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Differences in the morphological body condition index of sea turtles between species and size classes

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Abstract

The body condition of animals is an important indicator of their habitats and the effects of anthropogenic activities and pollution. Body condition indices calculated from morphometric measurements have been widely employed as they are easy to use and inexpensive. In sea turtles, Fulton's condition index, calculated as the bodyweight divided by the cube of straight carapace length (SCL), has been commonly used and it has been proposed that an index of ≥1.2 indicates a good body condition. However, comparing Fulton's condition index between different species and size classes is problematic as it does not consider the mass-length relationship. In this study, we conducted a meta-analysis to evaluate the differences between sea turtles. A literature review indicated that most studies reported the SCL-based Fulton's condition index for green turtles (Chelonia mydas), followed by loggerhead turtles (Caretta caretta) and hawksbill turtles (Eretmochelys imbricata). Therefore, we compared the values reported for healthy turtles of these three species. Meta-analysis supported the adequacy of 1.2 as a threshold in juvenile and adult green turtles and large juvenile and adult loggerhead turtles. High Fulton's condition index values were found for hatchlings and post-hatchlings of all three species and small loggerhead turtle juveniles. Low Fulton's condition index values were found for hawksbill turtles, particularly small juveniles. The differences in the Fulton's condition index between species and size classes indicated that it should be used carefully as a threshold for health condition evaluation.

Introduction

The health and body condition of endangered animals provide fundamental information in conservation biology. Body condition is an important indicator for evaluating habitats and the effects of anthropogenic activities and pollution (Johnson, 2007; Clukey *et al.*, 2017; Rodriguez & Heck, 2020). Body condition has been assessed using various techniques, including haematology and plasma biochemistry (Stevenson & Woods, 2006; Wang *et al.*, 2020; Kophamel *et al.*, 2022). The morphological body condition indices of endangered animals have been widely employed because they are easy to use and inexpensive. Various morphological condition indices have been suggested (Stevenson & Woods, 2006; Peig & Green, 2010; Sönmez, 2019); Fulton's condition index is one of the most common and is calculated as the bodyweight divided by the cube of body length (Ricker, 1975).

The body condition of sea turtles has recently become an important topic regarding their conservation as affected by marine debris (Clukey *et al.*, 2017) and fibropapillomatosis prevalence (Rossi *et al.*, 2019). Body condition indices based on morphometry have been widely used since Bjorndal *et al.* (2000*a*) calculated Fulton's condition index for juvenile green turtles (*Chelonia mydas*) as bodyweight/(straight carapace length [SCL])³. In addition, the haematology and plasma biochemistry of sea turtles have also been investigated (Anderson *et al.*, 2011; Komoroske *et al.*, 2011). Morphological condition indices of sea turtles include not only the Fulton's index, but also simple mass and length ratios (Patino-Martinez *et al.*, 2012), relative factors incorporating mass-length relationships (Fukuoka *et al.*, 2015), and residuals from the mass-length relationship (Jessop *et al.*, 2004).

Fulton's condition index is a widely used simple metric, but it should be carefully interpreted. The index assumes isometric growth; therefore, comparing values between different size classes may be problematic (Peig & Green, 2010). Interspecific or interpopulation comparisons are also difficult when body dimensions or growth patterns differ. In sea turtles, Fulton's condition index has been widely used as a rough measure of nutritional status and health (Bjorndal *et al.*, 2000*a*; Diez & van Dam, 2002) and values exceeding 1.2 have conventionally been interpreted to indicate a good body condition (Norton & Wyneken, 2015; Maulida *et al.*, 2017; Adnyana *et al.*, 2020). However, the threshold value may change, considering that there are interspecific and/or intraspecific differences in the body shape and growth pattern of sea turtles (Wabnitz & Pauly, 2008; Álvarez-Varas *et al.*, 2019). Additionally, the carapace length, which has been used as a representative length for calculating the index, can be measured in several ways, such as by using the SCL *vs* curved carapace length (CCL) (Bolten, 1999). Evaluating these differences is important to establish a baseline condition index for sea turtles. In this study, we reviewed the literature on morphological condition indices in sea turtles and conducted a meta-analysis of Fulton's condition index in sea turtles. This study summarizes the prevalence of various morphological condition indices among sea turtle species to elucidate the knowledge gap regarding their health status. We then evaluated the differences in Fulton's condition index between species and size classes to establish baseline sea turtle body conditions. We also evaluated differences in the index values when different length metrics were used.

Materials and methods

Literature review

We searched for studies using Google Scholar and Web of Science with the queries 'sea turtle' and 'body condition index' or 'Fulton index' on 5–7 August 2020 and 12–13 April 2021. We additionally searched PubMed on 5–6 April 2022, but did not include references published after April 2021. We reviewed the references therein and retained literature on morphological condition indices.

Meta-analysis of Fulton's condition index

The average and standard deviation (SD) or standard error (SE) of Fulton's condition indices $(\text{kg cm}^{-3} \times 10^4)$ calculated from the SCL in the literature were used. When the data appeared only in figures, they were extracted using Plot Digitizer 2.6.8 (Huwaldt, 2001). When the data were presented as median, maximum, minimum and/or quantile values, we estimated the average and SD using the method reported by Wan et al. (2014). The SCL can be measured as the length from the anterior point at the midline to the posterior notch at the midline (minimum SCL [SCLmin]) or the tip (standard SCL [SCLnt]) (Bolten, 1999). We could not differentiate these measurements in the following analysis as the literature sometimes did not clearly present which was used; however, we simulated the effects based on conversion equations (see below). We excluded studies that reported the body condition indices of unhealthy turtles to explore the standard baseline values for healthy turtles. Unhealthy turtles included dead and injured turtles, those noted as 'unhealthy' in the original texts, and those with tumours with scores (Work & Balazs, 1999) of 2-3 or labelled as 'developed', 'moderate' or 'severe'; however, we retained the data of turtles with 'mild' tumours or a tumour score of ~1. We also removed literature that may have contained data on the same individuals based on the authors, locations and study periods.

In addition to the dataset from the literature, we calculated Fulton's condition indices from the unstructurally searched literature that provided the bodyweights and SCLs of individuals. Furthermore, to complement the data of hawksbill turtle (*Eretmochelys imbricata*) hatchlings, we measured the bodyweight and SCL of 20 hawksbill turtle hatchlings each from 8 and 13 nests at Lankayan and Selingaan hatcheries, Sabah, Malaysia, respectively. We calculated the Fulton's condition index and its average \pm SD at each rookery by randomly selecting one hatchling from one nest. A full list of literature compiled in this study is provided in Supplementary Table S1.

Fulton's condition index has mainly been reported for three species: green turtles, loggerhead turtles (*Caretta caretta*) and hawksbill turtles (see Results). Therefore, we focused on these three species in this study. Additionally, we categorized the data into one of three size classes: 'hatchling and post-hatchling', 'small juvenile' and 'large juvenile and adult'. The 'hatchling and post-hatchling' category included hatchlings measured just after emergence from the nests and post-hatchlings that were

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reared for several months (SCL of ~15 cm). The 'small juvenile' and 'large juvenile and adult' categories were separated at 50 cm SCL according to Bjorndal et al. (2000b), Gorham et al. (2014) and Hamabata et al. (2018). The 'small juvenile' category included juveniles recruited to their foraging grounds after oceanic dispersal, with SCLs ranging from 20-50 cm. The 'large juvenile and adult' category included nesting turtles, matured males and large juveniles with SCLs larger than 50 cm. When it was difficult to clearly assign these categories to the literature because average and SD or SE values were reported from individuals including both small juveniles and large juveniles or adults, categorization was based on whether or not the average SCL exceeded 50 cm. Regional information was also adopted and categorized into 'North Atlantic', 'South Atlantic', 'North-west Pacific', 'Central Pacific' and 'East Pacific' based on the regional management units (RMU) in Wallace et al. (2010) and distinct population segments (DPS) in Conant et al. (2009) and Seminoff et al. (2015).

The differences in Fulton's condition index between species and size classes were tested by random-effects modelling using the metafor package (Viechtbauer, 2010) in R ver 4.0.0 (R Core Team, 2020). First, we assumed a multilevel model that included regions as the upper level and studies as the lower level. We confirmed that the variance attributable to regions was small by the likelihood ratio test and variance distribution calculation using the dmetar package (Harrer *et al.*, 2019) (see Results); thus, we estimated a single-level model that included studies as random effects. Overall averages and 95% confidence intervals (CIs) were estimated for each species and size class.

Effects of different carapace length measurement

For the simulation, we randomly generated SCLnt values (N = 100) from a uniform distribution ranging from 30-100 cm. We then estimated the ratios of SCLnt³/CCLnt³ or SCLnt³/SCLmin³ using the relationship between SCLnt and CCLnt (i.e. the CCL measured from notch to tip) and SCLnt and SCLmin based on regression analyses (Limpus, 1992; Teas, 1993; Iwase & Kuroyanagi, 1999; Seminoff *et al.*, 2003; Peckham *et al.*, 2008; Okamoto *et al.*, 2012; Bjorndal *et al.*, 2013, 2016, 2017; Table 1). These ratios indicate the ratios of SCLnt-based vs CCLnt-based (or SCLnt-based vs SCLmin-based) Fulton's condition indices as follows:

$$\frac{\text{Bodyweight /CCLnt}^3}{\text{Bodyweight /SCLnt}^3} = \frac{\text{SCLnt}^3}{\text{CCLnt}^3}$$

We used three equations to convert SCLnt to CCLnt for green, loggerhead and hawksbill turtles estimated from Atlantic and Pacific data. To convert SCLmin to SCLnt, we used equations estimated from Atlantic turtles because we could not find conversion equations for Pacific turtles.

Results

We identified 77 articles that reported morphological condition indices. Most studies focused on green (N = 51), followed by loggerhead (N = 16) and hawksbill turtles (N = 6) (Table 2, Supplementary Table S2). Fulton's condition index was calculated based on the SCL in most studies (N = 54); however, some studies reported CCL-based indices (N = 7) (Table 2, Supplementary Table S2). Two studies calculated the modified Fulton's index considering carapace length × carapace width × carapace depth, instead of (carapace length)³ (Barco *et al.*, 2016; Cammilleri *et al.*, 2017). The mass-to-length ratio (mass/SCL) has been

Table 1. Equations for converting the curved carapace length of sea turtles measured from notch to tip (CCLnt) or notch to notch straight carapace length (SCLmin) to the notch to tip straight carapace length (SCLnt)

Conversion	Species	Location	Equation	References	
CCLnt to SCLnt	Green	West Atlantic	SCLnt (cm) = 0.294 + (0.937 × CCLnt)	Teas (1993)	
		West Atlantic	SCLnt (cm) = -0.5385 + (0.9698 × CCLnt)	Bjorndal <i>et al</i> . (2017)	
		Japan, Pacific	SCLnt (mm) = 4.584 + (0.946 × CCLnt)	Okamoto et al. (2012)	
		East Pacific	SCLnt (cm) = -2.168 + (0.965 × CCLnt)	Seminoff et al. (2003)	
	Loggerhead	West Atlantic	SCLnt (cm) = -1.442 + (0.948 × CCLnt)	Teas (1993)	
		West Atlantic	SCLnt (cm) = -0.899 + (0.939 × CCLnt)	Bjorndal <i>et al</i> . (2013)	
		Japan, Pacific	SCLnt (mm) = 8.621 + (0.940 × CCLnt)	Okamoto et al. (2012)	
		East Pacific	SCLnt (cm) = 0.369 + (0.932 × CCLnt)	Peckham et al. (2008)	
	Hawksbill	West Atlantic	SCLnt (cm) = -0.212 + (0.955 × CCLnt)	Teas (1993)	
		West Atlantic	SCLnt (cm) = 0.4496 + (0.9326 × CCLnt)	Bjorndal <i>et al</i> . (2016)	
		Japan, Pacific	SCLnt (cm) = 1.91 + (0.920 × CCLnt)	lwase & Kuroyanagi (1999)	
		Australia	SCLnt (cm) = 0.449 + (0.935 × CCLnt)	Limpus (1992)	
SCLmin to SCLnt	Green	West Atlantic	SCLnt (cm) = 0.238 + (1.0138 × SCLmin)	Bjorndal <i>et al</i> . (2017)	
	Loggerhead	West Atlantic	SCLnt (cm) = 0.999 + (1.003 × SCLmin)	Bjorndal <i>et al</i> . (2013)	
	Hawksbill	West Atlantic	SCLnt (cm) = 0.1424 + (1.0409 × SCLmin)	Bjorndal <i>et al</i> . (2016)	

used for hatchlings (van de Merwe *et al.*, 2005, 2010; Patino-Martinez *et al.*, 2012) or post-hatchlings (Mansfield *et al.*, 2012); however, Fulton's condition index has recently been applied to hatchlings (Banerjee *et al.*, 2020; Fleming *et al.*, 2020).

We included studies that reported the SCL-based Fulton's index for green, loggerhead and hawksbill turtles in further meta-analyses. After removing potential duplicate data and adding the data calculated in the present study, data from 68 studies were used to evaluate the differences between species and size classes (Supplementary Table S3). The multilevel model showed that regions and studies explained 25.7 and 34.3% of the variation, respectively, and the effects of regions were not significant (likelihood ratio test: $\chi^2 = 0.27$, P = 0.603). The single-level model attributed 53.3% of the total variance to between-study heterogeneity but showed a significant effect of moderators (Q = 186.4, df =8, P < 0.0001). A high Fulton's condition index was observed in 'hatchling and post-hatchling' turtles (averages for green, loggerhead and hawksbill turtles: 2.24 [95% CI: 1.87-2.61], 2.13 [1.97-2.28], 2.06 [1.82-2.30], respectively) (Figure 1). The CIs overlapped between 'small juveniles' and 'large juveniles and adults' for each species (green turtle: 1.31 [1.25-1.36] and 1.41 [1.34-1.47], loggerhead turtle: 1.59 [1.45-1.73] and 1.40 [1.33-1.48], hawksbill turtle: 1.09 [0.98-1.20] and 1.26 [1.07-1.45], respectively); however, the value of small juvenile hawksbill turtles was smaller than that of green and loggerhead turtles (Figure 1).

The averages and ranges of estimated SCLnt³/CCLnt³ ratios of green turtles based on equations from Teas (1993), Bjorndal *et al.* (2017), Okamoto *et al.* (2012) and Seminoff *et al.* (2003) were 0.835 (range: 0.830–0.847), 0.887 (range: 0.865–0.897), 0.867 (range: 0.858–0.887) and 0.805 (range: 0.729–0.842), respectively. The ratios for loggerhead turtles based on equations from Teas (1993), Bjorndal *et al.* (2013), Okamoto *et al.* (2012) and Peckham *et al.* (2008) were 0.791 (range: 0.740–0.816), 0.790 (range: 0.758–0.806), 0.869 (range: 0.853–0.906), and 0.825 (range: 0.819–0.840), respectively. The ratios for hawksbill turtles based on equations from Teas (1993), Bjorndal *et al.* (2018), Bjorndal *et al.* (2016), Iwase and Kuroyanagi (1999), and Limpus (1992) were 0.861 (range: 0.853–0.865), 0.831 (range: 0.822–0.849), 0.863 (range: 0.825–0.948) and 0.837 (range: 0.829–0.855), respectively. The estimated

SCLnt³/SCLmin³ ratios for green, loggerhead and hawksbill turtles were 1.055 (range: 1.049–1.067), 1.061 (range: 1.040–1.114) and 1.016 (range: 1.013–1.023), respectively.

Discussion

Fulton's condition index has been widely applied in sea turtle studies, excluding flatback turtles (*Natator depressus*). Values of Fulton's condition index based on SCLs \geq 1.2 have been interpreted to indicate a relatively good body condition for sea turtles (Norton & Wyneken, 2015; Maulida *et al.*, 2017; Adnyana *et al.*, 2020). Although index values \geq 1.3 were generally observed in large green and loggerhead turtles, the meta-analysis in this study supported the adequacy of this threshold for juvenile and adult green turtles and large juvenile and adult loggerhead turtles. This study also indicated further differences in Fulton's condition index between species and size classes; thus, it should be carefully applied on body condition evaluation.

The meta-analysis indicated high Fulton's condition index values for hatchlings and post-hatchlings of all three species. This is to be expected because the bodyweight of sea turtles is not proportional to SCL³, but SCL^{2.7}-SCL^{2.9} (Wabnitz & Pauly, 2008), resulting in a decrease in Fulton's condition index as bodyweight increases (Figure 2). The relationship between bodyweight and SCL also supports the finding that Fulton's condition index of small loggerhead juveniles was lower than that of hatchlings and post-hatchlings, but slightly higher than that of large juveniles and adults. This tendency was not observed in green and hawksbill turtles, which may be because the index values from foraging grounds included both small juveniles and large juveniles or adults, and the categorization was based on the average SCL. Evaluating hatchling and post-hatchling sea turtles using Fulton's condition index requires caution. Additionally, a threshold higher than 1.2 is more suitable to indicate the good body condition of small juvenile loggerhead turtles.

A lower Fulton's condition index was observed for hawksbill turtles, particularly small juveniles. The relationships between the bodyweight and SCL (Wabnitz & Pauly, 2008) indicated that the bodyweight of hawksbill turtles in relation to SCL (i.e. Fulton's condition index) is lower than that of green and

Table 2. Number of studies that have reported the morphometric body condition index for	r each sea turtle species
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Index	Ν	Green	Loggerhead	Hawksbill	Olive Ridley	Kemp's Ridley	Leatherback
Fulton (SCL-based)	54	34	14	5	4	3	2
Fulton (CCL-based)	7	6				1	
Modified Fulton	2		2				
Relative	4	4					
Residual	6	4		1			1
Mass/Length	4	2	1				1
log(Mass)/log(Length)	3	3					
Scaled mass index	1	1					
Total ^a	77	51	16	6	4	4	4

^aSome studies have reported indices of multiple species or multiple indices; therefore, the total numbers are different from the summation of the columns. See Supplementary Table S2 for further details.

loggerhead turtles (Figure 2). This difference is likely due to the relatively depressed plastron of hawksbill turtles, which is supported by the relationship between body depth and SCL (van Dam & Diez, 1998), when compared with loggerhead turtles (Marn *et al.*, 2015). In addition, carapace widening is observed in juvenile green and loggerhead turtles (Salmon & Scholl, 2014), but not in juvenile hawksbill turtles (Salmon *et al.*, 2018), possibly resulting in lower bodyweights of juvenile hawksbill turtles in relation to SCL. Considering the differences in body proportion and the results of the meta-analysis, Fulton's condition index of values of ~1.0 rather than 1.2 could be a threshold for indicating good body condition in juvenile and adult hawksbill turtles.

SCL has been used as the representative body length for calculating Fulton's condition index in sea turtles, as used by Bjorndal *et al.* (2000*a*). Some studies measured the CCL but converted it to SCL to calculate the SCL-based Fulton's condition factor (López-Mendilaharsu *et al.*, 2016; Rossi *et al.*, 2019; Lamont & Johnson, 2021). We found seven studies that calculated Fulton's condition factor directly using CCL. Fulton's condition index values calculated from the CCL were ~0.81–0.89 times lower than those calculated using the SCL in green and hawksbill turtles. Therefore, an SCL-based index value of 1.2 is equivalent to a CCL-based index value of 1.0. Moreover, CCL-based values were lower in Atlantic loggerhead turtles ($0.79 \times$ SCL-based values). There may be a regional difference in the relationship between SCL and CCL for Atlantic and Pacific loggerhead turtles that results in differences in the CCLnt-based index/SCLnt-based index ratio among conversion equations (~0.79 based on Teas, 1993 and Bjorndal *et al.*, 2013 *vs* 0.82–0.87 based on Okamoto *et al.*, 2012 and Peckham *et al.*, 2008).

We only evaluated three species of sea turtles, i.e. green, loggerhead and hawksbill turtles, because data are scarce for the other species. Further studies are required to evaluate other sea turtle species. Kemp's Ridley turtle (*Lepidochelys kempii*) may have a higher Fulton's condition index than green turtles due to

Species and size class							Mean [95% CI]
Hatchling & post-hatchling							
Green turtle					•		2.24 [1.87, 2.61]
Loggerhead turtle				⊢	-		2.13 [1.97, 2.28]
Hawksbill turtle			⊢ ∎–-i				2.06 [1.82, 2.30]
Small juvenile Green small			-				1.31 [1.25, 1.36]
Loggerhead small			- 				1.59 [1.45, 1.73]
Hawksbill small		+=-					1.09 [0.98, 1.20]
Large juvenile & adult Green large			HEH				1.41 [1.34, 1.47]
Loggerhead large			HEH				1.40 [1.33, 1.48]
Hawksbill large		H	•				1.26 [1.07, 1.45]
	0.5	1.0	1.5	2.0	2.5	3.0	
		Fultor	n's body	conditio	on index		

Fig. 1. Forest plot of Fulton's body condition index values estimated using meta-analysis. The mean and 95% confidence interval (CI) values are shown in the right column, and the dashed line shows the value of 1.2.

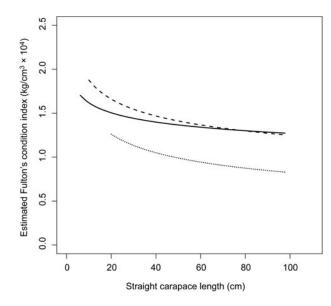


Fig. 2. The relationship between Fulton's body condition index and straight carapace length (SCL) estimated from the relationships between bodyweight and SCL in green (Bodyweight = 0.000206 SCL^{2.895}), loggerhead (Bodyweight = 0.000282 SCL^{2.823}) and hawksbill turtles (Bodyweight = 0.000278 SCL^{2.736}) (Wabnitz & Pauly, 2008). Green, loggerhead and hawksbill turtles are illustrated by solid, dashed and dotted lines, respectively.

interspecific morphological differences (Lamont & Johnson, 2021). Additionally, we did not evaluate the eastern Pacific green turtle subspecies, the black turtle (*Chelonia mydas agassizii*) because foraging grounds may contain both black turtle-like and ordinal green turtle-like morphotypes, and values have not been reported separately (Sielfeld *et al.*, 2019). However, a smaller Fulton's condition index has been reported in small juveniles of black turtle-like morphotypes than in ordinary green turtles (Sampson *et al.*, 2014).

In the present study, the effect of region was not significant; however, regional differences were possible sources of betweenstudy heterogeneity. Fulton's condition index has not been reported equally from all regions and was tested as a random effect in this study. Further studies are necessary to explore regional differences. In addition, foraging aggregations sometimes contain turtles from various rookeries (Amorocho et al., 2012; Nishizawa et al., 2013, 2018), which may result in high individual differences and within-study heterogeneity in the condition index. Another factor for heterogeneity is the difference in carapace length measurement. SCL can be measured as notch-to-notch (SCLmin) or notch-to-tip (SCLnt) (Bolten, 1999). Calculating the index using SCLmin slightly increases the index from that based on SCLnt by 1.01-1.06 times. Defining which length is used clearly will be important for further establishing baseline body condition index values in sea turtles.

In conclusion, caution should be applied when using Fulton's condition index as a body condition indicator for sea turtles. Using Fulton's condition index for different species and size classes is problematic, as it does not consider the mass-length relationship (Peig & Green, 2010). Different threshold values for good body condition must be implemented for species and size classes. Morphometric body condition indices that incorporate mass-length relationships have been calculated for sea turtles (relative condition index: Labrada-Martagón *et al.*, 2010, 2011, 2013; Fukuoka *et al.*, 2015; scaled mass index: Bell *et al.*, 2019). Fulton's condition index is a simple metric that can be used to assess sea turtle body conditions. Because accidental errors can always occur when measuring bodyweight and length, the proposed threshold values for good body condition in this study

must be carefully applied for individual body condition evaluation. Nonetheless, this study proposed baseline Fulton's condition index values for adequate sea turtle habitats and body conditions, which will be compared in future studies.

Data. The data that support the findings of this study are available from the online supplementary materials.

Supplementary material. The supplementary material for this article can be found at https://doi.org/10.1017/S0025315422000765.

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Author contributions. HN: formulating the research questions, designing the study, carrying out the study, analysing the data, interpreting the findings and writing the article. JJ: formulating the research questions, providing financial support, carrying out the study, revising the article.

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Conflict of interest. The authors declare no conflict of interests.

Ethical standards. Fieldwork in Sabah, Malaysia followed the guidelines and permitted under the Sabah Biodiversity Centre (SaBC) Access Licence: JKM/ MBS.1000-2/2 JLD.12(23) and Sabah Parks: TTS/IP/100-6/2 JLD.11(119).

References

- Adnyana IBW, Christianen MJA, Hitipeuw C and Dethmers K (2020) The body condition index and genetic connectivity among foraging green turtle populations in Indonesia at different scales: a case study from Berau green turtle rookery, East Kalimantan–Indonesia. *International Journal of Life Sciences Research* **8**, 46–61.
- Álvarez-Varas R, Véliz D, Vélez-Rubio GM, Fallabrino A, Zárate P, Heidemeyer M, Godoy DA and Benítez HA (2019) Identifying genetic lineages through shape: an example in a cosmopolitan marine turtle species using geometric morphometrics. *PLoS ONE* 14, e0223587.
- Amorocho DF, Abreu-Grobois FA, Dutton PH and Reina RD (2012) Multiple distant origins for green sea turtles aggregating off Gorgona Island in the Colombian eastern Pacific. *PLoS ONE* 7, e31486.
- Anderson ET, Harms CA, Stringer EM and Cluse WM (2011) Evaluation of hematology and serum biochemistry of cold-stunned green sea turtles (*Chelonia mydas*) in North Carolina, USA. Journal of Zoo and Wildlife Medicine 42, 247–255.
- Banerjee SM, Frey A, Kurle CM, Perrault JR and Stewart KR (2020) Morphological variation in leatherback (*Dermochelys coriacea*) hatchlings at sandy point national wildlife refuge, US Virgin Islands. *Endangered Species Research* **41**, 361–372.
- Barco S, Law M, Drummond B, Koopman H, Trapani C, Reinheimer S, Rose S, Swingle WM and Williard A (2016) Loggerhead turtles killed by vessel and fishery interaction in Virginia, USA, are healthy prior to death. *Marine Ecology Progress Series* 555, 221–234.
- Bell IP, Meager J, van de Merwe JP and Hof CAM (2019) Green turtle (*Chelonia mydas*) population demographics at three chemically distinct foraging areas in the northern great barrier reef. *Science of the Total Environment* **652**, 1040–1050.
- Bjorndal KA, Bolten AB and Chaloupka MY (2000a) Green turtle somatic growth model: evidence for density dependence. *Ecological Applications* 10, 269–282.
- Bjorndal KA, Bolten AB, Chaloupka M, Saba VS, Bellini C, Marcovaldi MAG, Santos AJB, Bortolon LFW, Meylan AB, Meylan PA, Gray J, Hardy R, Brost B, Bresette M, Gorham JC, Connett S, Crouchley BVS, Dawson M, Hayes D, Diez CE, van Dam RP, Willis S, Nava M, Hart KM, Cherkiss MS, Crowder AG, Pollock C, Hillis-Starr Z, Muñoz Tenería FA, Herrera-Pavón R, Labrada-Martagón V, Lorences A, Negrete-Philippe A, Lamont MM, Foley AM, Bailey R, Carthy RR, Scarpino R, McMichael E, Provancha JA, Brooks A, Jardim A, López-Mendilaharsu M, González-Paredes D, Estrades A, Fallabrino A,

Martínez-Souza G, Vélez-Rubio GM, Boulon Jr RH, Collazo JA, Wershoven R, Hernández VG, Stringell TB, Sanghera A, Richardson PB, Broderick AC, Phillips Q, Calosso M, Claydon JAB, Metz TL, Gordon AL, Landry Jr AM, Shaver DJ, Blumenthal J, Collyer L, Godley BJ, McGowan A, Witt MJ, Campbell CL, Lagueux CJ, Bethel TL and Kenyon L (2017) Ecological regime shift drives declining growth rates of sea turtles throughout the West Atlantic. *Global Change Biology* 23, 4556–4568.

- Bjorndal KA, Bolten AB and Martins HR (2000b) Somatic growth model of juvenile loggerhead sea turtles *Caretta caretta*: duration of pelagic stage. *Marine Ecology Progress Series* **202**, 265–272.
- Bjorndal KA, Chaloupka M, Saba VS, Diez CE, van Dam RP, Krueger BH, Horrocks JA, Santos AJB, Bellini C, Marcovaldi MAG, Nava M, Willis S, Godley BJ, Gore S, Hawkes LA, McGowan A, Witt MJ, Stringell TB, Sanghera A, Richardson PB, Broderick AC, Phillips Q, Calosso MC, Claydon JAB, Blumenthal J, Moncada F, Nodarse G, Medina Y, Dunbar SG, Wood LD, Lagueux CJ, Campbell CL, Meylan AB, Meylan PA, Burns Perez VR, Coleman RA, Strindberg S, Guzmán-H V, Hart KM, Cherkiss MS, Hillis-Starr Z, Lundgren IF, Boulon Jr RH, Connett S, Outerbridge ME and Bolten AB (2016) Somatic growth dynamics of West Atlantic hawksbill sea turtles: a spatio-temporal perspective. *Ecosphere* 7, e01279.
- Bjorndal KA, Schroeder BA, Foley AM, Witherington BE, Bresette M, Clark D, Herren RM, Arendt MD, Schmid JR, Meylan AB, Meylan PA, Provancha JA, Hart KM, Lamont MM, Carthy RR and Bolten AB (2013) Temporal, spatial, and body size effects on growth rates of loggerhead sea turtles (*Caretta caretta*) in the Northwest Atlantic. *Marine Biology* 160, 2711–2721.
- Bolten AB (1999) Techniques for measuring sea turtles. In Eckert KL, Bjorndal KA, Abreu-Grobois FA and Donnelly M (eds), Research and Management Techniques for the Conservation of Sea Turtles. Washington, DC: IUCN/SSC Marine Turtle Specialist Group Publication 4, pp. 110–114.
- Cammilleri G, Calvaruso E, Pantano L, Cascio GL, Randisi B, Macaluso A, Vazzana M, Caracappa G, Giangrosso G, Vella A and Ferrantelli V (2017) Survey on the presence of non-dioxine-like PCBS (NDL-PCBS) in loggerhead turtles (*Caretta caretta*) stranded in south Mediterranean coasts (Sicily, southern Italy). *Environmental Toxicology and Chemistry* 36, 2997–3002.
- Clukey KE, Lepczyk CA, Balazs GH, Work TM and Lynch JM (2017) Investigation of plastic debris ingestion by four species of sea turtles collected as bycatch in pelagic Pacific longline fisheries. *Marine Pollution Bulletin* 120, 117–125.
- Conant TA, Dutton PH, Eguchi T, Epperly SP, Fahy CC, Godfrey MH, MacPherson SL, Possardt EE, Schroeder BA, Seminoff JA, Snover ML, Upite CM and Witherington BE (2009) Loggerhead sea turtle (*Caretta caretta*) 2009 status review under the U.S. Endangered Species Act. Report of the Loggerhead Biological Review Team to the National Marine Fisheries Service, August 2009, 222 pp.
- Diez CE and van Dam RP (2002) Habitat effect on hawksbill turtle growth rates on feeding grounds at Mona and Monito Islands, Puerto Rico. *Marine Ecology Progress Series* 234, 301–309.
- Fleming KA, Perrault JR, Stacy NI, Coppenrath CM and Gainsbury AM (2020) Heat, health and hatchlings: associations of *in situ* nest temperatures with morphological and physiological characteristics of loggerhead sea turtle hatchlings from Florida. *Conservation Physiology* **8**, coaa046.
- Fukuoka T, Narazaki T and Sato K (2015) Summer-restricted migration of green turtles *Chelonia mydas* to a temperate habitat of the northwest Pacific Ocean. *Endangered Species Research* 28, 1–10.
- Gorham JC, Clark DR, Bresette MJ, Bagley DA, Keske CL, Traxler SL, Witherington BE, Shamblin BM and Nairn CJ (2014) Characterization of a subtropical hawksbill sea turtle (*Eretmochelys imbricata*) assemblage utilizing shallow water natural and artificial habitats in the Florida keys. *PLoS ONE* 9, e114171.
- Hamabata T, Nishizawa H, Kawazu I, Kameda K, Kamezaki N and Hikida T (2018) Stock composition of green turtles *Chelonia mydas* foraging in the Ryukyu Archipelago differs with size class. *Marine Ecology Progress Series* 600, 151–163.
- Harrer M, Cuijpers P, Furukawa T and Ebert DD (2019) dmetar: Companion R Package For The Guide 'Doing Meta-Analysis in R. R package version 0.0.9000. Available at http://dmetar.protectlab.org/ (Accessed 21 April 2021).
- Huwaldt JA (2001) PlotDigitizer. Available at http://plotdigitizer.sourceforge. net (Accessed 16 September 2020).

- Iwase F and Kuroyanagi K (1999) Relationship between straight carapace length and curved carapace length of green and hawksbill turtles. Umigame Newsletter Japan 39, 12. (in Japanese).
- Jessop TS, Hamann M and Limpus CJ (2004) Body condition and physiological changes in male green turtles during breeding. *Marine Ecology Progress Series* 276, 281–288.
- Johnson MD (2007) Measuring habitat quality: a review. Condor 109, 489– 504.
- Komoroske LM, Kewison RL, Seminoff JA, Deheyn DD and Dutton PH (2011) Pollutants and the health of green sea turtles resident to an urbanized estuary in San Diego, CA. *Chemosphere* **84**, 544–552.
- Kophamel S, Illing B, Ariel E, Difalco M, Skerratt LF, Hamann M, Ward LC, Méndez D and Munns SL (2022) Importance of health assessments for conservation in noncaptive wildlife. *Conservation Biology* 36, e13724.
- Labrada-Martagón V, Méndez-Rodríguez LC, Gardner SC, Cruz-Escalona VH and Zenteno-Savín T (2010) Health indices of the green turtle (*Chelonia mydas*) along the Pacific coast of Baja California Sur, Mexico. II. Body condition index. *Chelonian Conservation and Biology* 9, 173–183.
- Labrada-Martagón V, Méndez-Rodríguez LC, Mangel M and Zenteno-Savín T (2013) Applying generalized linear models as an explanatory tool of sex steroids, thyroid hormones and their relationships with environmental and physiologic factors in immature East Pacific green sea turtles (*Chelonia mydas*). Comparative Biochemistry and Physiology, Part A 166, 91–100.
- Labrada-Martagón V, Tenorio Rodríguez PA, Méndez-Rodríguez LC and Zenteno-Savín T (2011) Oxidative stress indicators and chemical contaminants in East Pacific green turtles (*Chelonia mydas*) inhabiting two foraging coastal lagoons in the Baja California peninsula. *Comparative Biochemistry and Physiology, Part C* 154, 65–75.
- Lamont MM and Johnson D (2021) Variation in species composition, size and fitness of two multi-species sea turtle assemblages using different neritic habitats. *Frontiers in Marine Science* 7, 608740.
- Limpus CJ (1992) The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern great barrier reef feeding ground. *Wildlife Research* 19, 489–505.
- López-Mendilaharsu M, Vélez-Rubio GM, Lezama C, Aisenberg A, Bauzá A, Berrondo L, Calvo V, Caraccio N, Estrades A, Hernández M, Laporta M, Martínez-Souza H, Morales M, Quirici V, Ríos M and Fallabrino A (2016) Demographic and tumour prevalence data for juvenile green turtles at the coastal-marine protected area of Cerro Verde, Uruguay. *Marine Biology Research* 12, 541–550.
- Mansfield KL, Wyneken J, Rittschof D, Walsh M, Lim CW and Richards PM (2012) Satellite tag attachment methods for tracking neonate sea turtles. *Marine Ecology Progress Series* 457, 181–192.
- Marn N, Klanjscek T, Stokes L and Jusup M (2015) Size scaling in western North Atlantic loggerhead turtles permits extrapolation between regions, but not life stages. *PLoS ONE* 10, e0143747.
- Maulida FF, Hadi S, Imron MA and Reischig T (2017) Geometry morphometry and health status of hawksbill turtle (Eretmochelys imbricata Linnaeus, 1766) in Maratua Island, East Kalimantan-Indonesia. ICBS Conference Proceedings International Conference on Biological Science (2015) 2017, 100–110.
- Nishizawa H, Joseph J, Chong YK, Syed Kadir SA, Isnain I, Ganyai TA, Jaaman S and Zhang X (2018) Comparison of the rookery connectivity and migratory connectivity: insight into movement and colonization of the green turtle (*Chelonia mydas*) in Pacific–Southeast Asia. *Marine Biology* 165, 77.
- Nishizawa H, Naito Y, Suganuma H, Abe O, Okuyama J, Hirate K, Tanaka S, Inoguchi E, Narushima K, Kobayashi K, Ishii H, Tanizaki S, Kobayashi M, Goto A and Arai N (2013) Composition of green turtle feeding aggregations along the Japanese archipelago: implications for changes in composition with current flow. *Marine Biology* 160, 2671–2685.
- Norton T and Wyneken J (2015) Body condition scoring the sea turtle. 27 January 2015. LafeberVet Web site. Available at https://lafeber.com/vet/ body-condition-scoring-the-sea-turtle/ (Accessed 27 August 2021).
- Okamoto K, Ouchi Y, Ishihara T and Kamezaki N (2012) Straight carapace length calculation of the loggerhead and green sea turtles from some morphological characters. *Umigame Newsletter Japan* **91**, 8–12 (in Japanese).
- Patino-Martinez J, Marco A, Quiñones L and Hawkes L (2012) A potential tool to mitigate the impacts of climate change to the Caribbean leatherback sea turtle. *Global Change Biology* 18, 401–411.

- Peckham SH, Maldonado-Diaz D, Koch V, Mancini A, Gaos A, Tinker MT and Nichols WJ (2008) High mortality of loggerhead turtles due to bycatch, human consumption and strandings at Baja California Sur, Mexico, 2003 to 2007. Endangered Species Research 5, 171–183.
- Peig J and Green AJ (2010) The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology* 24, 1323–1332.
- **R Core Team** (2020) *R: A Language and Environment for Statistical Computing.* Vienna: R Foundation for Statistical Computing. Available at https://www.R-project.org/ (Accessed 21 August 2020).
- Ricker WE (1975) Computation and interpretation of biological statistics of fish populations. Bulletin of the Fisheries Research Board of Canada 191, 1–382.
- Rodriguez AR and Heck KL (2020) Green turtle herbivory and its effects on the warm, temperate seagrass meadows of St. Joseph Bay, Florida (USA). *Marine Ecology Progress Series* 639, 37–51.
- Rossi S, Sánchez-Sarmiento AM, Santos RG, Zamana RR, Prioste FES, Gattamorta MA, Ochoa PFC, Grisi-Filho JHH and Matushima ER (2019) Monitoring green sea turtles in Brazilian feeding areas: relating body condition index to fibropapillomatosis prevalence. *Journal of the Marine Biological Association of the United Kingdom* 99, 1879–1887.
- Salmon M, Coppenrath C and Higgins B (2018) Allometric growth in juvenile marine turtles: possible role as an antipredator adaptation. *Zoology* 117, 131–138.
- Salmon M and Scholl J (2014) The early ontogeny of carapace armoring in hawksbill sea turtles (*Eretmochelys imbricata*), with comparisons to its close relatives (Loggerhead, *Caretta caretta*; Kemp's Ridley, *Lepidochelys kempii*). Journal of Morphology 279, 1224–1233.
- Sampson L, Payán LF, Amorocho DF, Seminoff JA and Giraldo A (2014) Intraspecific variation of the green turtle, *Chelonia mydas* (Cheloniidae), in the foraging area of Gorgona natural national park (Colombian Pacific). Acta Biológica Colombiana 19, 461–470.
- Seminoff JA, Allen CD, Balazs GH, Dutton PH, Eguchi T, Haas HL, Hargrove SA, Jensen M, Klemm DL, Lauritsen AM, MacPherson SL, Opay P, Possardt EE, Pultz S, Seney E, Van Houtan KS and Waples RS (2015) Status review of the green turtle (*Chelonia mydas*) under the endangered species act. NOAA Technical Memorandum, NOAANMFS-SWFSC-539, 571 pp.
- Seminoff JA, Jones TT, Resendiz A, Nichols WJ and Chaloupka MY (2003) Monitoring green turtles (*Chelonia mydas*) at a coastal foraging area in Baja California, Mexico: multiple indices describe population status. *Journal of the Marine Biological Association of the United Kingdom* 83, 1355–1362.
- Sielfeld W, Salinas-Cisternas P, Contreras D, Tobar M, Gallardo J and Azocar C (2019) Population status of green turtles (*Chelonia mydas*) foraging in Arica Bay, Chile. *Pacific Science* 73, 501–514.

- Sönmez B (2019) Morphological variations in the green turtle (*Chelonia mydas*): a field study on an eastern Mediterranean nesting population. *Zoological Studies* 58, 16.
- Stevenson RD and Woods WA (2006) Condition indices for conservation: new uses for evolving tools. Integrative and Comparative Biology 46, 1169–1190.
- Teas WG (1993) Species composition and size class distribution of marine turtle strandings on the Gulf of Mexico and southeast United States coasts, 1985–1991. NOAA Technical Memorandum NMFS-SEFSC-315.
- van Dam RP and Diez CE (1998) Caribbean Hawksbill turtle morphometrics. Bulletin of Marine Science 62, 145–155.
- van de Merwe J, Hodge M, Whittier JM, Ibrahim K and Lee SY (2010) Persistent organic pollutants in the green sea turtle *Chelonia mydas*: nesting population variation, maternal transfer, and effects on development. *Marine Ecology Progress Series* **403**, 269–278.
- van de Merwe J, Ibrahim K and Whittier J (2005) Effects of hatchery shading and nest depth on the development and quality of *Chelonia mydas* hatchlings: implications for hatchery management in Peninsular, Malaysia. *Australian Journal of Zoology* **53**, 205–211.
- Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36, 1–48.
- Wabnitz C and Pauly D (2008) Length-weight relationships and additional growth parameters for sea turtles. In Palomares MLD and Pauly D (eds), *Von Bertalanffy Growth Parameters of Non-Fish Marine Organisms*. Fisheries Centre Research Reports, no. 16. Vancouver: Fisheries Centre, University of British Columbia, pp. 92–101.
- Wallace BP, DiMatteo AD, Hurley BJ, Finkbeiner EM, Bolten AB, Chaloupka MY, Hutchinson BJ, Abreu-Grobois FA, Amorocho D, Bjorndal KA, Bourjea J, Bowen BW, Dueñas RB, Casale P, Choudhury BC, Costa A, Dutton PH, Fallabrino A, Girard A, Girondot M, Godfrey MH, Hamann M, López-Mendilaharsu M, Marcovaldi MA, Mortimer JA, Musick JA, Nel R, Pilcher NJ, Seminoff JA, Troëng S, Witherington B and Mast RB (2010) Regional management units for marine turtles: a novel framework for prioritizing conservation and research across multiple scales. *PLoS ONE* 5, e15465.
- Wan X, Wang W, Liu J and Tong T (2014) Estimating the sample mean and standard deviation from the sample size, median, range and/or interquartile range. *BMC Medical Research Methodology* 14, 135.
- Wang Y-F, Li T-H, Jiang Y-F, Chi C-H, Cheng I-J, Cheng C-H, Sun R and Yu P-H (2020) Light microscopic and ultrastructural characteristics of heterophil toxicity and left-shifting in green sea turtles (*Chelonia mydas*) from Taiwan. *Zoological Studies* 59, 52.
- Work TM and Balazs GH (1999) Relating tumor score to hematology in green turtles with fibropapillomatosis in Hawaii. *Journal of Wildlife Diseases* 35, 804–807.