, C. R., Lang, B. J., Mandelman, J. W., & Rummer, J. L. (2022). The upper thermal limit of epaulette sharks (*Hemiscyllium ocellatum*) is conserved across three life history stages, sex and body size. *Conservation Physiology*, *10*(1), coac074.

Wheeler, C. R., Rummer, J. L., Bailey, B., Lockwood, J., Vance, S., & Mandelman, J. W. (2021). Future thermal regimes for epaulette sharks (*Hemiscyllium ocellatum*): growth and metabolic performance cease to be optimal. *Scientific Reports*, *11*(1), 454.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Wheeler, C. R., Irschick, D. J., Mandelman, J. W., & Rummer, J. L. (2023). Nonlethally assessing elasmobranch ontogenetic shifts in energetics. *Journal of Fish Biology*, 1–12. https://doi.org/10.1111/jfb.15425