Received: 15 March 2018 | Accepted: 20 August 2018
DOI: 10.1111/jfb.13785

JOURNAL OF FISH BIOLOGY fsbi

REGULAR PAPER

An evaluation of body condition and morphometric relationships within southern California juvenile white sharks *Carcharodon carcharias*

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Length, mass and girth relationships are presented for 112 juvenile white sharks (JWS) *Carcharodon carcharias* caught in the Southern California Bight (SCB) nursery area between June 2008 and August 2017. No difference was found between male and female JWS length–mass relationships, but data suggest that JWS in the SCB gain more mass per unit length for the juvenile size classes compared with other *C. carcharias* populations. Condition-factor-to-liver-mass and condition-factor-to-liver-lipid-content relationships revealed that length and mass (*i.e.*, condition factor) can be used as a non-invasive proxy for body condition for juveniles of this species. The parameters estimated in this study are key information for population assessments of juvenile *C. carcharias* in the north-east Pacific Ocean and will contribute to the conservation and management of this IUCN Red List Vulnerable species.

KEYWORDS

body condition, hepato-somatic index, length–mass, morphometrics, southern California, white shark

1 | INTRODUCTION

Species biomass is an important variable used in stock assessments for managers to evaluate the health of target species and draft appropriate management plans. However, obtaining actual mass measurements in the field can be logistically difficult and at times prohibitive. The development of length–mass and length–length conversion factors to estimate biomass from external measurements has overcome this challenge and is especially useful for large-bodied fishes such as sharks. In addition, establishing accurate morphometric relationships allows for the inclusion of individuals with only partial measurements (*i.e.*, only one length reported), thereby increasing sample sizes of population level assessments. Morphometric relationships are especially important for protected species where the type of data that can be collected is limited or difficult to obtain. For example, the White Shark *Carcharodon carcharias* (L. 1758) has a naturally low abundance (Chapple *et al.*, 2011) and is internationally recognized as a species that warrants protection measures because of their vulnerability to overexploitation (Curtis *et al.*, 2014; Dulvy *et al.*, 2008; Fergusson *et al.*, 2009). Much of our knowledge of morphometric relationships comes from fishery-dependent sources (Dicken & Booth, 2013; Lowe *et al.*, 2012; Lyons *et al.*, 2013; Oñate-González *et al.*, 2017); however, as *in situ* measuring devices increase in popularity around the globe (*e.g.*, drones, autonomous underwater vehicles (AUV), remotely operated vehicles (ROV) and baited remote underwater videos (BRUV) outfitted with parallel lasers) (Cimino *et al.*, 2018; Harasti *et al.*, 2017; Kiszka *et al.*, 2016; Rogers *et al.*, 2017), information on length–mass relationships is critical for being able to incorporate these data in a meaningful way for management. For inherently rare species like *C. carcharias*, obtaining information of size from any method can aid in estimations of biomass from a particular area (Cowley & Whitfield, 2002; Friedlander & DeMartini, 2002; Liao *et al.*, 1995).

Another important factor in species management is the successful recruitment of younger age classes (juvenile to subadult) to the adult population. In order for this to occur, juveniles must be able to successfully exploit habitat resources (Heupel *et al.*, 2007). Since we cannot retrospectively know specifically what individuals ate or where they foraged, body condition represents a useful proxy for foraging success (Bolger & Connolly, 1989; Jakob *et al*., 1996), as individuals that are better at obtaining resources may be heavier than comparably sized individuals that are poor feeders. As the liver is the major site of energy storage, particularly for lipids, in elasmobranchs (Del Raye *et al*., 2013; Hussey *et al*., 2009; Springer, 1967; Watson & Dickson, 2001), it follows that the condition of this organ would give insights into the foraging success of young sharks (Hussey *et al*., 2010). Quantifying liver condition can be accomplished by examining the relationship between liver mass and total mass (hepato-somatic index) or measuring hepatic lipid content (Bolger & Connolly, 1989). However, assessing liver condition often requires lethal sampling, which is unsustainable for species of conservation concern. Thus, there is a need to determine if condition indices calculated using length and mass accurately reflect lipid reserves and liver mass in juvenile white sharks (JWS; *C. carcharias* < 300 cm L_{nT}).

Development of these condition conversion factors can then be useful in determining foraging success of nursery habitat of JWS, of which there are relatively few worldwide (Bruce & Bradford, 2012; Casey & Pratt, 1985; Oñate-González *et al*., 2017). Coastal southern California, U.S.A., to Baja California, Mexico, functions as an important nursery habitat for JWS (Klimley, 1985; Oñate-González *et al*., 2017) and has been the focus area of a number of studies examining the movement ecology and fishery interactions of JWS (Lowe *et al*., 2012; Lyons *et al*., 2013; Weng *et al*., 2007, 2012), but fewer studies have investigated morphometric relationships within this population. Most previous morphometric relationships presented for this species come from other aggregation sites around the world (*e.g*., U.S. Atlantic coast, South Africa, Australia); yet, nursery habitat quality and prey availability can vary among regions leading to the condition of neonate sharks being highly location-dependent. For example, Lowe (2002) reported low energetic condition of neonate Scalloped Hammerhead Sharks *Sphyrna lewini* (Griffith & Smith 1834) in Kaneohe Bay, Hawaii, U.S.A. It was ultimately hypothesized that a substantial proportion of animals in this population die from starvation (Lowe, 2002). Additionally, Duncan and Holland (2006) demonstrated that mass and body condition of young-of-the-year (YOY) *S. lewini* declined during their first summer in the same nursery. In contrast, Adams and Paperno (2007) used stomach content analysis to show that neonate *S. lewini* off the Atlantic coast of Florida are sufficiently able to feed and Castro (1993) notes an abundance of potential prey items (*e.g*., menhaden *Brevoortia tyrannus* [Latrobe 1802], shrimp *Farfantepenaeus aztecus* and *Litopenaeus setiferus*) during peak pupping season in Bulls Bay, South Carolina where newborn *S. lewini* are abundant. Consequently, determining how the morphometric relationships from the current population of JWS in southern California compare to other populations and previous estimates may provide insights into the suitability of southern California nursery grounds.

In the present study, length, mass and lipid data were used to identify morphometric conversion factors that are useful for future stock assessments of JWS caught in the Southern California Bight (SCB). The availability of individuals for necropsy allowed for relationships such as hepato-somatic index, liver lipid to length, liver mass and liver lipids to condition factors to be obtained. Such relationships can be used to assess individual health and ultimately the relative health of a population using only external measurements. Lastly, we compared the length–mass relationship of JWS in the SCB to *C. carcharias* from other regions of the world in an attempt to assess quality of the SCB nursery habitat.

2 | MATERIALS AND METHODS

All capture and handling techniques of JWS were reviewed and approved by California Department of Fish and Wildlife (permit # 3450) and California State University Long Beach Institutional Animal Care and Use Committee (IACUC) protocol # 319.

Carcharodon carcharias were collected from Goleta (34° 24′N, 119° 50′W) to Oceanside (33° 12′N, 117° 23′W), California from June 2008 to August 2017 using a variety of capture techniques, but most were the result of by-catch from local White Seabass *Atractoscion nobilis* (Ayres 1860) and California Halibut *Paralichthys californicus* (Ayres 1859) gillnet fisheries in southern California (n = 91, 81.2%). Other methods included research directed fishing using a purse seine or gillnet (n = 16, 14.3%) and hook and line (n = 5, 4.5%). Sharks that were captured alive were measured, weighed and released, while sharks that were dead at landing were measured and weighed at time of necropsy. Individuals were measured to the nearest cm (natural total length (L_{nT}), fork length (L_F), precaudal length (L_{PC}), girth (G)) and kg (total mass, M_T) when a scale was available. For a portion of necropsied sharks, liver mass (M_H, kg) was measured and liver lipid content (% wet mass) was determined by extracting lipids via Soxhlet extraction and obtaining dried lipid mass (M_{DL}) gravimetrically. Precaudal length and L_F were measured as the straight-line length from the tip of the snout to the dorsal notch in the caudal peduncle or fork of the tail, respectively. Natural total length was defined as the straight-line length from the tip of the snout to a point on the horizontal axis intersecting a perpendicular line extending from the tip of the upper caudal lobe (Kohler *et al*., 1996). Girth was measured as the circumference of the animal anterior to the dorsal fin and just behind the insertion of the pectoral fins (Supporting Information in Figure S1).

All statistical analyses were conducted in R Studio 1.0.136 (RStudio Team, 2015). Allometric length–mass and girth–mass relationships were determined using the $\log y = \log a + b \log x$ formula, which allowed for parameter calculation from linear regression and presented as: $M_T = aL^b$, where M_T is total mass (kg) and L is length (cm; L_{nT}, L_F or L_{PC} depending on relationship being examined). Similar calculations were performed for girth measurements, where G replaced L in specified calculations (Table 1). The 95% C.I. were also calculated for parameters a and b from the log–log transformed regressions. We assumed that when the slope of the regression [b] was equal to 3, the relationship was considered to be isometric and where $b \neq 3$, allometric (Froese, 2006). A Student's t-test was used to determine if b values were significantly different from the null hypothesis for isometric growth (H_0: b = 3; Ortega-Garcia *et al*., 2017; Zar, 2010). To determine if morphometric relationships differed between juvenile males and females, an analysis-of-covariance (ANCOVA) was used to test whether mass gain with increasing length differed by sex (α = 0.05). Length–length and girth–length relationships were calculated by simple linear-regression models. Individual body condition

TABLE 1 Summary of morphometric relationship parameters for juvenile *Carcharodon carcharias* caught in the Southern California Bight

		Regression coefficients		95% C.I.		
Relationship	*n*	*a*	*b*	*a*	*b*	r^2
$M_T = a\,L_F^{\,b}$	88	3.56×10^{-6}	3.25	$1.37–9.19 \times 10^{-6}$	3.06, 3.44	0.96
$M_T = a\,L_{nT}^{\,b}$	88	3.85×10^{-6}	3.18	$0.13–1.11 \times 10^{-5}$	2.97, 3.39	0.95
$M_T = a\,L_{PC}^{\,b}$	77	$5.95 \times 10–^{6}$	3.22	$0.20–1.76 \times 10^{-5}$	3.0, 3.45	0.96
$M_T = a\,G^b$	87	9.35×10^{-4}	2.43	$0.47–1.85 \times 10^{-3}$	2.27, 2.58	0.95
$M_H = a\,G^b$	20	2.84×10^{-5}	2.75	$0.03–2.63 \times 10^{-4}$	2.24, 3.25	0.95
$L_F = a + b\,L_{nT}$	112	1.79	0.9	−2.89, 6.47	0.87, 0.93	0.97
$L_F = a + b\,L_{PC}$	87	−0.16	1.12	−4.43, 4.11	1.09, 1.16	0.98
$L_{PC} = a + b\,L_{nT}$	89	1.79	0.8	−3.91, 7.51	0.76, 0.84	0.96
$G = a + b\,L_{nT}$	106	−14.09	0.59	−-21.4, −6.81	0.55, 0.64	0.86
$G = a + b\,L_F$	103	−14.76	0.66	−21.9, −7.61	0.6, 0.7	0.87
$G = a + b\,L_{PC}$	82	−16.62	0.74	−24.7, −8.56	0.68, 0.81	0.88

Relationships are presented for fork length (L_F), natural total length (L_{nT}), precaudal length (L_{PC}), total mass (M_T), girth (G), and liver mass (M_H). Length and mass were measured in cm and kg, respectively.

was evaluated using Fulton's condition factor $K = 10^5 M_T(L_F^{\,3})^{-1}$ (Fulton, 1904) and hepato-somatic index (I_H) was calculated as $I_H = M_H M_T^{\,-1}$, where M_T is total mass, L_F is fork length and M_H is total liver mass per individual shark. Lipid content and M_H were linearly regressed with the K to determine if field obtained estimates of K could be related to M_H and lipid content and therefore the energy reserves of an individual. Because of the large range of values (0.9–26.5 kg) and skewed distribution, liver mass was log(x + 1) transformed. To determine if SCB juvenile *C. carcharias* followed a similar pattern to other juvenile elasmobranchs where liver mass and lipid content decrease in the first few months of life (Francis, 1996; Hussey *et al*., 2010; Oñate-González *et al*., 2017), liver mass and lipid content were regressed against L_F for YOY sharks (< 160 cm L_F).

Finally, the L_F–M_T relationship determined in this study was compared with *C. carcharias* from other geographic regions (U.S. Atlantic coast, South Africa and Worldwide, which included measurements from Australia, U.S. Atlantic coast, Cuba, Azores and U.S. Pacific coast) to compare relative condition (Cliff *et al*., 1989; Kohler *et al*., 1996; Mollet & Cailliet, 1996). Length–mass relationships reported in L_T or L_{PC} were converted to L_F using the relationships presented in the respective paper. As we did not have access to the observation data used in these studies, we were unable to use an ANCOVA to test for differences due to slope and simply comparing the slopes of the lines ignores the variability and uncertainty present in the other studies. To overcome this, we simulated data from other studies using information on their regression coefficients (a, b), sample size (n), coefficient of determination (r^2) and length distribution. Length distributions were estimated differently depending on available data presented in each study, which used 5 cm length classes (Cliff *et al*., 1989), size classes (110–200, 200–325, 425–460 cm; Kohler *et al*., 1996), or size ranges (125–400 cm; Mollet & Cailliet, 1996). Within each of these classes, individuals were assumed to be uniformly distributed and were randomly sampled to generate possible datasets. Mass for individuals were assumed to be normally distributed around their regression line with an error related to their r^2. We were then able to generate length and mass estimates according to their regression coefficients and r^2 and the associated 95% C.I. An iterative process was used (1,000 iterations) to account for possible variability between runs by random sampling. From these 1,000 iterations, we were then able to evaluate if the 95% C.I. between our regression and the simulated regressions overlapped and if so, to what extent. If they did not overlap, the mass at length was determined to be significantly different. To ensure there was not a systematic bias for simulated *v.* observed data, we simulated our own data using the same method and compared the simulated results to our observed data.

3 | RESULTS

As not all sampled sharks were weighed and measured in the same manner, 88 JWS were used to determine length–mass relationships, 87 for girth–mass relationships, 112 for length–length and 103 for girth–length relationships (Figure 1 and Table 1). The male–female ratio was evenly split between the sexes (0.9:1). Sex did not have a significant effect on the slope or y-intercept of the log transformed length–mass relationship ($P > 0.05$; Table 2), so sexes were combined in all analyses. Positive allometric growth was found for all length–total mass relationships (L_{PC}, L_F and L_{nT}; $H_0 > 3$; t-test, $P < 0.05$) and negative allometric growth for the girth–total mass relationship ($H_0 < 3$; $T_{85} = -7.3$, $P < 0.001$). However, the girth–liver mass regression slope was not significantly different from the predicted slope of 3, suggesting isometric growth of the liver ($T_{18} = -1.04$, $P > 0.05$), but the large 95% C.I. (2.24–3.25) suggest caution with this interpretation (Figure 1). In addition, all length–length and girth–length relationships exhibited strong linear relationships (all $r^2 > 0.86$, $P < 0.001$). Parameters for these relationships are reported in Table 1 and condition information for male and female sharks is reported in Table 2.

To determine if YOY *C. carcharias* (those < 160 cm L_F) were losing liver mass or lipid content soon after birth, the relationship of L_F–M_H and lipid content were investigated; however, no relationship was found for liver M_H ($P > 0.05$) or lipid content with L_F ($P > 0.05$; Figure 2). For all sharks with available data, a significant positive relationship was found between the logM_H and K ($F_{1,19} = 8.3$, $P < 0.01$,

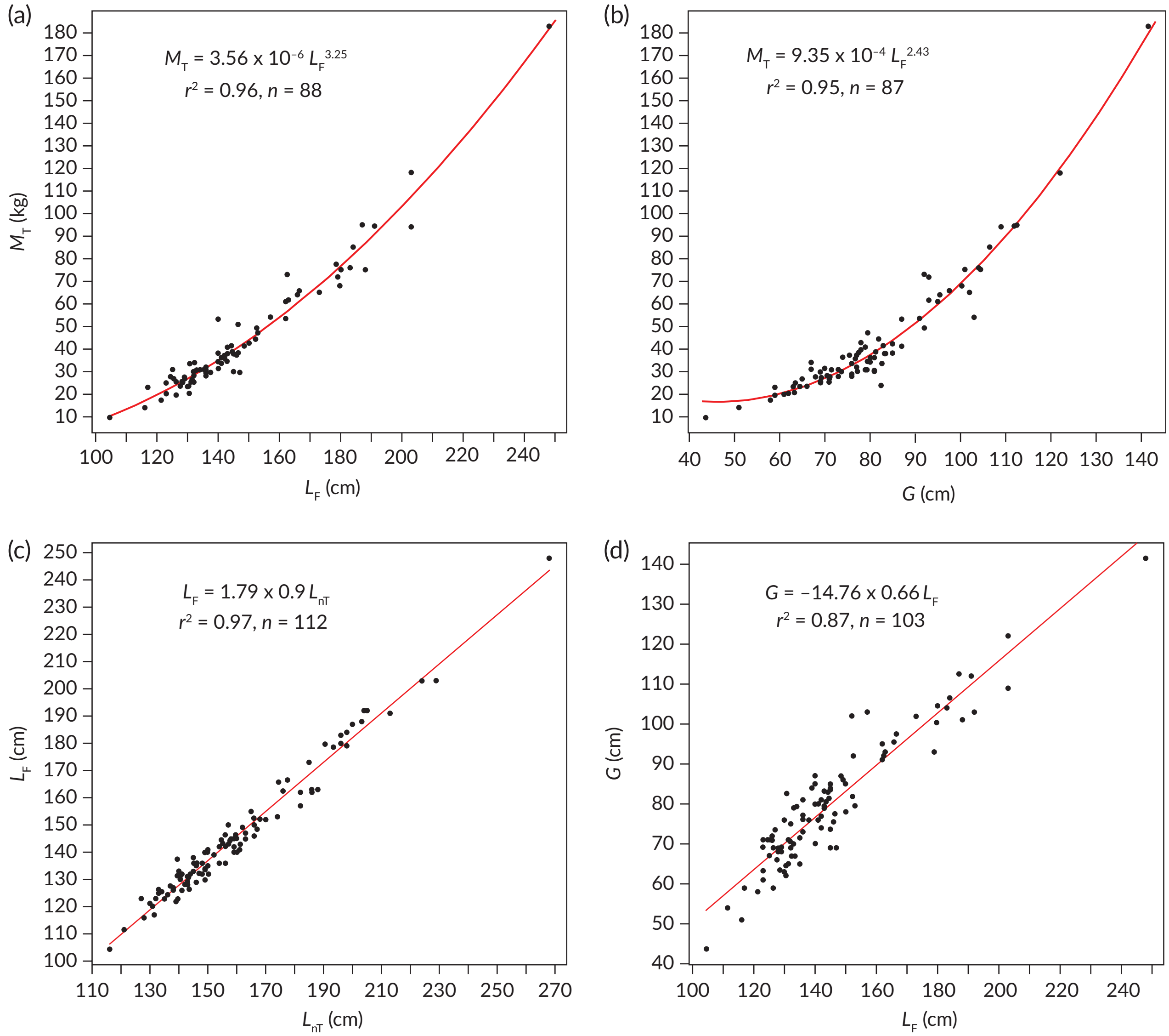

FIGURE 1 Relationships (a) total mass (M_T) *v.* fork length (L_F), (b) M_T *v.* girth (*G*), (c) L_F *v.* natural total length (L_{nT}) and (d) *G v.* L_F for juvenile *Carcharodon carcharias* caught in the Southern California Bight

$r^2 = 0.27$; Figure 3a). There was an increasing, albeit insignificant ($P > 0.05$), trend in the lipid content and condition factor relationship. This relationship became stronger and statistically significant when one outlier with unusually low liver lipid content (25.5%) was removed from analysis ($F_{1,19} = 8.02$, $P < 0.01$, $r^2 = 0.29$; Figure 3b).

When compared with JWS from other populations, SCB JWS had significantly greater relative mass for their size (Figure 4). This observation did not become apparent until the sharks reached *c.* 130–170 cm L_F (roughly 1+ years old), at which point the confidence intervals of observed and predicted data presented here no longer

TABLE 2 Condition indices (mean ± s.d., range in parentheses) of juvenile *Carcharodon carcharias* caught in the Southern California Bight

Sex	L_F (cm)	G (cm)	M_T (kg)	M_H (kg)	I_H	K
Male	144.9 ± 20 (120.2–203) *n* = 54	79.5 ± 14.2 (58–112) *n* = 51	40.6 ± 20.6 (17.4–94.4) *n* = 42	6.2 ± 2.8 (2.2–10.1) *n* = 10	0.13 ± 0.02 (0.11–0.17) *n* = 10	1.22 ± 0.14 (0.92–1.58) *n* = 42
Female	144.7 ± 24.5 (104.5–248) *n* = 57	79.4 ± 16.6 (43.7–141.5) *n* = 54	43.4 ± 28.4 (9.7–182.9) *n* = 46	6.9 ± 7.0 (0.9–26.5) *n* = 11	0.12 ± 0.03 (0.07–0.16) *n* = 11	1.29 ± 0.19 (0.85–1.94) *n* = 46
Total	144.6 ± 22.3 (104.5–248) *n* = 111	79.4 ± 15.3 (43.7–141.5) *n* = 105	42.1 ± 24.9 (9.7–182.9) *n* = 88	6.6 ± 5.3 (0.9–26.5) *n* = 21	0.13 ± 0.03 (0.07–0.17) *n* = 21	1.26 ± 0.17 (0.85–1.94) *n* = 88

L_F, Fork length; G, girth; M_T, total mass; M_H, liver mass; I_H, hepato-somatic index; *K*, Fulton's condition factor.

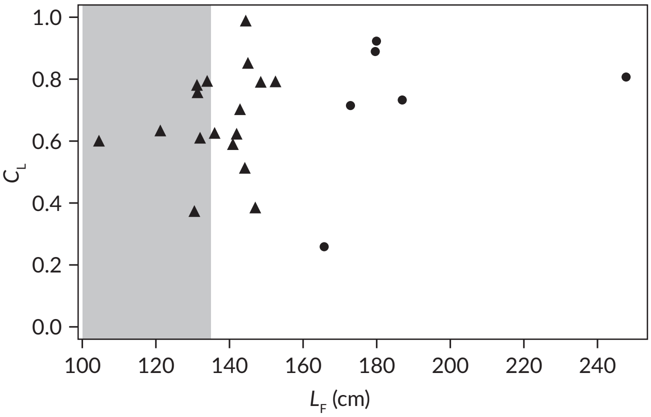

FIGURE 2 Liver lipid concentration–fork length (L_F) relationship for juvenile *Carcharodon carcharias* caught in the Southern California Bight. ▲, Young-of-the-year (YOY) sharks, *i.e.*, < 160 cm L_F; and ●, sharks older than 1 year; ▢, the range of sizes at birth (Francis, 1996)

overlapped with confidence intervals predicted from previous studies (Figure 4 and Supporting Information Figure S2).

4 | DISCUSSION

The information gained from this study will be important for future evaluations of JWS in the SCB and increases our understanding of the relationships between length, mass, girth and condition in *C. carcharias*, which to our knowledge, have yet to be evaluated in any population. The opportunity to necropsy a significant number of individuals of a state and federally protected species allowed determination of morphometric relationships applicable for future estimations of animal or population health via non-lethal measurements. For example, liver mass and lipid content were positively correlated with higher condition factors, indicating that condition factor may provide a strong metric of body condition for live-caught JWS. This finding has the potential for immediate use in assessing habitat quality or food availability in nursery habitat for management and conservation purposes if length and mass can be obtained in the field.

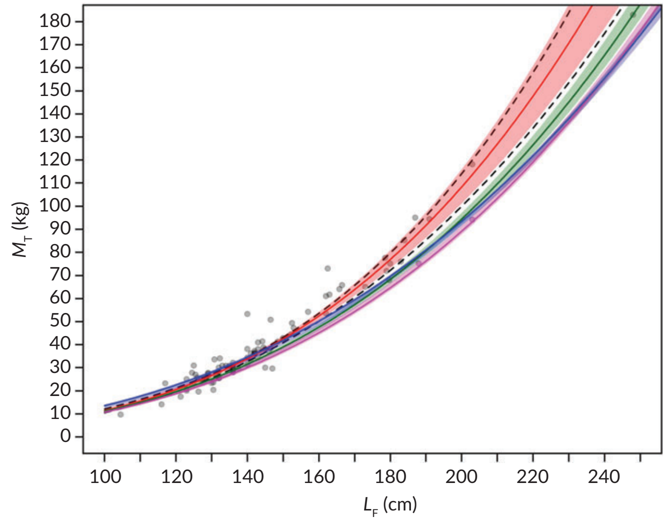

FIGURE 4 Fork length (L_F) to total mass (M_T) relationships among the current study and previously published studies of *Carcharodon carcharias*. The solid lines represent lines of best fit to the observed or simulated data and shaded regions indicate 95% C.I. from 1,000 iterations. Dashed lines indicate the edges of the southern California simulated data C.I. to distinguish them from the observed southern California data C.I. (in red). ●, Measurements of juvenile *C. carcharias* taken in the Southern California Bight ■ Southern California (present study), ⬚ Southern California simulated, ■ US East Coast Kohler *et al.* (1996), ■ South Africa, Cliff *et al.* (1989) and ■ Worldwide, Mollet and Cailliet (1996)

As with Cliff *et al.* (1989), there was no significant difference between males and females for the length–mass relationship for the size classes examined. While it is typical for females to reach a greater maximum length and mass than males for many species of shark, this pattern is most often observed when individuals approach sexual maturity and is less evident during early life stages (Hoenig and Gruber, 1990). The absence of animals > 268 cm L_{nT} in this study prevents the extrapolation of the length–mass curve presented here to subadult and adult *C. carcharias* in the north-east Pacific Ocean. However, these data suggest that JWS in the Southern California Bight (SCB) obtain a greater mass per unit length than other populations globally. These differences could be due in part to previous studies

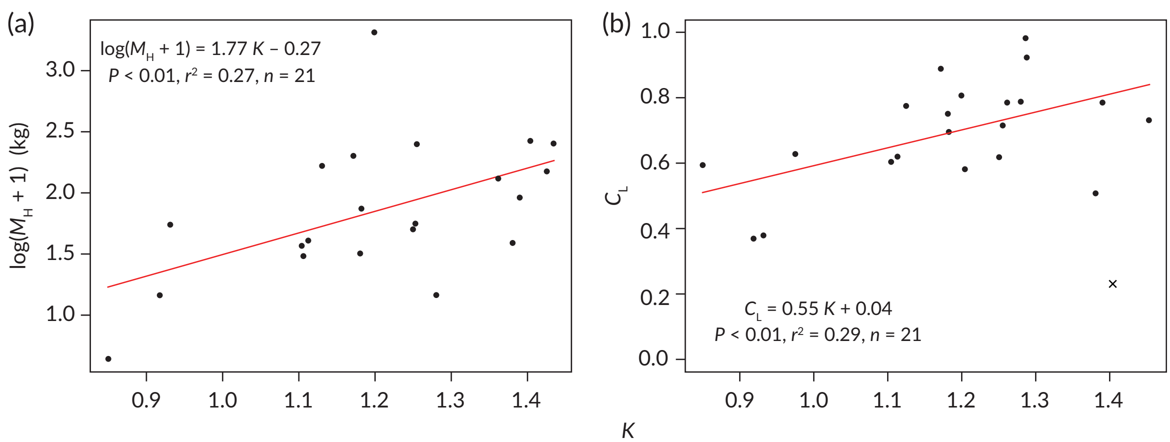

FIGURE 3 Relationship of (a) liver mass (M_H) and (b) lipid content (C_L) *v.* Fulton's condition factor (K) for juvenile *Carcharodon carcharias* caught in the Southern California Bight. (Regression statistics in (b) omit an outlier shown as "×" in lower right corner of the plot)

including larger size classes of sharks with slower growth rates, potentially biasing the curve at small sizes. For instance, analyses in Cliff *et al*. (1989), Kohler *et al*. (1996) and Mollet & Cailliet (1996) included sharks with a maximum L_{nT} 92, 58 and 108% longer, respectively, than the largest shark analysed in this study. However, all studies also included YOY and juvenile sharks where the majority of analyzed sharks were < 3 m, providing a strong fit for this size class (refer to Kohler *et al*. (1996), Cliff *et al*. (1989) and Mollet & Cailliet 245 (1996)).

Greater mass per unit length would imply that *C. carcharias* in this study had greater condition factors than other populations, suggesting that females may be better provisioning the embryos, the SCB nursery habitat provides more abundant and profitable prey, or environmental conditions in the SCB provide for optimal foraging and growth (Allen *et al*., 2007; Pondella & Allen, 2008). However, the lack of differentiation in length–mass curves for YOY *C. carcharias* suggests that mothers contributing to the north-east Pacific population do not necessarily provision more to their embryos than mothers from other areas, as it is only after the sharks have grown to 1+ years old that the difference in mass between populations becomes apparent (Figure 4). This suggests that environmental conditions and enough food resources in the SCB may be driving this pattern rather than pups being better provisioned at birth. There is evidence of high prey abundance in the SCB which may provide ample food resources, as known JWS prey such as round stingray *Urobatis helleri* (Cooper 1863), bat ray *Myliobatis californica* Gill 1865 and other groundfishes occur in high densities along the southern California coast in areas where JWS frequent (Lowe *et al*., 2007; C. Lowe, personal communication, 2018). While data on stomach contents were not collected at the time of necropsy, anecdotal evidence suggests stomachs often contained prey at various states of digestion, indicating recent successful foraging events (R. Logan, personal observation, 2017).

Abundant prey could also help explain why there was not a decline in YOY *C. carcharias* liver mass or lipid content after birth as in other shark species (Hussey *et al*., 2010). However, the high variability in the liver lipids seen here could also be related to the variability in the size (105–160 cm L_F, this study; Francis, 1996) and time of birth (June–September; Francis, 1996; Klimley, 1985). Thus, given the low sample size of YOY sharks for which liver and lipid measurements were obtained (n = 16), there may not have been enough power to detect a pattern of decreasing liver size or lipids after birth. In addition, the isometric relationship and wide confidence intervals observed between liver mass and girth highlights the plasticity of this organ relative to other static measurements such as length. Since elasmobranchs heavily rely on the liver, its condition is expected to change between periods of low to high resource abundance (Baldridge, 1972). Thus, the apparent lack of a consistent positive allometric relationship between liver mass and girth is not surprising.

Carcharodon carcharias is one of the largest, most widely distributed apex predators in the world. Like other *k*-selected species, they are dependent on the high survival rates of young sharks to ensure recruits to the adult population. Results herein suggest that condition factor from external measurements can be indicative of liver mass and lipid reserves of this species and that JWS in southern California obtain greater mass per unit length than JWS in other areas of the world. Accelerated mass gain in this population has the potential to increase individual fitness and possibly to reduce juvenile natural mortality of this IUCN Red List Vulnerable species (Fergusson *et al*., 2009). As Heithaus (2007) points out, predation risk and food availability are the major factors that influence juvenile shark habitat selection. As oceanic temperatures are predicted to increase due to climate change and coastal anthropogenic modification is only predicted to intensify (Heithaus, 2007), the morphometric relationships presented here can serve as a baseline to compare future catch records of JWS in the SCB and around the world, as coastal nursery habitats may decline in productivity, or be shifted into less profitable habitats (Perry *et al*., 2005).

ACKNOWLEDGEMENTS

The authors thank all the current and previous members of the Juvenile White Shark (JWS) Rapid Response Team of the California State University Long Beach (CSULB) Shark Labratory for various measurements of live caught-and-released and necropsied JWS: M. Blasius, K. Loke-Smith, H. Zemel, C. Mull, C. Mireles, K. Anthony, T. Mason, E. Jarvis-Mason, L. Hale, K. Jirik, C. Martin, T. Farrugia, M. Espinoza, B. Rogers, C. Espasandin, M. McKinzie, T. TinHan, B. Wolfe, M. Farris, R. Freedman, D. Frantz, B. Ahr, D. Crear, G. Teesdale, J. Sawyna, A. Barilotti, S. Luongo, E. Burns, E. Meese, C. McGarigal and A. Clevenstine. We also gratefully acknowledge all the fishermen who have called our team after incidentally capturing a shark, this work could not have been done without their assistance. This work was supported by the Monterey Bay Aquarium and California State University Long Beach.

Contributions

R. K. L. and C. G. L. conceived the ideas and designed methodology, R. K. L., C. F. W., K. L., C. W., S. J. J., J. B. O. and C. G. L collected the data, R. K. L. and C. F. W. analysed and interpreted the data, R. K. L. and K. L. wrote the manuscript, R. K. L. prepared the manuscript for submission and C. G. L., C. W., S. J. J. and J. B. O. secured the funding to support the work.

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SUPPORTING INFORMATION

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

How to cite this article: Logan RK, White CF, Winkler C, et al. An evaluation of body condition and morphometric relationships within southern California juvenile white sharks *Carcharodon carcharias*. *J Fish Biol*. 2018;93:842–849. https://doi.org/10.1111/jfb.13785