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The condition conundrum: application of multiple condition indices to the dusky shark *Carcharhinus obscurus*

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ABSTRACT: Measuring fish condition has become a standard practice in the management of fishes, both at the individual and population level. The comparative application of several condition indices to sharks, however, has not yet received a rigorous evaluation. Data for a total of 2120 dusky sharks *Carcharhinus obscurus* (Lesueur, 1818), ranging in size from newborns (≤79 cm precaudal length [PCL]) to mature adults (≥210 cm PCL), were used to calculate seasonal trends in condition and to facilitate index comparisons. Four commonly used condition measures were selected, including a somatic measure, hepatosomatic index (HSI), and 3 morphometric measures, condition factor (CF), relative condition (Kn) and residual condition (Rr_{PCL}). The effect of month was significant for most condition analyses by size class, sex and reproductive state. HSI was found to be the most sensitive index and rapid indicator of condition, but its appropriate use requires the disaggregation of data by clearly defined life stages and reproductive states. The relatively large liver size of neonates and the relatively small liver size of pregnant and postpartum females may otherwise bias interpretations of seasonal variations in condition. HSI was also affected by increasing size of the animal, which confounds inter-size-class comparisons and may require the further division of life-stage data into additional size classes. The results of the 3 morphometric measures were comparable but were not correlated with HSI. CF, Kn and Rr_{PCL} lagged behind HSI, were unable to differentiate between neonate and juvenile animals and were insensitive to short-term variations. The effect of increasing size did not affect calculated CF and Rr_{PCL}, but Kn demonstrated a negative correlation. The fact that large predators may consume large volumes of food in a single feeding event was identified as a possible complicating factor in interpreting condition indices.

KEY WORDS: Hepatosomatic index · Condition factor · Morphometric condition indices · *Carcharhinus obscurus* · Ontogenetic variation

INTRODUCTION

The use of condition indices to assess ‘health’ or ‘energetic state’ has been applied widely to both marine and terrestrial animals. In vertebrates, these condition indices have been used to assess the effects of environmental threats (pollution and climate change), life-history strategies (migration and reproduction) and ecological interactions (diet, competitive interactions and parasite load) on animal condition (reviewed in Stevenson & Woods 2006). Condition indices typically are calculated from morphological and somatic measures of the animal (e.g. Fulton's condition factor [CF], relative condition [Kn] and relative weight, and hepatosomatic [HSI] and gonadosomatic index, respectively) and the biochemistry of body fluids and tissues or total body composition (e.g. protein and lipid content). Modern thought is that the biochemical measures should correlate and complement the more traditional morphological and somatic approaches. Within the spectrum of traditional condition indices, particularly for fishes, debate exists over the appropriate con-

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dition index to use and the type of analysis to be undertaken (Bolger & Connolly 1989, Springer et al. 1990, Jakob et al. 1996, Pope & Kruse 2007).

Sharks, members of the class Chondrichthyes, have received limited attention with regard to the application of condition indices. Under most circumstances the required data for large and/or highly migratory species are difficult to obtain, restricting comparative condition analyses. Considering the volume of published literature on the use of condition indices for the management of teleost fishes, coupled with the important biological and ecological information that can be elucidated through this approach, it is appropriate to address the subject for this large group of fishes.

The most widely applied measure of condition in sharks is HSI, which expresses liver weight relative to body weight, and is often used as an estimate of the energy status of a fish (Pope & Kruse 2007). The livers of sharks can constitute up to 25% of body mass and are principally formed of lipids (Baldridge 1970, 1972, Watson & Dickson 2001). Springer (1967) first suggested that they act as a food store or energy resource; however, research has primarily focused on its function in buoyancy control and in providing hydrostatic lift (Bone & Roberts 1969, Baldridge 1970, 1972). More recently, Hoffmayer et al. (2006) examined the energy storage capability of the liver of the Atlantic sharpnose shark *Rhizoprionodon terraenovae* using HSI and found that there was a seasonal pattern in the energetic condition of the species. Consequently it would appear that the liver may act as an indicator of the state of balance between food consumed and food required for body metabolism (King 1984). In sharks, HSI has been applied in the study of shark migration ecology (Rossouw 1983, King 1984) and, most frequently, in studies examining the reproductive development/state of sharks (Allen & Cliff 2000, de Bruyn et al. 2005, Dudley et al. 2005, Lucifora et al. 2005).

Morphometric measures of condition, such as CF (Ricker 1975, Nash et al. 2006) and Kn (Le Cren 1951), measure individual variation from an expected weight at a given length. Fulton's condition index has been used to examine seasonal condition patterns in sharks (Atlantic sharpnose shark, Parsons & Hoffmayer 2005; scalloped hammerhead shark *Sphyrna lewini*, Duncan & Holland 2006) and Kn has been correlated with survival rates of newborn/juvenile lemon sharks *Negaprion brevirostris* (Dibattista et al. 2007). The application of morphometric condition indices to sharks, however, has been limited.

A rigorous comparative approach is required to determine the suitability of the various traditional condition indices when applied to sharks. For teleost fishes this has been resolved by calculating multiple condition indices and performing inter-condition index comparisons (Bolger & Connolly 1989, Jakob et al. 1996). The present paper reports a similar comparison of condition indices for sharks by making use of a comprehensive long-term data set on the dusky shark *Carcharhinus obscurus* caught in beach protection nets in KwaZulu-Natal (KZN), South Africa. The objectives of the present study were to calculate 3 standard morphometric indices and a somatic index for dusky sharks to (1) examine seasonal trends in condition by life stage, (2) facilitate a comparison of the 4 calculated condition indices by life stage and examine the effect of increasing animal size, (3) examine the sensitivity of the condition indices and (4) discuss why differences between condition indices occur.

MATERIALS AND METHODS

Study location. Data for the dusky shark were accessed from the KwaZulu-Natal Sharks Board (KZNSB) archived database (1982 to 2007). All sharks were caught in beach protection nets set at popular bathing localities along the coastline of KZN. Dead sharks, with the exception of those in an advanced state of decomposition, were returned to the KZNSB laboratory for dissection and included in the analyses. For specific details of the net locations, net types, KZNSB service operations, and modifications in net installations for the study period, refer to Cliff et al. (1988) and Dudley et al. (2005). On an annual basis, sea surface temperatures in KZN range from 21 to 27°C (van der Elst 1981). The cooler autumn/winter season and warmer spring/summer season are defined by the months of April to September and October to March, respectively.

The dusky shark was selected as the model species for the present study due to its high catch rate (20% of total annual shark catch) and the sampling of all size classes (Dudley et al. 2005). Sufficient data were available to allow detailed statistical analyses to be conducted in relation to changes in condition indices by season, life stage (size), sex and reproductive state.

The KZN coast is a nursery ground for dusky sharks (Bass et al. 1973, Dudley et al. 2005) with juveniles remaining in the region until they attain a size of approximately 100 cm precaudal length (PCL). As a result, juveniles (including neonates) are caught in the nets throughout the year. Larger dusky sharks — sub-adults and adults of both sexes — are caught less frequently; however, both pregnant and postpartum animals are sampled. June and July form the peak catch period for both sub-adult and adult animals, corresponding with the migration of sardines *Sardinops sagax* along the KZN coastline (Armstrong et al. 1991). For details on the geographic and spatial distribution of dusky shark catches in KZN waters refer to Dudley et al. (2005).

The data required for the condition analyses included sex, date of capture, capture location, PCL (cm), total body mass (kg), total liver mass (kg), stomach mass (kg), total pup mass (kg) (for pregnant sharks), reproductive state and the seasonal catch of postpartum dusky sharks. PCL was measured as the straight line distance from the tip of the snout to the precaudal notch as defined by Dudley et al. (2005). Visual assessment of maturity and reproductive state were based on the criteria defined by Bass et al. (1973).

Data division by size class. Prior to analyses, the data were divided into size classes as recommended by Pope & Kruse (2007). Three size classes were selected: small, <100 cm PCL; medium, 100 to 209 cm PCL; and large, ≥210 cm PCL, approximating maturity states. The small sharks were further subdivided into ≤79.0 cm PCL (assumed to be neonates after Dudley et al. 2005) and 79.1 to 99.9 cm PCL (assumed to be > 1 yr old), hereinafter referred to as neonates and juveniles, respectively. Small male and female sharks were combined since they inhabit the same nursery region. Because larger animals may pursue distinct sex-specific life strategies, medium and large sharks were divided by sex and large sharks further subdivided by reproductive state. Large males (≥210 cm PCL) included immature (Stage 2), and mature (Stage 3) individuals, as well as individuals with regressed testes (Stage 6). No males considered to be in mating condition were recorded in the data. All large males were therefore amalgamated into 1 data set. Large females included immature (Stage 2), mature but inactive or non-gravid (Stage 3), pregnant (Stage 5) and postpartum (Stage 6) animals. Given the large energetic demand on pregnant sharks during the gestation phase, pregnant and postpartum animals were isolated from the large female data set (≥210 cm PCL) and presented independently.

Condition indices. For each size class, 4 commonly used condition indices were calculated. HSI, the most widely used somatic measure (Stevenson & Woods 2006, Pope & Kruse 2007), was calculated using:

$$\text{HSI} = [\text{liver mass (kg)} / \text{total body mass (kg)}] \times 100 \quad (1)$$

The morphometric indices of condition assessed in the present study included CF (Ricker 1975, Nash et al. 2006), Kn (Le Cren 1951) and residual morphometric condition, Rr_{PCL} (Fechhelm et al. 1995). CF was calculated using:

$$\text{CF} = [\text{total body mass (kg)} / \text{PCL (cm)}^3] \times 10^5 \quad (2)$$

whereby the linear measure of length is raised to the power of 3, assuming that mass and the linear dimension increase isometrically. Kn was calculated using:

$$\text{Kn} = [\text{total body mass (kg)} \times \text{PCL (cm)}^{-b}] \times 10^5 \quad (3)$$

where b = slope of a regression plot of $\log_{10}$ mass vs. $\log_{10}$ PCL. In the present study a value for b of 3.04 was used (n = 2627, $p < 0.001$; Dudley et al. 2005). To determine Rr_{PCL}, a linear least-squares regression model was applied to the $\log_{10}$-transformed length and mass data (Fechhelm et al. 1995, Schulte-Hostedde et al. 2005). Individual sharks were then assigned their residual value of predicted body mass (Rr_{PCL}) from the fitted model for all subsequent analyses. Rr_{PCL} measures the variability in the data after variation tied to increasing size/mass of an animal has been removed. To standardise pregnant female data prior to the calculation of all condition indices, actual body mass was calculated by subtracting the total mass of the near-term pups. For the selected condition indices, total body mass included viscera and stomach contents, in line with standard practices (Bolger & Connolly 1989). Monthly mean somatic and morphometric condition index values (±1 SE) were then plotted for each size class and sex/reproductive state.

Statistical analysis. HSI, CF, Kn and Rr_{PCL} were each tested using a 2-factor ANOVA in which each condition index was entered as the response variable, and month and size class (for small sharks, i.e. neonates and juveniles), month and sex (for medium and large sharks), and month and reproductive state (for large reproductively active pregnant and postpartum females) entered as treatments. Respective interaction terms were included in all models. Because the sample sizes were unbalanced, adjusted Bonferroni pairwise comparisons were undertaken to test for monthly variations in condition indices within and between defined treatments. To examine for possible length-related bias in HSI, CF, Kn and Rr_{PCL} within the medium and large size classes, a 2-factor ANOVA was performed with PCL as the response variable and the treatments per size class. For neonates and juveniles, a 1-factor ANOVA tested each size class with PCL as the response variable and month as the treatment. The testing for the assumptions of the ANOVA was undertaken as recommended by Underwood (1997). For data that did not meet the requirement of normality and homogeneity of variance, the graphical approach recommended by McGuinness (2002) was adopted prior to accepting non-parametric tests. Observation of residual vs. fitted plots/variance vs. mean plots indicated adequate conformity to homoscedasticity. To test for differences in condition between reproductively inactive large sharks and pregnant/postpartum females, a 2 sample *t*-test was undertaken for each condition index. To examine the influence of increasing size on the condition indices and possible complications in interpreting and comparing the results between size classes, each shark's calculated value for each condition index was plotted as a function of PCL

(Colautti et al. 2006). Each condition index was then correlated with PCL using Pearson's r (Jakob et al. 1996). To investigate the relationship between the condition indices, Pearson correlation coefficients were calculated for all pairwise combinations of the 4 condition indices. The level of statistical significance for all the above tests was set at $\alpha = 0.05$.

RESULTS

A total of 2120 dusky sharks (1384 females and 736 males) were used to calculate the condition indices. Sample sizes, mean (±1 SE) and range of PCL, total body mass, liver mass and stomach mass for each size class are presented in Table 1. On average stomach mass accounted for 0.75% of the total body mass (Table 1). A least-squares regression of $\log_{10}$ PCL vs. $\log_{10}$ total body mass for all data resulted in a significant relationship from which residual values for Rr_{PCL} for each shark were calculated (Fig. 1). For sample sizes of sharks per month for each size class/sex and reproductive state, see Figs. 2e, 3e, 4e & 5e.

Comparison of condition indices by size class

Small neonate and juvenile sharks

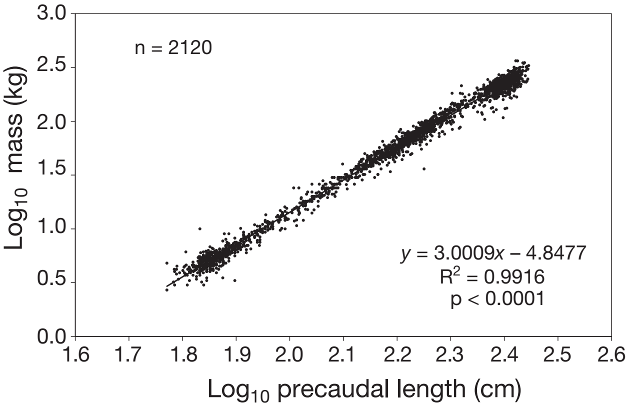

Fig. 1. *Carcharhinus obscurus*. Least-squares linear regression of $\log_{10}$ total body mass against $\log_{10}$ precaudal length for all sharks sampled between 1982 and 2007

The seasonal trend of HSI was markedly different for neonates and juveniles (Fig. 2a, Table 2). HSI of the neonates increased from April to a peak in June to August followed by a gradual decline throughout the rest of the year. A significant effect of month was detected (Table 2, Fig. 2a). The peak in neonate HSI correlated with the highest catch rate of postpartum sharks (Fig. 2a). For the juveniles, HSI remained constant (Fig. 2a). Direct month-to-month comparisons between the 2 size classes showed significant differences in HSI for 7 of the 12 months (Table 3, grey section). The trends for all 3 morphometric indices, CF, Kn and Rr_{PCL}, were similar on an annual cycle for neonates and juveniles (Fig. 2b–d). In contrast to HSI, no significant difference was detected in direct month-to-month comparisons of CF, Kn and Rr_{PCL} between the 2

Table 1. *Carcharhinus obscurus*. Precaudal length (PCL), body mass, liver mass and stomach mass for each predetermined size classification (mean ± SE). Values in brackets indicate min. and max. range. Codes determining maturity/reproductive state: 1 = immature, 2 = adolescent, 3 = mature but inactive; for males, 6 = regressed testis; for females, 5 = pregnant and 6 = postpartum (after Bass et al. 1973). Total pup mass is subtracted from mass of pregnant sharks

Size class PCL (cm)	Sex	Maturity/ reprod. state	n	PCL (cm)	Body mass (kg)	Liver mass (kg)	Stomach mass (kg)
Small neonate ≤79		1	469	71.8 ± 0.2 (59.0–79.0)	5.3 ± <0.1 (2.7–10.0)	0.58 ± 0.01 (0.10–1.70)	0.03 ± 0.04 (0–0.60)
Small juvenile 79.1–99.9		1	129	87.9 ± 0.5 (79.4–99.4)	9.6 ± 0.2 (6.0–16.0)	0.58 ± 0.02 (0.15–1.60)	0.13 ± 0.02 (0–1.09)
Medium 100–209	M	1, 2	374	159.7 ± 1.2 (101.2–209.0)	63.5 ± 1.5 (10.7–214.0)	6.17 ± 0.21 (0.42–24.00)	0.31 ± 0.05 (0–8.14)
	F	1, 2	584	161.4 ± 1.1 (101.0–209.1)	67.3 ± 1.3 (12.0–182.0)	6.77 ± 0.19 (0.50–25.00)	0.31 ± 0.05 (0–17.12)
Large inactive ≥210	M	2, 3, 6	106	238.7 ± 0.9 (210.0–256.0)	198.7 ± 2.6 (128.0–270.0)	27.54 ± 0.86 (5.90–46.00)	2.48 ± 0.61 (0–29.80)
	F	2, 3	104	238.2 ± 1.6 (210.0–275.0)	195.3 ± 4.8 (104.0–365.0)	25.41 ± 1.25 (7.30–66.00)	1.79 ± 0.49 (0–30.00)
Large active ≥210	F	5	208	253.4 ± 0.8 (222.0–279.0)	268.3 ± 3.2 (122.2–349.2)	21.20 ± 0.55 (5.70–56.00)	0.31 ± 0.10 (0–11.10)
	F	6	146	255.2 ± 1.0 (224.0–276.0)	228.8 ± 3.4 (108.0–350.0)	25.90 ± 1.00 (6.40–70.00)	1.96 ± 0.46 (0–36.19)
Total			2120				

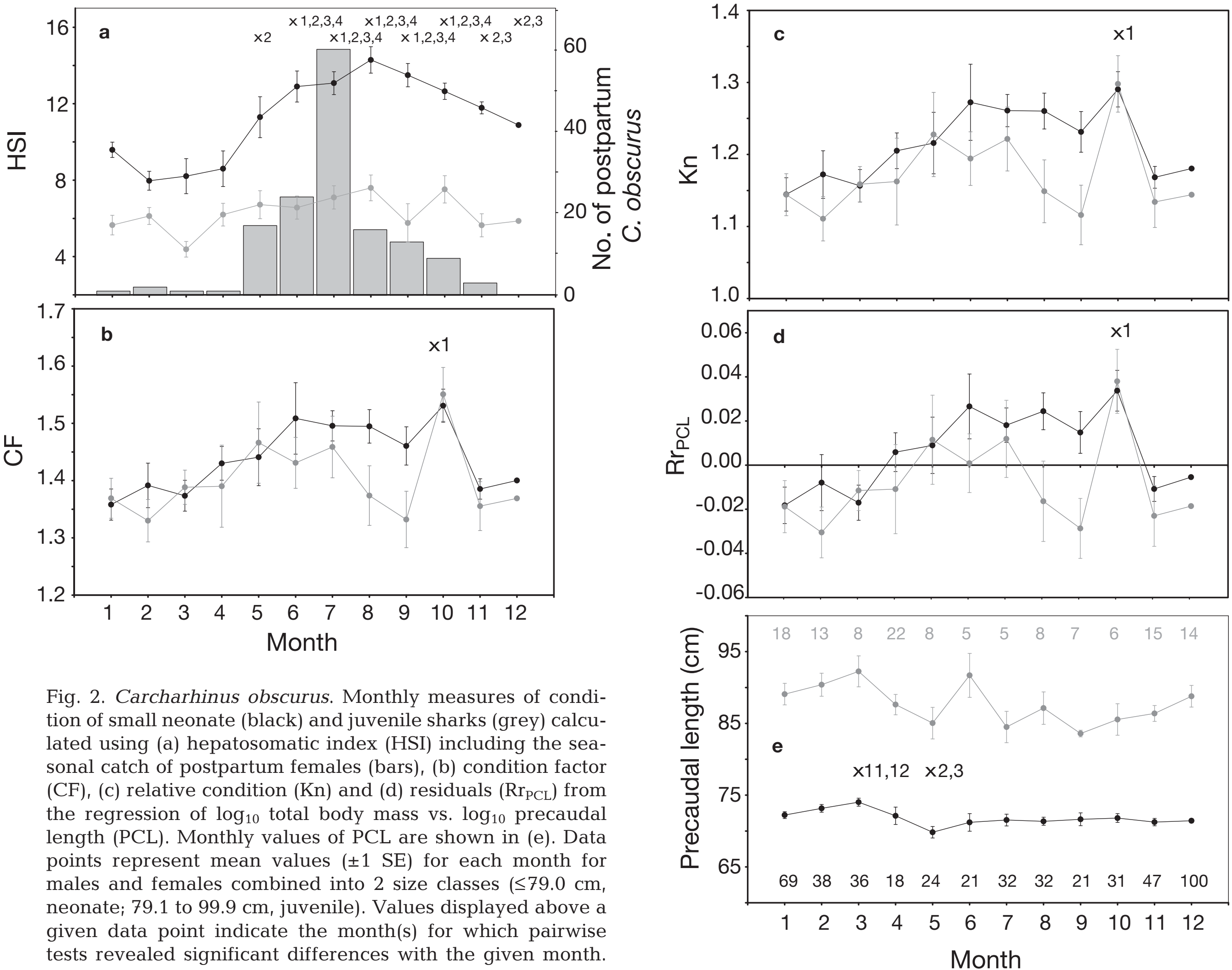

Fig. 2. *Carcharhinus obscurus*. Monthly measures of condition of small neonate (black) and juvenile sharks (grey) calculated using (a) hepatosomatic index (HSI) including the seasonal catch of postpartum females (bars), (b) condition factor (CF), (c) relative condition (Kn) and (d) residuals (Rr_{PCL}) from the regression of $\log_{10}$ total body mass vs. $\log_{10}$ precaudal length (PCL). Monthly values of PCL are shown in (e). Data points represent mean values (±1 SE) for each month for males and females combined into 2 size classes (≤79.0 cm, neonate; 79.1 to 99.9 cm, juvenile). Values displayed above a given data point indicate the month(s) for which pairwise tests revealed significant differences with the given month. Number of observations (n) for each month is shown in (e) for both size classes of shark

size classes. The monthly mean PCL of neonates was variable throughout the year, in contrast to juveniles, where no significant effect of PCL was observed ($F = 2.62$, df = 11, $p < 0.003$ and $F = 1.81$, df = 11, $p = 0.06$, respectively; Fig. 2e).

Medium sharks

The mean HSI value of male medium sharks was significantly different to females (Table 2). HSI of both sexes peaked in June and July but was relatively constant throughout the rest of the year (Fig. 3a). There was an effect of month for both sexes, with significantly higher HSI values in June and July than all other months (Table 2, Fig. 3a). In the 2 periods February/March and September/October, males showed a trend for lower HSI values than females (Fig. 3a). CF, Kn and Rr_{PCL} for both sexes followed a similar monthly trend to HSI, with 'slump' periods in condition for males in March and October. All morphometric indices for both sexes peaked in July but, unlike HSI, not in June (Fig. 3b–d, Table 2). Mean monthly PCL values of males and females increased in June and July (Fig. 3e) following a similar annual trend to all condition indices (Fig. 3a–d). Both sexes were significantly larger in size in June and July than all other months ($F = 8.00$, df = 11, $p < 0.0001$; Fig. 3e).

Large reproductively inactive sharks

Sample sizes restricted data analysis of large sharks to the months of June, July and August only (Fig. 4e). No significant effects of month or sex were detected for HSI (Table 2, Fig. 4a). For all 3 morphometric condition

Table 2. *Carcharhinus obscurus*. 2-factor ANOVA to test for effects of month and size class (≤79 or ≤100 cm precaudal length [PCL]) for small neonate and juvenile sharks, month and sex for medium (100 to 209 cm PCL) and large reproductively inactive sharks (≥210 cm PCL), and month and reproductive state for reproductively active pregnant and postpartum females (≥210 cm PCL) for each of the condition indices. All model interactions are included. HSI = hepatosomatic index, CF = condition factor, Kn = relative condition and Rr_{PCL} = residuals from the regression of $\log_{10}$ body mass vs. $\log_{10}$ PCL. Significant p-values in **bold**

Source	Small[a]			Medium[b]			Large					
							Reproductively inactive[b]			Reproductively active females[c]		
	df	*F*	p	df	*F*	p	df	*F*	p	df	*F*	p
HSI												
Month	11	5.38	**<0.001**	11	27.14	**<0.001**	2	1.80	0.169	4	4.92	**<0.001**
Treatment	1	194.26	**<0.001**	1	6.72	**0.010**	1	3.18	0.076	1	0.21	0.651
Month × Treatment	11	2.33	**0.008**	11	1.56	0.107	2	0.68	0.508	4	6.92	**<0.001**
CF												
Month	11	2.27	**0.010**	11	8.46	**<0.001**	2	5.13	**0.007**	4	3.22	**0.013**
Treatment	1	3.32	0.069	1	4.24	**0.040**	1	0.35	0.557	1	3.58	0.060
Month × Treatment	11	0.50	0.906	11	0.92	0.523	2	0.92	0.401	4	3.95	**0.004**
Kn												
Month	11	2.28	**0.010**	11	7.65	**<0.001**	2	5.12	**0.007**	2	3.22	**0.014**
Treatment	1	5.55	**0.019**	1	3.73	0.054	1	0.34	0.560	1	3.49	0.063
Month × Treatment	11	0.49	0.912	11	0.91	0.527	2	0.93	0.397	2	3.97	**0.004**
Rr_{PCL}												
Month	11	2.44	**0.006**	**11**	7.73	**<0.001**	2	5.57	**0.005**	2	2.57	**0.039**
Treatment	1	2.87	0.09	11	5.05	**0.025**	1	0.79	0.375	1	3.94	**0.048**
Month × Treatment	11	0.58	0.848	11	1.03	0.415	2	1.13	0.325	2	3.20	**0.014**

[a] Treatment is size class
[b] Treatment is sex
[c] Treatment is reproductive state

indices (CF, Kn and Rr_{PCL}), month had a significant effect (Table 2). Reproductively inactive females had significantly higher CF, Kn and Rr_{PCL} values in June than in August (Fig. 4b–d). The interaction term month × sex was not significant for any somatic or morphometric condition index, indicating large sharks of both sexes exhibited similar trends in condition over the 3 mo. The mean size of both sexes was similar across the 3 mo period ($F = 0.47$, df = 2, $p = 0.63$; Fig. 4e).

Large pregnant and postpartum females

Sample size restricted data analysis for pregnant and postpartum sharks to the months of May to Sep-

Table 3. *Carcharhinus obscurus.* All monthly hepatosomatic index (HSI) pairwise comparisons between neonates (≤79.0 cm PCL) and juveniles (79.1 to 99.9 cm PCL). •••, $p < 0.001$; ••, $p < 0.01$; •, $p < 0.05$. Grey shading: direct month-to-month comparisons between the 2 size classes

	Neonatal *C. obscurus*											
Month	1	2	3	4	5	6	7	8	9	10	11	12
Juvenile *C. obscurus* 1	•			•••	•••	•••	•••	•••	•••	•••	•••	
2				••	•••	•••	•••	•••	•••	•••	••	
3	•				•••	•••	•••	•••	•••	•••	•••	•••
4	•				•••	•••	•••	•••	•••	•••	•••	•••
5						•	••	•••	•••	••	•	
6						•	•	••	•	•		
7							•	••	•			
8						•	•	•••	•	•		
9					•	•••	•••	•••	•••	•••	•	•
10							•	••	•			
11	•				•••	•••	•••	•••	•••	•••	•••	•••
12	•				••	•••	•••	•••	•••	•••	•••	•••

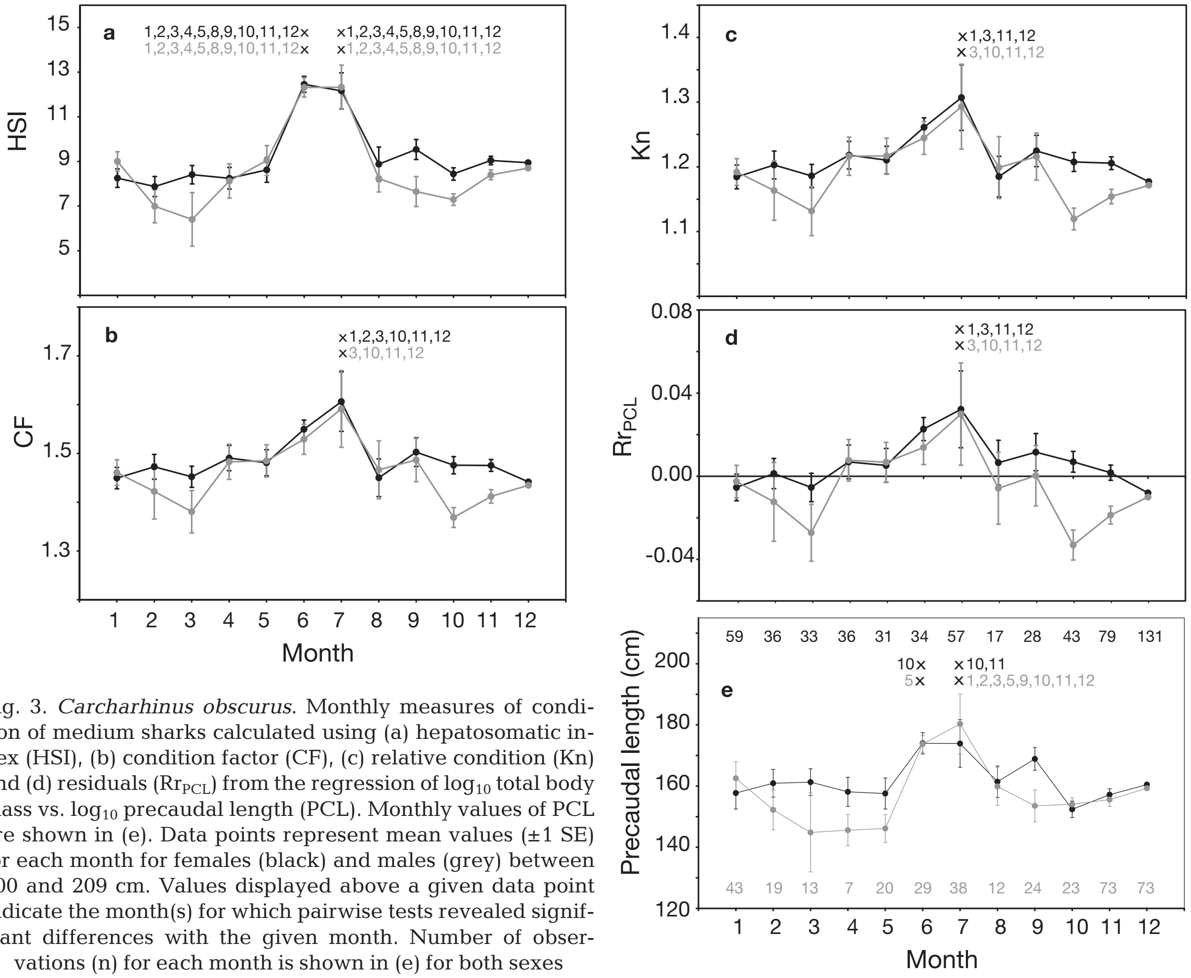

Fig. 3. *Carcharhinus obscurus*. Monthly measures of condition of medium sharks calculated using (a) hepatosomatic index (HSI), (b) condition factor (CF), (c) relative condition (Kn) and (d) residuals (Rr_{PCL}) from the regression of $\log_{10}$ total body mass vs. $\log_{10}$ precaudal length (PCL). Monthly values of PCL are shown in (e). Data points represent mean values (±1 SE) for each month for females (black) and males (grey) between 100 and 209 cm. Values displayed above a given data point indicate the month(s) for which pairwise tests revealed significant differences with the given month. Number of observations (n) for each month is shown in (e) for both sexes

tember only (Fig. 5e). HSI of pregnant sharks increased to a peak in July with a gradual reduction throughout the rest of the year, before a second peak in December. Monthly mean HSI values of postpartum sharks were more variable (Fig. 5a). A significant effect of month was detected (Table 2, Fig. 5a). The trend of morphometric condition of pregnant and postpartum animals was dissimilar between August and November (Fig. 5b–d). For pregnant sharks, all 3 morphometric condition indices remained constant between February and July, increasing to a peak in September (Fig. 5b–d). For the months of May, August and October, postpartum sharks showed small peaks in CF, Kn and Rr_{PCL} similar to HSI (Fig. 5c–e). The mean size of both pregnant and postpartum sharks was similar across the 5 mo period ($F = 2.31$, df = 4, $p = 0.058$; Fig. 5e). Large reproductively inactive males and females were in significantly higher condition than pregnant/postpartum females for all calculated condition indices (Table 4).

Effect of PCL on condition indices

Plots of calculated HSI, CF, Kn and Rr_{PCL} values vs. PCL for each individual shark for all size classes and reproductive states are shown in Fig. 6a–d. Neonates had HSI values ranging from 2.4 to 26.2 (Fig. 6a). Between juvenile and mature adults, HSI followed an asymmetric distribution, with maximum HSI values increasing with size of animal (Fig. 6a). HSI of pregnant females was lower than that of large reproductively inactive males and females (Fig. 6a, Table 4). The peak HSI values of the reproductively inactive sharks were equivalent to that of the neonates. HSI was positively correlated with increasing body length ($r_{2118} = 0.164$, $p < 0.001$). CF, Kn and Rr_{PCL} values plotted against PCL revealed little effect of increasing PCL on the morphometric condition indices (Fig. 6b–d). Pearson's r correlation found that CF and Rr_{PCL} were not significantly correlated with shark length ($r_{2118} = -0.025$ and $r_{2118} = -0.030$ respectively, $p > 0.05$), while for Kn there was a significant negative correlation (r_{2118}

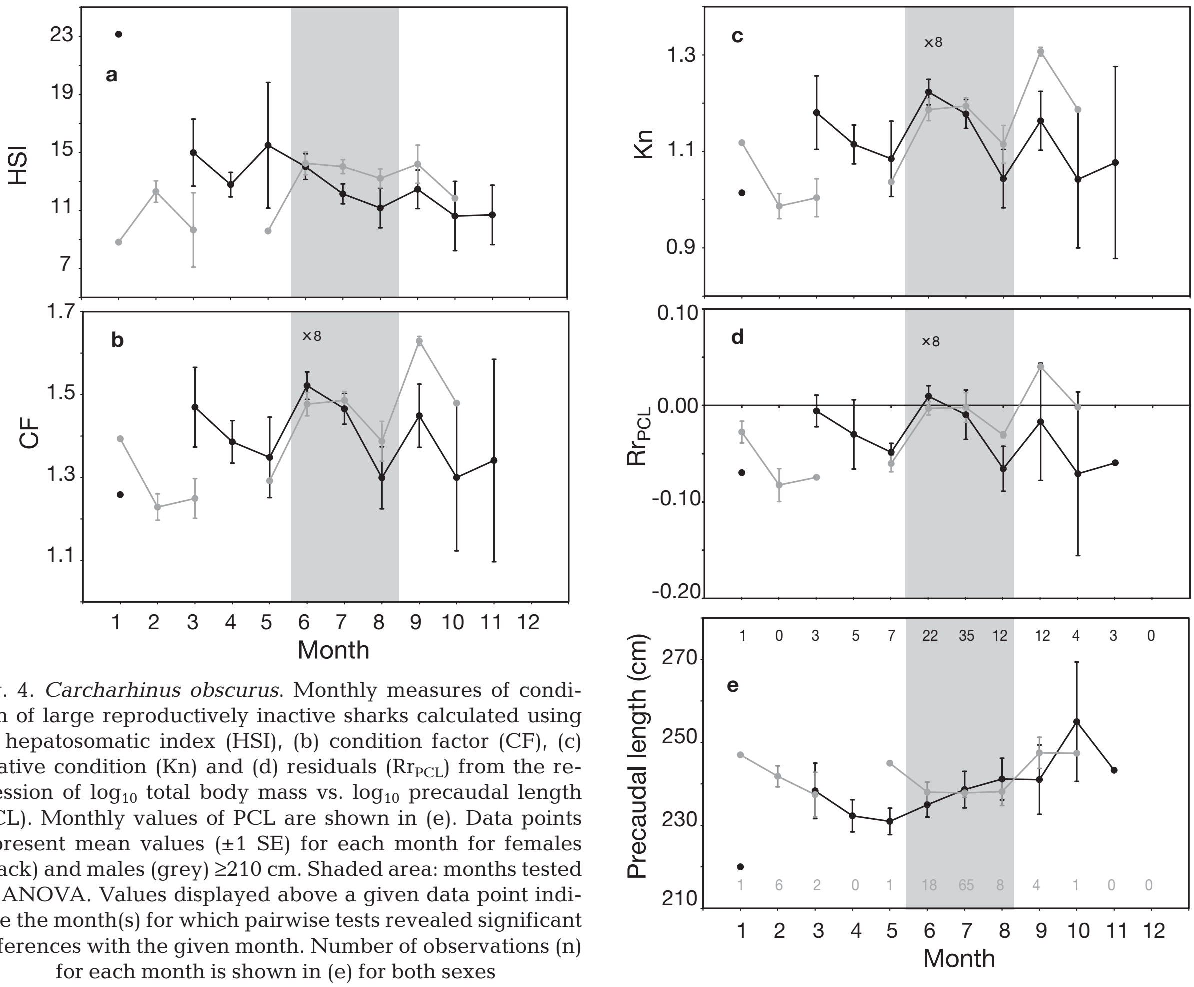

Fig. 4. *Carcharhinus obscurus*. Monthly measures of condition of large reproductively inactive sharks calculated using (a) hepatosomatic index (HSI), (b) condition factor (CF), (c) relative condition (Kn) and (d) residuals (Rr_{PCL}) from the regression of $\log_{10}$ total body mass vs. $\log_{10}$ precaudal length (PCL). Monthly values of PCL are shown in (e). Data points represent mean values (±1 SE) for each month for females (black) and males (grey) ≥210 cm. Shaded area: months tested by ANOVA. Values displayed above a given data point indicate the month(s) for which pairwise tests revealed significant differences with the given month. Number of observations (n) for each month is shown in (e) for both sexes

$= -0.166$, $p < 0.001$). Pearson correlation coefficients for all pairwise comparisons of the 4 condition indices are presented in Table 5. CF, Kn and Rr_{PCL} were highly correlated with each other but the 3 morphometric condition measures were not correlated with HSI.

DISCUSSION

The data of the present study are unique in that 2120 dusky sharks were available to enable a comprehensive comparison of multiple condition indices for a large predator. Generally, such data are both scarce and difficult to obtain, considering the necessity for mortalities coupled with the global declines observed for many large sharks. By applying several widely used condition indices, the present study enabled a detailed comparison of their sensitivity, their seasonal variability within each life stage and for sex and reproductive state, and the effect of increasing animal size. For teleosts, differences between condition indices have been identified and the appropriate application of selected condition indices proposed. The present study on an elasmobranch found that differences between somatic and morphometric condition indices occur and that several confounding factors require attention when examining the condition of sharks. The data underscore the value of condition indices for elucidating seasonal condition patterns for various life stages of a large shark.

Comparison of condition by size class, sex and reproductive state

Small neonate and juvenile sharks

Marked differences in the seasonal trends in HSI between neonate and juvenile sharks were evident.

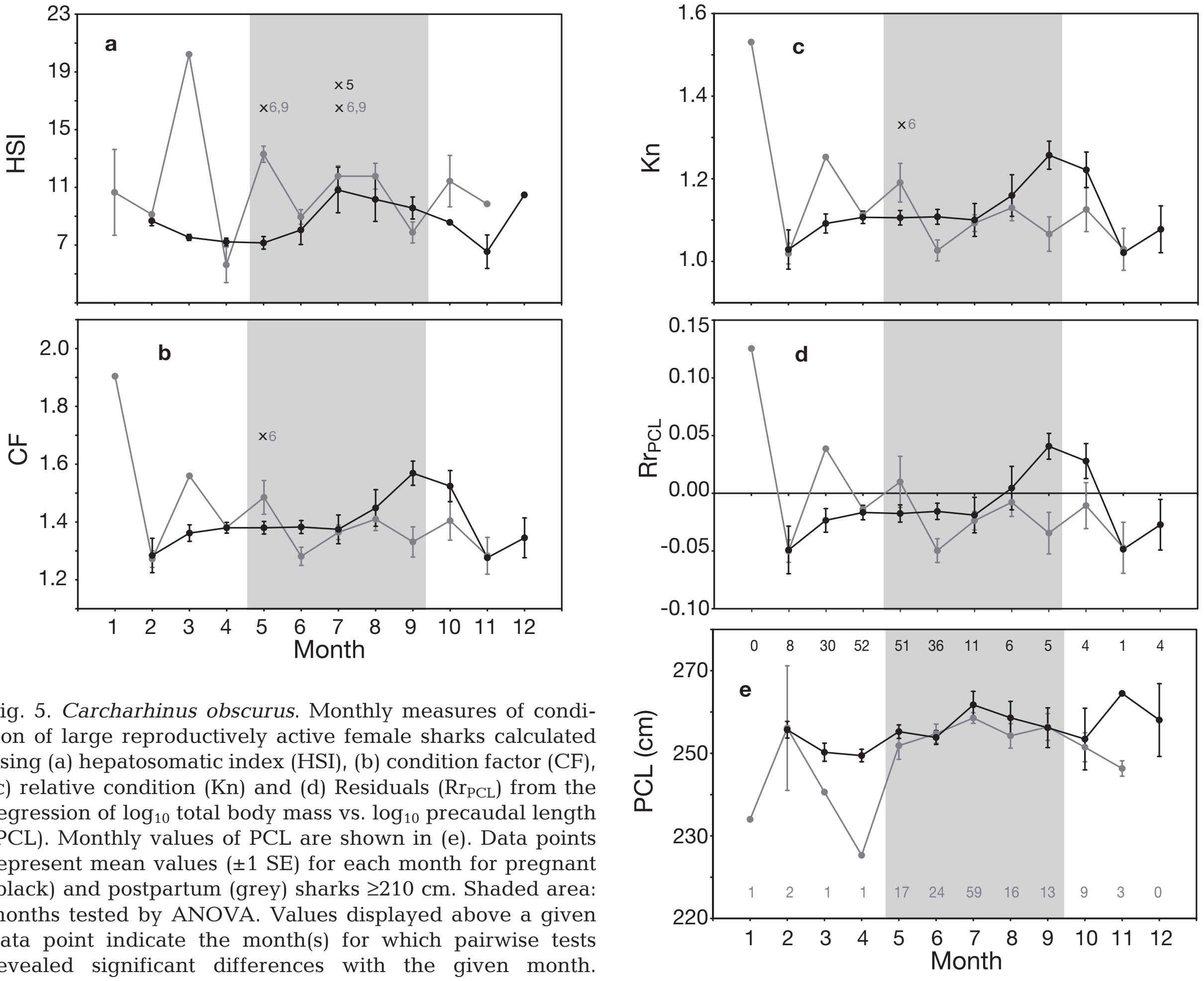

Fig. 5. *Carcharhinus obscurus.* Monthly measures of condition of large reproductively active female sharks calculated using (a) hepatosomatic index (HSI), (b) condition factor (CF), (c) relative condition (Kn) and (d) Residuals (Rr_{PCL}) from the regression of $\log_{10}$ total body mass vs. $\log_{10}$ precaudal length (PCL). Monthly values of PCL are shown in (e). Data points represent mean values (±1 SE) for each month for pregnant (black) and postpartum (grey) sharks ≥210 cm. Shaded area: months tested by ANOVA. Values displayed above a given data point indicate the month(s) for which pairwise tests revealed significant differences with the given month. Number of observations (n) for each month is shown in (e) for both reproductive states

The observed HSI peak for neonates corresponded with the highest catch rate of postpartum sharks and the reported peak pupping period (Bass et al. 1973, Dudley et al. 2005). Our data are in agreement with Francis & Stevens (2000), who reported that near-term porbeagle shark *Lamna nasus* embryos had higher HSI levels than juveniles. Dudley et al. (2005) amalgamated the small and medium dusky sharks included in the present analysis to examine HSI and detected peak values for the months of June and July, which they attributed to the abundant food resource of the sardine run. While this conclusion is consistent with the high incidence of sardines in the stomachs of medium sharks, sardines were infrequently recorded in the stomachs of small sharks (Dudley et al. 2005). The lack of a June/July HSI peak for juveniles in the present study supports this latter observation. The peak observed by Dudley et al. (2005) in June/July was influenced, in part, by the inclusion of neonates in their data

Table 4. *Carcharhinus obscurus.* Mean condition values (±1 SE) for all pregnant or postpartum females and for reproductively inactive large males and females for all calculated condition indices: HSI = hepatosomatic index, CF = condition factor, Kn = relative condition and Rr_{PCL} = residuals from the regression of $\log_{10}$ body mass vs. $\log_{10}$ precaudal length. Associated *t*-test statistics (parentheses: df) are detailed

Index	Mean condition value (±1 SE)		*t*-test	p
	Pregnant & postpartum	Non-reproductively active large (M & F)		
HSI	10.01 ± 0.18	13.26 ± 0.30	(356) 9.25	<0.0001
CF	1.38 ± 0.01	1.45 ± 0.01	(383) 4.17	<0.0001
Kn	1.10 ± 0.01	1.16 ± 0.01	(382) 4.38	<0.0001
Rr_{PCL}	−0.019 ± 0.003	0.002 ± 0.004	(393) 3.80	<0.0001

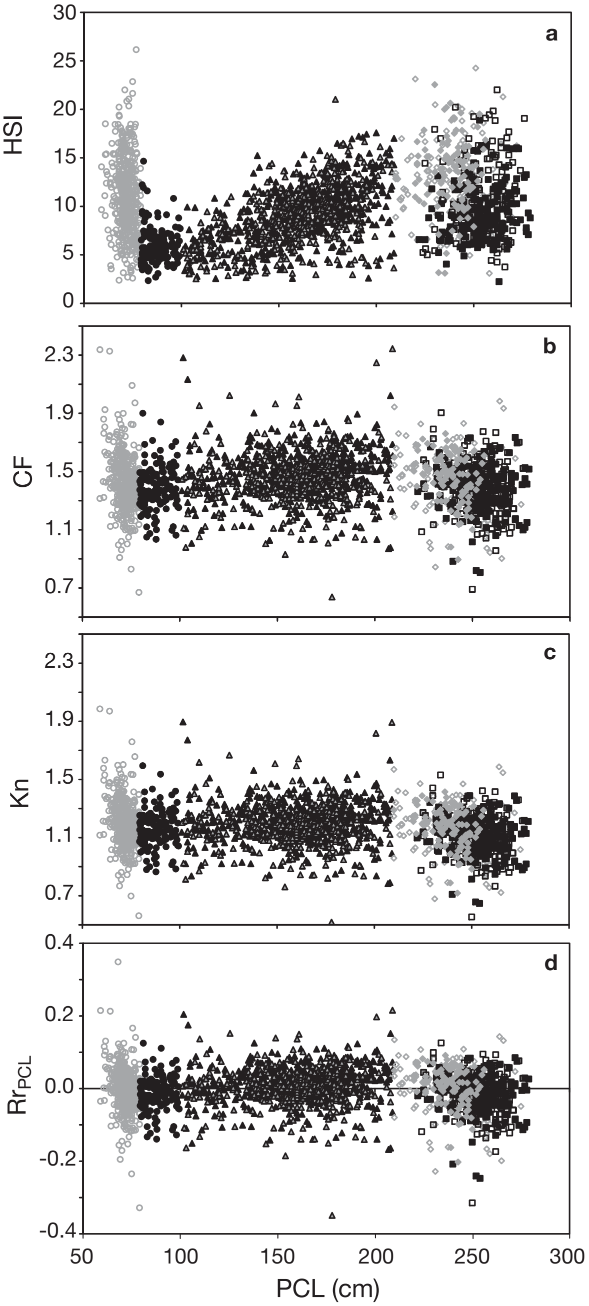

Fig. 6. *Carcharhinus obscurus*. Effect of precaudal length (PCL) on all calculated indices used to assess the condition of sharks: (a) hepatosomatic index (HSI), (b) condition factor (CF), (c) relative condition (Kn) and (d) residuals from the regression of $\log_{10}$ total body mass vs. $\log_{10}$ PCL (Rr_{PCL}). ○ = neonate, ● = juvenile, ▲ = medium female, ▲ = medium male, ◇ = large reproductively inactive female, ◆ = large reproductively inactive male, ■ = pregnant female and □ = postpartum female

Table 5. *Carcharhinus obscurus*. Pearson correlation coefficients for all pairwise comparisons of the 4 condition indices calculated in the present study for the complete data set. HSI = hepatosomatic index, CF = condition factor, Kn = relative condition and Rr_{PCL} = residuals from the regression of $\log_{10}$ body mass vs. $\log_{10}$ precaudal length. *p < 0.001

Index	HSI	CF	Kn
CF	0.19		
Kn	0.17	0.99*	
Pr_{PCL}	0.19	0.99*	0.98*

set. The seasonal HSI cycles observed for neonate and juvenile dusky sharks confirms the importance of separating condition data into ecologically relevant size classes prior to analysis (Pope & Kruse 2007). Differentiating between neonates and juveniles can be achieved through either umbilical scar presence/healing or by determining approximate size-at-age classes. If these data are unavailable, simple plots of liver mass vs. PCL for the species in question will identify the inclusion of neonates in the data. No seasonal fluctuations in HSI of the juvenile sharks were observed in the present study, indicating a tolerance of the summer-winter temperature regime, in contrast to the findings of Hoffmayer et al. (2006) for the Atlantic sharpnose shark.

The morphometric condition indices did not clearly distinguish between juveniles and neonates. Dusky sharks are born at variable sizes in KZN (Bass et al. 1973, Dudley et al. 2005) and it is likely that our proposed neonates included some >1 yr old animals. This dilution effect combined with the low sensitivity of the morphometric indices may explain why CF, Kn and Rr_{PCL} were not able to clearly separate the 2 life stages. The peak in morphometric condition of juveniles in October correlated with a slight increase in HSI in the same month. Dudley et al. (2005) reported that larger near-term embryos were found in pregnant sharks caught towards the end of the year, and hence it is possible that some of the animals categorized as juveniles were actually large neonates.

Medium sharks

The peak in HSI for medium-size dusky sharks during June and July correlates with the presence of the sardine run and the reported high incidence of sardines *Sardinops sagax* in the stomach contents of this size class (Dudley et al. 2005). The increase in HSI in June is dramatic (from ca. 8 to 12%), suggesting an immediate response by the liver to the increased feeding regime. The lipid content, and hence the energetic value, of sardines is extremely high (van der Elst 1979), which may enable rapid storage as lipid in shark livers. Mature spinner sharks *Carcharhinus brevipinna* exhibited a similar trend in HSI (from ca. 10 to 15%) in the study region (Allen & Cliff 2000). Craik (1978) identified an increase in HSI (from ca. 5 to 8%) for female lesser spotted catsharks *Scyliorhinus canicula* in the Irish Sea. For medium-size sharks in the present study, larger individuals of both sexes were caught in June and July. It is likely when assessing HSI of a large size range of animals grouped within 1 class (100 to 209 cm PCL) that interpretation of HSI is confounded by PCL. The notable 'slump' periods in condition of the males are the months when the larger animals within the medium-size category are not normally present in the study region (Dudley et al. 2005). Rossouw (1983) found that the lesser guitarfish *Rhinobatos annulatus* had lower liver lipid content after migration. These slump periods may indicate male dusky sharks that have undertaken migrations. Alternatively, the 'slump' periods may reflect the smaller sharks in the medium category that are present in KZN waters year-round (Dudley et al. 2005). CF, Kn and Rr_{PCL} demonstrated similar seasonal patterns. The marked distinction between the morphological indices and HSI was the gradual increase in condition from May to a peak in July. This may suggest that the morphometric indices lag behind HSI in reflecting improved condition. Alternatively, it may further highlight the effect of PCL on HSI. The general similarity in trend of somatic and morphometric indices for the medium dusky sharks corresponds to the findings of Parsons & Hoffmayer (2005) and Hoffmayer et al. (2006) for CF and HSI of Atlantic sharpnose sharks.

Large reproductively inactive sharks

Considering the limited sample size, there was no apparent influence of the sardine run on HSI of the large sharks, in contrast to medium sharks. Large dusky sharks, particularly males, feed primarily on sardines in June and July (Dudley et al. 2005, KZNSB unpubl. data). This suggests that the absence of an HSI peak may be an artifact of the small sample size, an issue previously raised by Bolger & Connolly (1989). HSI remained relatively constant throughout the year for both sexes (ignoring single datum points). Large reproductively inactive sharks may therefore be in good condition prior to the sardine run, indicating an optimum HSI value or a maximum size the liver can attain for a given life stage. The existence of the latter would be expected, as the abdominal cavity size limits liver size. The peak values of HSI for neonates are equivalent to those of the reproductively inactive sharks, further indicating an optimal HSI value. All 3 morphometric indices followed identical seasonal trends but indicated a more pronounced peak in condition in June than HSI. Large sharks can consume up to 26.6 kg of sardines or 11.3% of total body mass in 1 feeding event (KZNSB unpubl. data). The inclusion of gutted mass could therefore result in lower HSI and higher morphometric condition values than expected. Within our data, it is unlikely that the inclusion of gutted mass had a significant overall influence on our results, considering most individuals had empty stomachs and only a few sharks had a high stomach mass. Although observed annual trends of both somatic and morphometric measures of condition were similar, the inclusion of gutted mass for a few individuals during June/July, i.e. the sardine run, may have resulted in this discrepancy between HSI and CF, Kn and Rr_{PCL}. Measuring morphometric condition of fish is traditionally undertaken on live animals and therefore the inclusion of gut mass is viewed as a contributor to the measure of fitness (Weatherley 1972). Considering global declines in shark populations worldwide, the future application of condition measures will typically be non-invasive (Duncan & Holland 2006, Dibattista et al. 2007), which will preclude the removal of gutted mass. Gutted mass data were unavailable in the present study; however future work could address this point through the calculation of Clarke's isometric and allometric CFs (Ricker 1975) using archived data sets.

Large pregnant and postpartum sharks

The condition of pregnant sharks was similar to that of postpartum sharks, but both were lower than that of reproductively inactive sharks for all condition indices. King (1984) found that pregnant and postpartum female rig *Mustelus lenticulatus* had the lowest HSI values of all mature reproductive stages. Dudley & Cliff (1993) and Allen & Cliff (2000) also found that the HSI of blacktip sharks *Carcharhinus limbatus* and spinner sharks peaked during mating and then decreased during the pregnant and postpartum phases. The energetic cost of gestation and pupping is likely to account for this decrease in condition (Ranzi 1933 cited in Bone & Roberts 1969). For postpartum dusky sharks, there was no clear evidence of an increase in condition relative to pregnant females, except for the month of May. King (1984) reported that the HSI of postpartum rig rapidly increased after pregnancy and pupping ceased. This suggests that most postpartum dusky sharks are caught directly after pupping and that their residency in coastal waters is limited. For both postpartum and pregnant sharks, the minor improvement in HSI in July might be correlated with the sardine run. It would be expected that postpartum sharks would take advantage of the sardine run, but there was no immediate peak in condition in June. This supports dietary data (Dudley et al. 2005, KZNSB unpubl. data) showing that pregnant and postpartum sharks do not actively feed on the sardine run, which may be a result of their weakened condition. The reduced liver size of pregnant sharks coupled with the additional near-term pup mass (ca. 50 kg) would suggest that these sharks were approaching negative buoyancy. Baldridge (1970) reported that pregnant sandbar sharks *C. plumbeus* had relatively low average densities in seawater in comparison with nonpregnant females due to the embryos' lower densities. The reduction in parental liver mass is therefore likely a 2-fold process, providing nourishment to developing young while offsetting the increasing pup HSI throughout the gestation phase to regulate buoyancy. Differences between the morphometric indices and the somatic index for pregnant sharks occurred in the latter part of the year. If we accept a prolonged pupping season, neonates are born at a larger size towards the end of the year (Dudley et al. 2005); consequently, liver size of the mother may be smaller and calculated HSI would be lower than expected, while CF, KN and Rr_{PCL} would be higher. A further explanation may be the result of the high incidence of empty stomachs reported for pregnant dusky sharks (Dudley et al. 2005). Baldridge (1972) reported a significant increase in tissue water in starved sharks and calculated that to increase the water content of a 100 kg shark from the expected tissue water value of ca. 80% to the starved value of ca. 85% would require the addition of 33.3 kg of water. Baldridge (1972) further stated that the increase in water content of muscle tissue resulted in a decrease in observed weight-loss rate. Thus the trend of increasing morphometric condition of pregnant sharks later in the year, which are carrying larger pups, may be a result of an increase in water load in muscle tissue, hence reflecting sharks in extremely poor condition.

Comparison of somatic and morphometric condition indices

For dusky sharks, HSI was clearly a more sensitive measure of condition than the 3 morphometric indices. Adams & McLean (1985) reported similar findings for largemouth bass *Micropterus salmoides*. They concluded that HSI was a relatively rapid response indicator whereas CF was a long-term response indicator and insensitive to short-term variation. When examining seasonal condition trends in the Atlantic sharpnose shark, Parsons & Hoffmayer (2005) and Hoffmayer et al. (2006) found that CF and HSI followed a similar trend across months but the increase in HSI was more pronounced. The marked increase in HSI with increasing size of shark enforces the need for selecting appropriate size, maturity and reproductive-state categories for analysis and comparison, as previously stated by Pope & Kruse (2007). HSI is also complicated on a seasonal basis because it reflects short-term energetic and reproductive states, combined with metabolic demands regulated by temperature and other environmental factors (Adams & McLean 1985, Hoffmayer et al. 2006). Consequently, when using HSI to assess condition, it may be necessary to consider a more complex range of indices including reproductive measures and environmental parameters to fully understand trends in the data. There was minimal variation between the morphometric condition indices CF, Kn and Rr_{PCL} for each life stage, sex and reproductive state. This suggests that any of these condition indices would be suitable for intra-population comparisons. The negative correlation between Kn and PCL of shark was significant. This is surprising because Kn, based on the weight-length for the whole population, was developed to overcome biases of length with increasing size of fish identified in CF (Le Cren 1951).

Green (2001) questioned the use of residuals for understanding the condition of animals in ecological studies. Our findings suggest no observed difference in the ecological information provided when compared to standard morphometric condition measures, as found by Schulte-Hostedde et al. (2005).

Although the morphometric condition indices may have limited sensitivity, they provide a rapid, noninvasive measure of the physiological status of the fish (Brown & Murphy 1991, Neumann & Murphy 1991). This is an increasingly important consideration when studying large predators undergoing population declines; future work might investigate the utility of validating ultrasound techniques to devise a non-invasive method of estimating HSI. In order to advance the use of morphometric indices for elasmobranchs, it would be useful to calculate and test the reliability of relative weight indices to enable accurate inter-population comparisons. This is a requirement since comparative population analyses using CF, Kn and Rr_{PCL} are not possible, as they violate the basic assumptions of the indices (Bolger & Connolly 1989).

CONCLUSIONS

Condition indices are widely used as an ecological and management tool for monitoring the health or fitness of fishes. Their appropriate use may provide valuable insights into ecological and physiological processes (migration, lipid storage, growth and maturation) and the effect of components in the environment that the fish inhabits (prey availability, habitat and temperature). To date, a comprehensive comparative analysis of multiple condition indices for sharks has been limited by the scarcity of available data. The present study demonstrates that condition indices are a useful tool for studying the seasonal health or fitness of sharks but that the appropriate condition index and size range of animals must be selected. The significant effect of month for most size-class, sex and reproductive-state tests underlines that seasonal variations in both morphometric and somatic condition occur. Our data found that the application of CF, Kn and Rr_{PCL} would provide comparable results but that HSI is a more sensitive measure of condition, responding more rapidly to environmental/physiological cues. HSI was also more able to determine seasonal trends in condition of juvenile and neonate sharks. The effect of increasing animal size was most apparent for HSI, which confounds inter-size class comparisons. Considering the large liver size of neonates, the reduced liver size of pregnant and postpartum sharks and the notable effect of PCL on HSI, it is important to disaggregate data sets by clearly defined size class, sex and reproductive states for accurate interpretation of the data. Sample sizes and preliminary examination of the data to determine the suitability of statistical tests are also important considerations. Although gutted mass is unlikely to have significant effects on overall seasonal patterns, our results raise possible concerns over the inclusion of gutted mass when examining both somatic and morphometric condition of large predators. Considering that condition measures are usually undertaken on live animals, subsequent work should determine the possible effects of gutted mass for large individuals through the calculation of Clarke's isometric and allometric CFs (Ricker 1975). Non-invasive ultrasound methods may provide future alternative strategies to examine HSI, eliminating the requirement for animal mortalities.

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