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A new metric for measuring condition in large predatory sharks

D. J. Irschick* † ‡ and N. Hammerschlag§||

**Department of Biology, 221 Morrill Science Center, University of Massachusetts at Amherst, Amherst, MA, 01003, U.S.A., †Organismic and Evolutionary Biology Program, University of Massachusetts Amherst, Amherst, MA, 01003, U.S.A., §Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149-1098, U.S.A. and ||Leonard and Jayne Abess Center for Ecosystem Science and Policy, University of Miami, Coral Gables, FL 33146, U.S.A.*

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A simple metric (span condition analysis; SCA) is presented for quantifying the condition of sharks based on four measurements of body girth relative to body length. Data on 104 live sharks from four species that vary in body form, behaviour and habitat use (*Carcharhinus leucas*, *Carcharhinus limbatus*, *Ginglymostoma cirratum* and *Galeocerdo cuvier*) are given. Condition shows similar levels of variability among individuals within each species. *Carcharhinus leucas* showed a positive relationship between condition and body size, whereas the other three species showed no relationship. There was little evidence for strong differences in condition between males and females, although more male sharks are needed for some species (*e.g. G. cuvier*) to verify this finding. SCA is potentially viable for other large marine or terrestrial animals that are captured live and then released.

Key words: body mass; body shape; ecomorphology; elasmobranch; girth; morphometrics.

INTRODUCTION

Evaluating the health or vigour of animals is important for assessing their ability to migrate, feed, reproduce and ultimately survive in a given habitat (Krebs & Singleton, 1993; Jakob *et al.*, 1996; Weatherhead & Brown, 1996; Green, 2001; Schulte-Hostedde *et al.*, 2001; Bearhop *et al.*, 2004; Goymann *et al.*, 2010). Such measures are important for the broader field of ecology and evolutionary biology, and also for conservation (Lehnen & Krementz, 2007). Condition is typically viewed as an index of overall health, and is usually defined as body mass relative to body length (Jakob *et al.*, 1996). Definitions of condition vary greatly among study species (Jakob *et al.*, 1996; Green, 2001; Ardia, 2005), but some common definitions include ratios of mass and length (or some variant), or residuals of a mass measurement *v.* a metric of length (*e.g.* limb length and body length). Several reviews (Jakob *et al.*, 1996; Green, 2001) have discussed pitfalls of different metrics, which include co-linearity with size, lack of connection to the biology of the animal and undesirable statistical properties. In the context of conservation, establishing a metric of condition for

‡Author to whom correspondence should be addressed. Tel.: +1 413 545 1696; email: irschick@bio.umass.edu

threatened species is particularly important for predicting how they will respond to natural (*e.g.* predator–prey dynamics) or anthropogenic changes (*e.g.* climate change) and implementing effective conservation management strategies (Stevenson & Woods, 2006; Rode *et al.*, 2012; Hart *et al.*, 2013).

One group of animals for which there is a need to define and measure condition is sharks, especially apex predator sharks (Hussey *et al.*, 2009), many of which are undergoing dramatic population declines globally due to overexploitation (Dulvy *et al.* 2008; Worm *et al.*, 2013). Hussey *et al.* (2009) performed a thorough analysis of body condition in a large sample of dead dusky sharks *Carcharhinus obscurus* (Lesueur 1818), but those metrics included values of liver mass and body mass, which are limiting for large, live or rare sharks that cannot be weighed or sacrificed (Hammerschlag & Sulikowski, 2011). Thus, there is a need for a condition metric for large sharks that cannot be easily or safely weighed or sacrificed. Quantifying the condition of larger sharks is ecologically relevant because they often move long distances during migration (Boustany *et al.*, 2002; Goldman & Block, 2005; Hammerschlag *et al.*, 2012*a*; Del Raye *et al.*, 2013), and long-distance migrations are often energetically expensive in animals (Tucker, 1971; Klaassen, 1996). Tiger sharks *Galeocerdo cuvier* (Péron & Lesueur 1822) are known to travel long distances (>3000 km) from the Caribbean to the middle of the Atlantic Ocean and back, often in deep and cold waters (Hammerschlag *et al.*, 2012*a*). Other sharks such as whale sharks *Rhincodon typus* Smith 1828 also undertake deep dives exceeding 1 km (Rowat *et al.*, 2007; Brunnschweiler *et al.*, 2009). Finally, a recent study examined the relationship between estimated fuel reserves and migration in white sharks *Carcharodon carcharias* (L. 1758) (Del Raye *et al.*, 2013), and suggested that lipid reserves might affect how these sharks dive in deeper waters. These studies show why it is useful and valuable to study condition in sharks, given how many species undergo extensive migrations. Even for sharks that do not migrate long distances [*e.g.* nurse sharks *Ginglymostoma cirratum* (Bonnaterre 1788)], variation in condition among individuals may translate into variation in reproductive, feeding and predator avoidance opportunities.

Ideally, a measurement of total circumference would be the most accurate measure of girth, but for large sharks that are often captured and released by researchers in vessels on the open ocean, obtaining such measurements is challenging. In most cases, captured sharks are either restrained within the water alongside the boat or secured to a platform for processing. In these situations, accessing the ventral side of the shark for measurements is restrictive, if not impossible. Here, a new metric (termed span condition analysis; SCA) is presented for measuring the condition in the field for sharks. Condition data are provided for four different species of shark that differ greatly in life-history, mode of feeding and movement patterns: G. *cuvier*, bull shark *Carcharhinus leucas* (Müller & Henle 1839), blacktip shark *Carcharhinus limbatus* (Müller & Henle 1839) and *G. cirratum*. This metric of condition can be easily and rapidly used in the field (or laboratory) for a wide range of shark species, even large apex predator sharks (*e.g. C. carcharias* and *G. cuvier*).

MATERIALS AND METHODS

Sampling was done throughout the middle Florida Keys (U.S.A.), at Biscayne Bay, Florida Bay and the reefs off Islamorada, FL, U.S.A. Additional sampling was conducted off Grand

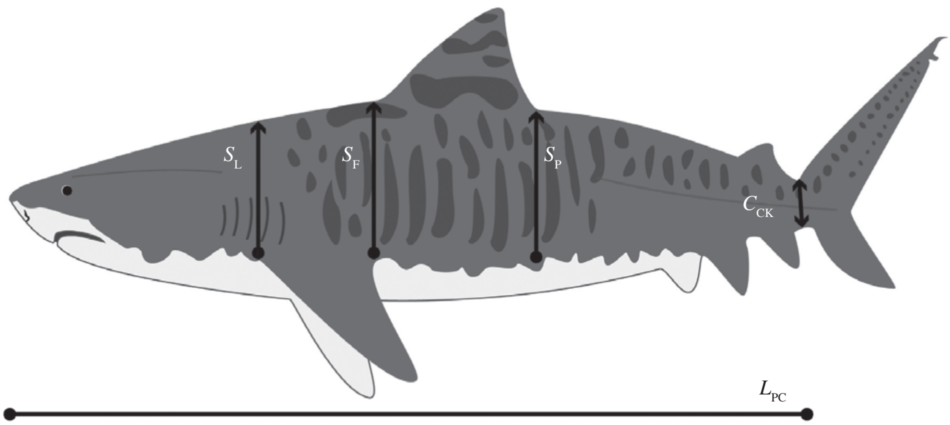

FIG. 1. A drawing of a typical *Galeocerdo cuvier* with the morphological variables measured in this study depicted. Note that all four variables shown (S_L = lateral span, S_F = frontal span, S_P = proximal span and C_{CK} = caudal keel circumference) along the body of the shark were measured across the body. L_{PC} = pre-caudal length.

Bahama, Bahamas. Sampling took place from July 2012 to October 2013, with samples obtained for most months throughout that period. Sharks were captured using standardized circle-hook drumlines following Hammerschlag *et al.* (2012*b*) and Gallagher *et al.* (2014a). Briefly, drumlines were composed of a weighted base that sits on the seafloor. Attached to the weight was a 23 m monofilament line (400 kg test) that terminated in a baited 16/0 offset circle hook. The gear was left for an hour before retrieval. When a shark was captured, it was restrained in the water alongside the back of the boat or secured to a partially submerged platform. A hose was then placed in the shark's mouth to pump fresh seawater over its gills to enable the shark to breathe, as even partial submersion in water will not enable full gill ventilation required by the sharks studied.

To calculate an index of condition that encompassed the body of the shark, several measurements were collected of body dimensions along the shark's dorsal surface. Accordingly, once the shark was secured, the following girth data were obtained (Fig. 1): (1) pre-caudal length (L_{PC}), the linear distance from the tip of the snout to the insertion of the caudal fin into the body, (2) lateral span (S_L), the distance spanning (*i.e.* around the curved dorsal surface of the shark) from the insertion point of the anterior edge of one pectoral fin to the same point on the other pectoral fin, (3) frontal span (S_F), the distance spanning (*i.e.* around the curved dorsal surface of the shark) from the insertion point of the anterior edge of the dorsal fin to a line oriented parallel to the horizontal plane of the pectoral fin, (4) proximal span (S_P), the distance spanning (*i.e.* around the curved dorsal surface of the shark) from the insertion point of the posterior edge of the dorsal fin to a line oriented parallel to the horizontal plane of the pectoral fin and (5) caudal keel circumference (C_{CK}), total circumference at the base of the tail as measured at the caudal keel. Condition, here referred to as span condition analysis (A_{SC}) was defined as: $A_{SC} = (S_L \pm S_F \pm S_P \pm C_{CK})\ L_{PC}^{-1}$. These variables were chosen because the aim was a holistic measure of the unique tapered shape of sharks which tends to be broader in the head and near the dorsal fin, and then tapers to the tail. Given that overall body volume and girth are likely to be reflected along the body axis, measures ranging from in front of the pectoral fin to the caudal keel were opted for. All measurements were taken with a tape measure in cm, and were accurate to one decimal place. After processing, sharks were released, usually within several minutes of capture.

To examine variation among the different measurements obtained, the standard deviation, variance and coefficient of variation (C.V.) for S_L, S_F, S_P, C_{CK} and L_{PC} were calculated. Linear least-squares regression was performed to evaluate the potential relationships between A_{SC} and L_{PC}. *t*-tests were used to compare males and females in species where sample sizes were

TABLE I. Descriptive statistics for morphological measurements for four shark species. Values are mean ± S.E., with ranges in parentheses

	Carcharhinus leucas $n = 14$	Carcharhinus limbatus $n = 11$	Ginglymostoma cirratum $n = 46$	Galeocerdo cuvier $n = 33$
L_{PC} (cm)	162·7 ± 7·1 (130–196)	118·6 ± 5·2 (79–140)	165·2 ± 2·2 (133–190)	220·5 ± 1·6 (113–303)
Lateral span (cm)	67·9 ± 3·7 (52·0–89·0)	44·2 ± 2·4 (24·0–53·0)	57·7 ± 1·1 (42·0–71·5)	72·4 ± 2·9 (38·0–97·0)
Frontal span (cm)	75·6 ± 4·6 (52·0–104·0)	48·0 ± 2·4 (29·5–59·0)	61·6 ± 1·5 (39·5–81·0)	77·1 ± 3·5 (34·5–111·0)
Proximal span (cm)	61·7 ± 4·0 (45·0–91·5)	41·8 ± 2·0 (31·0–52·0)	36·7 ± 0·9 (20·0–47·5)	69·5 ± 3·4 (31·5–111·0)
C_{CK} (cm)	27·9 ± 1·2 (22·0–35·0)	20·6 ± 0·9 (14·5–26·0)	27·9 ± 0·6 (12·0–42·0)	31·8 ± 1·2 (19·0–46·0)

n, number of individuals sampled; L_{PC}, pre-caudal length; C_{CK}, caudal keel circumference.

sufficient, and ANOVA to compare A_{SC} values among different species with species being the categorical variable. All measurements were ln-transformed and significance was set at $P < 0·05$.

RESULTS

Totals of 46 *G. cirratum* (16 females, 30 males), 14 *C. leucas* (12 females, two males), 33 *G. cuvier* (31 females, two males) and 11 *C. limbatus* (10 females, one male) were captured ($n = 104$ sharks, see Table I for descriptive statistics). For each shark species, a range of sizes were captured (Table I). Table II provides descriptive statistics for values of condition in each of the four shark species. Condition showed a generally normal distribution for each species (Fig. 2). In general, values of condition were largest for *C. leucas* (mean ± S.E. = 2·24 ± 0·03) and lowest for *G. cuvier* (mean ± S.E. = 1·14 ± 0·01). *Carcharhinus limbatus* and *G. cirratum* were intermediate between these extremes (Table II). Condition differed significantly among the four species ($F_{3,100} = 478·2$, $P < 0·001$).

Variability within each species, whether defined by the variance, the C.V. or the S.D., was similar among the four species (Table II). For three of the four species, condition showed no significant relationship with body size (*G. cuvier*: $F_{1,30} = 0·33$, $r^2 = 0·01$, $P > 0·05$; *C. limbatus*: $F_{1,9} = 0·14$, $r^2 = 0·01$, $P > 0·05$; *G. cirratum*: $F_{1,44} = 0·03$, $r^2 = 0·001$, $P > 0·05$) (Fig. 3). By contrast, in *C. leucas*, there was a significant and positive relationship between the two variables ($F_{1,12} = 11·64$, $r^2 = 0·45$, $P < 0·01$) (Fig. 3).

For all four species, females were more abundant than males: *G. cuvier* 88%, *C. leucas* 86%, *C. limbatus* 92% and *G. cirratum* 65%. Small samples prevented a statistical test for differences between males and females in the first three species, but in general, the few male sharks had somewhat lower values of condition compared to females (*G. cuvier*, females = 1·15, males = 1·08; *C. leucas*, females = 2·25, males = 2·13; *C. limbatus*, females = 2·02, males = 1·86). In *G. cirratum*, however, males had a slightly higher mean value (1·82) compared to females (1·78), but this difference was not statistically significant ($t = -1·02$, d.f. = 28, $P > 0·05$). Overall, little evidence was found

TABLE II. Descriptive statistics for values of condition for four shark species. All morphological values used to generate these condition values were in cm

	Carcharhinus leucas	*Carcharhinus limbatus*	*Ginglymostoma cirratum*	*Galeocerdo cuvier*
Mean	2·24	2·00	1·80	1·14
n	14	11	46	32
S.D.	0·11	0·13	0·12	0·08
S.E.	0·03	0·04	0·02	0·01
Maximum	2·44	2·19	2·04	1·25
Minimum	2·08	1·74	1·55	0·93
Variance	0·01	0·02	0·01	0·01
C.V.	0·05	0·06	0·07	0·08

n, number of individuals sampled.

that males and females differed in condition, but larger numbers of male sharks are needed for some species (*e.g. G. cuvier*) to verify this finding.

DISCUSSION

A simple and feasible metric (span condition analysis; A_{SC}) is provided for quantifying the condition in large apex predator sharks. It is shown that values of

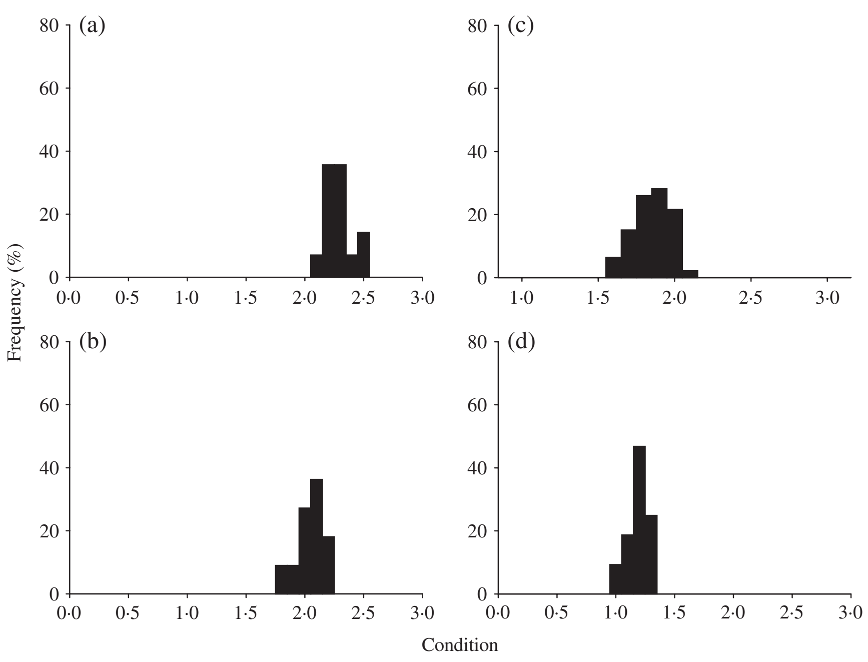

FIG. 2. Histograms of condition values for all four shark species: (a) *Carcharhinus leucas*, (b) *Carcharhinus limbatus*, (c) *Ginglymostoma cirratum* and (d) *Galeocerdo cuvier*.

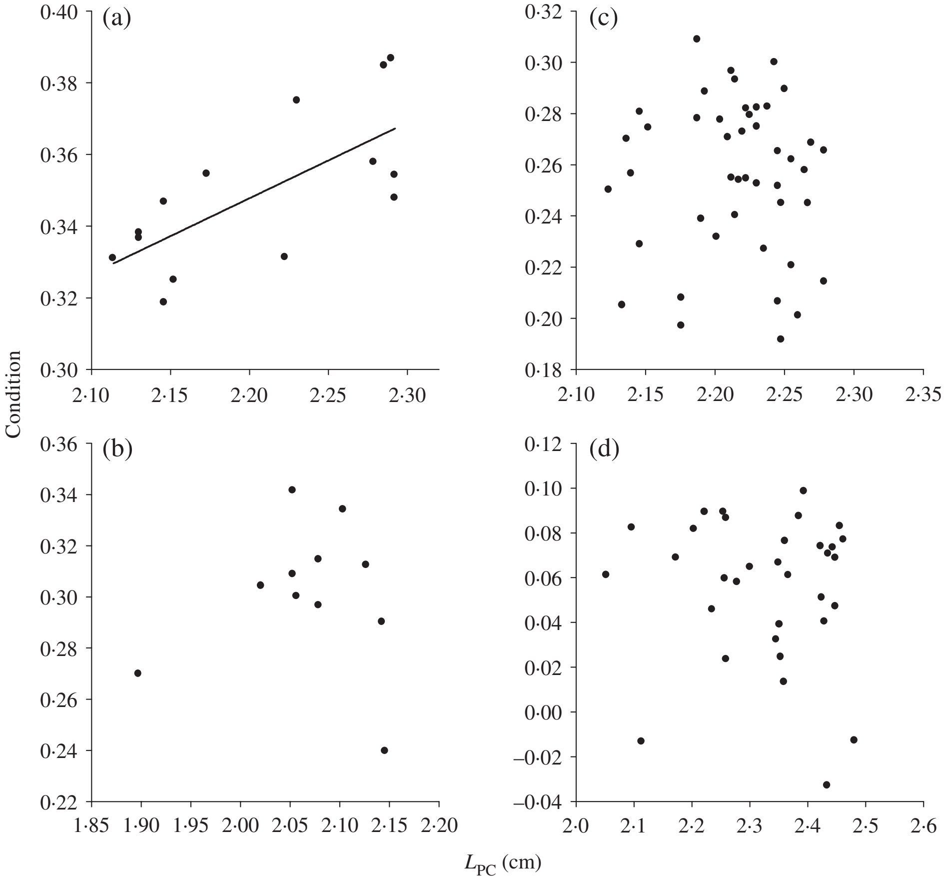

FIG. 3. Scatterplots of pre-caudal length (L_{PC}) and values of condition for all four shark species: (a) *Carcharhinus leucas*, (b) *Carcharhinus limbatus*, (c) *Ginglymostoma cirratum* and (d) *Galeocerdo cuvier*. (a) The curve was fitted by $y = 0·21x - 0·12$.

condition also do not seem to vary between male and female sharks, although data on more male sharks are needed for some species (*e.g. G. cuvier*) to verify this finding. Further, it is noteworthy that the merits of the present measure of condition may vary among species. For example, for three of the four species (*G. cuvier*, *C. limbatus* and *G. cirratum*) there was no relationship between the metric of condition and body length, whereas in *C. leucas* there was a positive and significant relationship. As co-linearity with body size is generally considered undesirable for condition measures (Jakob *et al.*, 1996), the present metric may not be fully applicable to all species.

The metric described here builds on prior metrics for quantifying the condition in fisheries science (Bolger & Connolly, 1988; Cone, 1989), but incorporates new elements that take into account the unique intra- and interspecific variation in the body form of sharks. If rapid sampling time is critical for species that exhibit pronounced physiological stress responses to capture (Gallagher *et al.*, 2014a,b), one possible simplification of the present condition metric would be to only use a single measurement of girth (such as the frontal span, Fig. 1) at the widest point on the shark's body. The present method of four variables across the length of the body was designed to assess the body axis of sharks in a more comprehensive manner; but in order to determine if one of the four variables could predict condition values to a high degree, a correlation matrix between each of the four measurements (S_L, S_F, S_P and C_{CK}) was created and condition among individuals within the species that had the greatest sample size (*G. cirratum*, $n = 46$) was quantified. It was found that S_F had the highest correlation with condition (Pearson $r = 0{\cdot}66$), whereas the others had lower values (r values: $S_L = 0{\cdot}47$; $S_P = 0{\cdot}53$; $C_{CK} = 0{\cdot}32$). This finding makes sense, as the measurement of frontal span is across the broadest part of the shark, but the still relatively low correlation value of 0·66 suggests that a combination of values is likely to prove more informative on the total body axis of the shark.

One goal of any useful metric of condition should be to estimate fat reserves (Jakob *et al.*, 1996). Sharks primarily store fat in their large bilobed livers, which run alongside the ventral side of sharks (Oguri, 1990; Hussey *et al.*, 2009; Del Raye *et al.*, 2013). In general, it is reasonable to assume that sharks with larger livers would be larger in circumference and overall volume compared with similarly sized sharks of the same species, although this assumption requires additional verification. In the most comprehensive study of condition in sharks to date, Hussey *et al.* (2009) showed in a sample of 2120 dead *C. obscurus*, that various metrics of condition changed seasonally, and that the hepato-somatic condition metric [liver mass in relation to body mass, I_L, Stevenson & Woods (2006); Pope & Kruse (2007)] was the most sensitive metric, but it also required obtaining liver masses. Liver masses might be estimated in live sharks through ultrasound (Hussey *et al.*, 2009), which would be interesting to compare with the present metric. Samples in the present study were across a wide time span (July 2012 to October 2013), and therefore, it is possible that some of the variation in condition could be due to seasonal changes. The data from Hussey *et al.* (2009) support the view that the overall size of shark livers is the most accurate metric of health, but the challenge remains to estimate liver size in live sharks. Anatomical studies relating the measure of condition on recently deceased sharks with liver size would be useful for testing this hypothesis. Further, relating blood assays of fatty acid levels to condition might inform whether the present metric of condition accurately reflects the overall fat level of individual sharks. Finally, no relationship was found between condition and body size for three of the four species examined, which indicates that this metric does not necessarily scale with body size, which is a primary concern for condition indices (Jakob *et al.*, 1996). The present data for the four divergent shark species in this study indicate very similar variability in condition within each species (Fig. 3).

Despite finding remarkably similar levels of variability in condition among the four divergent species examined, some individuals with relatively poor levels of condition were observed. For example, among the 33 *G. cuvier* sampled, a 273 cm female had a condition value of 0·93, which was the lowest among all the *G. cuvier* sampled. This shark exhibited severe lacerations on her head, eyes, dorsal fin and caudal fin, which appeared consistent with recent mating scars (Pratt & Carrier, 2001). The very low condition value for this female could be attributed to her compromised vision and damaged caudal fin, each of which would probably hamper her ability to attack and feed on mobile prey, such as turtles. Also noted here is the importance of gathering condition data on pregnant and non-pregnant females to determine the effects of pregnancy on overall body volume in live sharks. This variance in condition values offers an enticement for researchers interested in relating condition levels to movement patterns, diet, reproduction or a number of other ecological and life-history variables. For example, sharks could be captured, their condition and other physiological traits (*e.g.* fatty acid levels) measured, and then both variables could be related to how far and where sharks migrate. It could also be possible to assess any links between condition and diet, such as through isotope analyses (Hussey *et al.*, 2012; Shiffman *et al.*, 2012).

There is a large body of work examining the role of energetic limitations on the ability of animals to migrate, such as in birds, and large pelagic fishes. Research on some species (*e.g.* birds), show that variability in condition can dictate the success of migration, or the total fuel reserves available to animals once migration is completed (Merlla & Svensson, 1997; Bearhop *et al.*, 2004; Goymann *et al.*, 2010), but comparable studies have not been carried out on large sharks. It is hoped that the condition metric described here will enable a wider survey of relationships between condition and other ecological and behavioural traits in sharks. Further, it is believed that the present method could be modified for use in other animals for which capture is challenging, such as large marine mammals, and the non-invasive method could be modified as needed to provide an overall index of body shape and condition for species that are sensitive to capture.

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References

Ardia, D. R. (2005). Super size me: an experimental test for the factors affecting lipid content and the ability of residual body mass to predict lipid stores in nestling European starlings. *Functional Ecology* **19,** 414–420.

Bearhop, S. G., Hilton, M., Votier, S. C. & Waldron, S. (2004). Stable isotope ratios indicate that body condition in migrating passerines is influenced by winter habitat. *Proceedings of the Royal Society B* **271,** S215–218.

Brunnschweiler, J., Baensch, H., Pierce, S. & Sims, D. (2009). Deep-diving behaviour of a whale shark *Rhincodon typus* during long-distance movement in the western Indian Ocean. *Journal of Fish Biology* **74,** 706–714.

Bolger, T. & Connolly, P. (1988). The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology* **34,** 171–182.

Boustany, A. M., Davis, S. F., Pyle, P., Anderson, S. D., Le Boeuf, B. J. & Block, B. A. (2002). Expanded niche for white sharks. *Nature* **415,** 36.

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

Del Raye, G., Jorgensen, S. J., Krumhansl, K., Ezcurra, J. M. & Block, B. A. (2013). Travelling light: white sharks (*Carcharodon carcharias*) rely on body lipid stores to power ocean-basin scale migration. *Proceedings of the Royal Society B* **280**, 20130836. doi: 10.1098/rspb.2013.0836

Dulvy, N. K., Baum, K., Clarke, S., Compagno, L. J. V., Corte, E., Domingo, A., Fordham, S., Fowler, S., Francis, M. P., Gibson, C., Martinez, J., Musick, J. A., Soldo, A., Stevens, J.

D. & Valenti, S. (2008). You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* **18,** 459–482.

Gallagher, A. J., Serafy, J. E., Cooke, S. J. & Hammerschlag, N. (2014a). Physiological stress response, reflex impairment, and survival of five sympatric shark species following experimental capture and release. *Marine Ecology Progress Series* **496**, 207–218.

Gallagher, A. J., Orbesen, E. S., Hammerschlag, N. & Serafy, J. E. (2014b). Vulnerability of oceanic sharks as pelagic longline bycatch. *Global Ecology and Conservation*. doi: 10.1016/j.gecco.2014.06.003

Goldman, K. J. & Block, B. A. (2005). Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. *Science* **310,** 104–106.

Goymann, W., Spina, F., Ferri, A. & Fusani, L. (2010). Body fat influences departure from stopover sites in migratory birds: evidence from whole-island telemetry. *Biology Letters*. doi: 10.1098/rsbl.2009.1028

Green, A. J. (2001). Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* **82,** 1473–1483.

Hart, L. B., Wells, R. S. & Schwacke, L. H. (2013). Reference ranges for body condition in wild bottlenose dolphins *Tursiops truncatus*. *Aquatic Biology* **18,** 63–68.

Hammerschlag, N., Gallagher, A. J., Wester, J., Luo, J. & Ault, J. S. (2012a). Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. *Functional Ecology* **26,** 567–576.

Hammerschlag, N., Luo, J., Irschick, D. J. & Ault, J. S. (2012b). A comparison of spatial and movement patterns between sympatric predators: bull sharks (*Carcharhinus leucas*) and Atlantic Tarpon (*Megalops atlanticus*). *PLoS ONE* **7,** e45958. doi: 10.1371/journal.pone.0045958

Hammerschlag, N. & Sulikowski, J. (2011). Killing for Conservation: The Need for Alternatives to Lethal Sampling of Apex Predator Sharks. *Endangered Species Research* **14**, 135–140.

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., MacNeil, M. A., Olin, J. A., McMeans, B. C., Kinney, M. J. & Chapman, D. D. (2012). Stable isotopes and elasmobranchs: tissue types, methods, applications and assumptions. *Journal of Fish Biology* **80,** 1449–1484.

Jakob, E., Marshall, S. & Uetz, G. (1996). Estimating fitness: a comparison of body condition indices. *Oikos* **77,** 61–67.

Klaassen, M. (1996). Metabolic constraints on long-distance migration in birds. *Journal of Experimental Biology* **199,** 57–64.

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

Lehnen, S. E. & Krementz, D. G. (2007). The influence of body condition on the stopover ecology of Least Sandpipers in the Lower Mississippi Alluvial Valley during fall migration. *Avian Conservation and Ecology* **2,** 9.

Merlla, J. & Svensson, E. (1997). Are fat reserves in migratory birds affected by condition in early life? *Journal of Avian Biology* **28,** 279–286.

Oguri, M. (1990). A review of selected physiological characteristics unique to elasmobranchs. In *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries* (Pratt, J. H. L., Gruber, S. H. & Taniuchi, eds), pp. 49–54. *US Department of Commerce, NOAA Technical Report NMFS* **90**.

Pope, K. L. & Kruse, C. G. (2007). Condition. In *Analysis and Interpretation of Freshwater Fisheries Data* (Guy, C. S. & Brown, M. L., eds), pp. 423–471. Bethesda, MD: American Fisheries Society.

Pratt, H. L. & Carrier, J. (2001). A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. *Environmental Biology of Fishes* **60,** 157–188.

Rode, K. D., Peacock, K., Taylor, M., Stirling, I., Born, E. W., Laidre, K. L. & Wiig, O. (2012). A tale of two polar bear populations: ice habitat, harvest, and body condition. *Population Ecology* **54,** 3–18.

Rowat, D., Meekan, M., Engelhardt, U., Pardigon, B. & Vely, M. (2007). Aggregations of juvenile whale sharks (*Rhincodon typus*) in the Gulf of Tadjoura, Djibouti. *Environmental Biology of Fishes* **80,** 465–472.

Schulte-Hostedde, A. I., Millar, J. S. & Hickling, G. J. (2001). Evaluating body condition in small mammals. *Canadian Journal of Zoology* **79,** 1021–1029.

Shiffman, D. S., Gallagher, A. J., Boyle, M. D., Hammerschlag-Peyer, C. M. & Hammerschlag, N. (2012). Stable isotope analysis as a tool for elasmobranch conservation research: a primer for non-specialists. *Marine and Freshwater Research* **63,** 635–643.

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

Tucker, V. A. (1971). Flight energetics in birds. *American Zoologist* **11,** 115–124.

Weatherhead, P. J. & Brown, G. P. (1996). Measurement versus estimation of body condition in snakes. *Canadian Journal of Zoology* **74,** 1617–1621.

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C. A., Chapman, D., Heithaus, M. R., Kessel, S. T. & Gruber, S. H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy* **40,** 194–204.