Stable isotope profiles of large marine predators: viable indicators of trophic position, diet, and movement in sharks?

Nigel E. Hussey, Sheldon F.J. Dudley, Ian D. McCarthy, Geremy Cliff, and Aaron T. Fisk

Abstract: Understanding the role of predators is challenging but critical for ecosystem management. For community dynamics, predator-specific size-based variation in diet, trophic position, and habitat use are rarely accounted for. Using two applied tools (stable isotopes and stomach content data), we examined inter- and intra-species ontogenetic variability in diet (stomach contents), trophic position (TP_{SIA} for $\delta^{15}N$ and TP_{SCA} for stomach contents), and habitat use ($\delta^{13}C$) of two large sharks, the scalloped hammerhead (*Sphyrna lewini*) and the dusky (*Carcharhinus obscurus*). Stomach contents identified size-based and gender-specific shifts in diet indicating resource partitioning for and between species. Calculated TP for the two sharks varied by method, either TP_{SIA} or TP_{SCA} and with species, size, and gender, but were complicated by differing baselines and broad functional prey groups, respectively. TP increased with size for *S. lewini*, but was low in large *C. obscurus* compared with small sharks. Size-based $\delta^{13}C$ profiles indicated habitat partitioning by sex in *S. lewini* and a movement to shelf edge foraging in large *C. obscurus*. These results demonstrate that predators exert proportional size-based effects on multiple components of the marine system that are further complicated by species- and gender-specific strategies.

Résumé : Comprendre le rôle des prédateurs représente un défi, mais c'est essentiel pour la gestion des écosystèmes. Dans les études de dynamique des communautés, on tient rarement compte des variations reliées à la taille et spécifiques aux prédateurs dans le régime alimentaire, la position trophique et l'utilisation de l'habitat. À l'aide de deux méthodes, les isotopes stables et l'analyse des contenus stomacaux, nous avons examiné la variabilité inter- et intraspécifique durant l'ontogenèse du régime alimentaire (contenus stomacaux), de la position trophique (TP_{SIA} pour $\delta^{15}N$ et TP_{SCA} pour contenu stomacal) et de l'utilisation de l'habitat ($\delta^{13}C$) chez deux grands requins, le requin-marteau halicorne (*Sphyrna lewini*) et le requin obscur (*Carcharhinus obscurus*). Les contenus stomacaux permettent d'identifier des modifications dans le régime alimentaire reliées à la taille et spécifiques au sexe qui indiquent un partitionnement des ressources chez et entre les espèces. Les TP calculées pour les deux requins varient d'après la méthode utilisée, soit TP_{SIA} ou TP_{SCA}, et aussi en fonction de l'espèce, de la taille et du sexe et elles sont compliquées respectivement par des lignes de base différentes et par des groupes fonctionnels de proies distincts. La TP augmente en fonction de la taille chez *S. lewini*, mais elle est basse chez les grands *C. obscurus* par comparaison aux petits requins. Les profils de $\delta^{13}C$ indiquent un partitionnement de l'habitat en fonction du sexe chez *S. lewini* et un déplacement vers le bord de la plate-forme chez les grands *C. obscurus.* Ces résultats démontrent que les prédateurs exercent des effets proportionnels à leur taille sur plusieurs compartiments du système marin, qui sont de plus compliqués par des stratégies spécifiques à l'espèce et au sexe.

[Traduit par la Rédaction]

Introduction

Body size has long been recognized to have an important influence on the structural and functional complexity of aquatic food webs (Elton 1927). As predators are typically larger than their prey, trophic position (TP) is predicted to increase with body size (Cohen et al. 1993). Size as a surrogate measure of TP has therefore been used as a tool to examine human-induced impacts on community structure (Pinnegar et al. 2002; Dulvy et al. 2004), alterations in trophic linkages (Pauly et al. 1998), and (or) cascading effects of predator removal (Myers et al. 2007).

Large marine predators are typically mobile, undertaking large-scale movements and rapidly expanding home range with size (Bonfil et al. 2005). As a consequence, size-based variation in habitat use and relative TP of these predators

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can modify inferences on food web structure and assessments of community structure over time (Layman et al. 2005). Specifically, for analysis of community trophic structure (Jennings et al. 2001; Layman et al. 2005), (*i*) within-species size-based variation and (*ii*) associated size-based habitat shifts are not clearly defined and (or) generally accounted for.

Diet and trophic ecology of fish have been traditionally studied using stomach content analysis (Hyslop 1980; Cortés 1999). However, for sharks, as with many large, highly mobile predatory fish, stomach content analysis is hindered by insufficient sampling of all size classes and incomplete sampling across the geographic range of the animal both in temporal and spatial domains. More recently, the stable isotopes of nitrogen ($^{15}N/^{14}N$ expressed relative to a standard as $\delta^{15}N$) have been proven as a valuable tool in elucidating trophic relations in aquatic food webs (Vander Zanden et al. 1997; Post 2002) and have recently been applied in the study of sharks (Fisk et al. 2002; Estrada et al. 2006; Hussey et al. 2011).

The conservative fractionation of carbon ($^{13}C/^{12}C$ expressed relative to a standard as $\delta^{13}C$) between primary producers and top-level predators can also provide a tool to track animal movements between regions and to define habitat use (Hobson 1999; Rubenstein and Hobson 2004). When considering the inherent difficulties and expense involved in the examination of fine-scale movement patterns of predators through archival or satellite tracking telemetry (Block et al. 2001), there is a requirement to target specific life stages and sexes to provide the required data for effective management of exploited–threatened species. Size-based $\delta^{13}C$ data may provide the necessary coarse resolution movement profiles of little known species to guide the size-based application of telemetry methods, consequently improving the efficiency of yielded results.

The aim of the current study was threefold: (*i*) to examine size-based and gender-specific variations in diet, TP, and habitat use of two large marine predators, the scalloped hammerhead (*Sphyrna lewini*) and dusky shark (*Carcharhinus obscurus*), by combining stomach content analysis (from a long-term archived database) and stable isotope analysis ($\delta^{15}N$ and $\delta^{13}C$) of muscle tissue; (*ii*) to quantitatively compare and contrast TP calculated using these two commonly applied TP techniques; and (*iii*) to assess the utility of $\delta^{13}C$ as an indicator of coarse resolution ontogenetic movement profiles in these sharks, because $\delta^{13}C$ values have been shown to vary systematically across the geographic range of these species in South Africa (Hill et al. 2006; Hill and McQuaid 2008). With documented worldwide population declines of large sharks (Myers and Worm 2003) and gender and (or) size classes targeted by area-specific fishing practices (Mucientes et al. 2009), a more thorough understanding of species-specific trophic dynamics and movement patterns of large predators with relation to changes in body size is required (Layman et al. 2005). Concurrently, the increase in studies utilizing stable isotopes in sharks, coupled with current literature and archival stomach content data sets, requires an understanding of the issues associated with calculating TP and how the TP results vary by method.

Materials and methods

Location and sampling

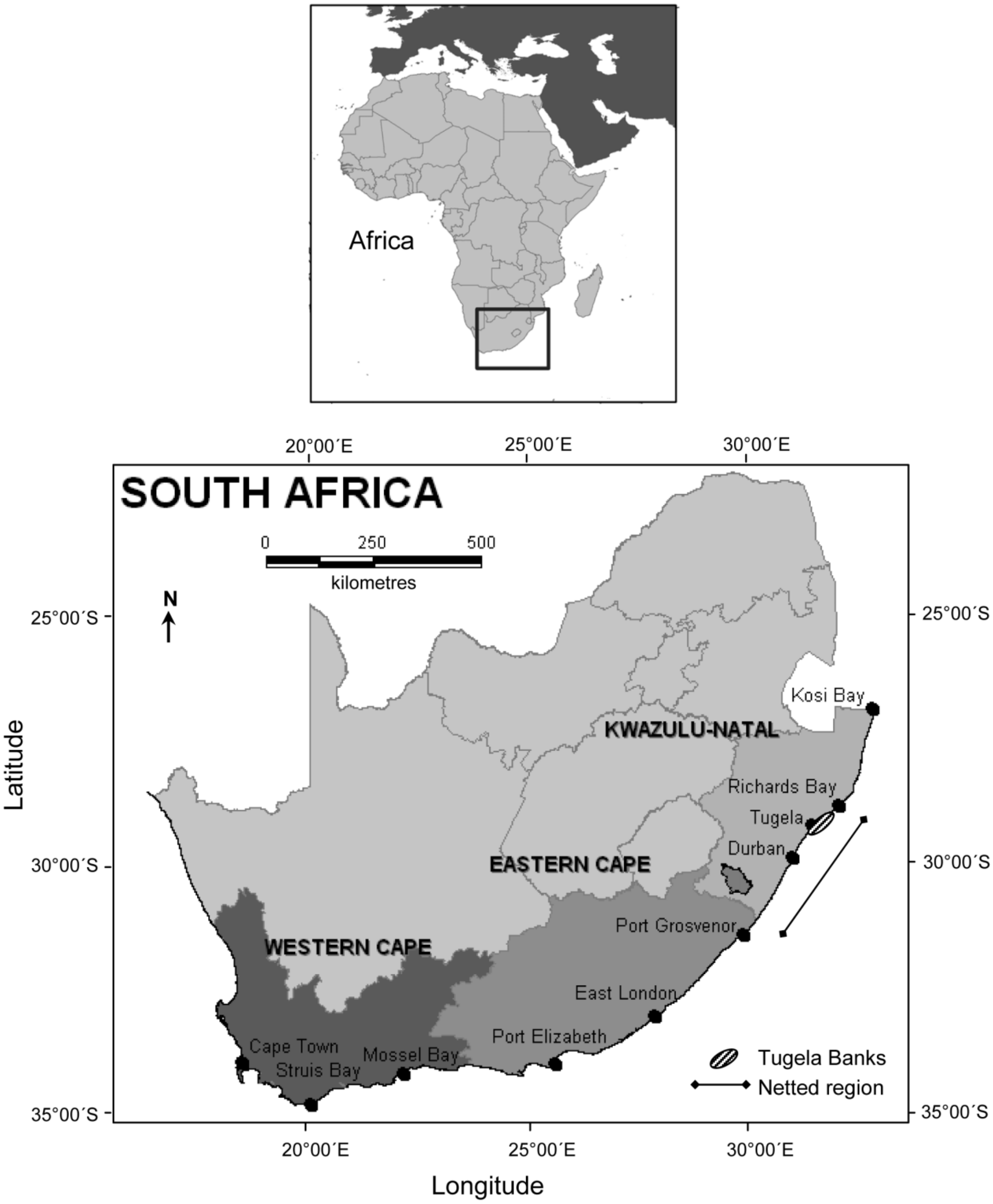
All scalloped hammerhead and dusky sharks were sampled from animals incidentally caught in beach protection nets in KwaZulu-Natal (KZN), South Africa, with the exception of five juvenile scalloped hammerhead sharks sampled from commercial trawl fisheries on the Tugela Banks (Fig. 1). Beach net installations were set parallel to the shoreline, approximately 300–500 m from the beach in 10–14 m (depth) of water. All shark mortalities that appeared to be recent mortalities and in good condition were retrieved, transported to the KwaZulu-Natal Sharks Board (KZNSB) laboratory, and stored frozen (–20 °C) until dissection. On arrival at the laboratory, basic data on species, sex, and morphological measurements, including precaudal length (PCL, cm), were recorded. For establishing the baseline inshore (coastal) and offshore (pelagic) stable isotope values of the KZN marine system, the grooved mullet (*Liza dumerili*) was sampled in shallow coastal waters off Durban, and whale sharks (*Rhincodon typus*) and devil rays (*Mobula* sp.) were sampled from beach strandings and KZNSB net catches, respectively.

Stomach content analysis

The diet of the scalloped hammerhead and dusky shark were quantified using stomach content data accessed from the KZNSB archived database (1983–2006). A total of 1018 scalloped hammerhead and 900 dusky sharks contained stomach contents and were included in the analysis. For specific details on species catch rates and seasonality of capture, refer to Dudley et al. (2005) and de Bruyn et al. (2005). For each shark, the complete stomach was removed, prey items identified to the lowest possible taxon, and the number and mass (to 0.1 g) of each prey item recorded. To summarize the stomach content data, all prey items were grouped to family level and then further grouped into eight functional prey groups, defined as elasmobranch, teleost, cephalopod, crustacean, mollusc, mammal, bird, and miscellaneous items (Cortés 1999). The percent mass contribution (% mass) of each functional prey group to the diet of the two shark species was then calculated. To examine size-based and gender shifts in diet for the two species, the data were divided by sex and into three size classes for scalloped hammerhead sharks (small, <110 cm; medium, 110–140 cm; and large, >140 cm) and for dusky sharks (small, <100 cm; medium, 100–209 cm, and large, ≥210 cm). Large female dusky sharks were further divided into reproductively inactive (Linact), pregnant (Lpreg), and postpartum (Lpost) sharks. The size classes selected approximate to maturity stage and relate to species-specific life strategies (Compagno 1984).

The % mass contribution of the functional prey groups for the two species of sharks divided by sex and the predefined size classes were (*i*) plotted in histogram form and (*ii*) subjected to nonmetric multidimensional scaling (MDS) ordination to infer the overall influence of species, sex, and body size on diet composition. Accepting the limited number of prey items–types per individual shark stomach, dietary data for groups of individual animals (approximately 10 per group) were randomly pooled within each size class, herein referred to as dietary samples (White et al. 2004). Prior to MDS ordination, the dietary samples were ARCSIN-transformed, and a similarity matrix was constructed using the Bray–Curtis similarity coefficient in PRIMER (PRIMER-E Ltd., Ivybridge, UK). A one-way analysis of similarities (ANOSIM) test was then employed to determine if statistical differences in diet

Fig. 1. The study region encompassing the area protected by beach protection nets and the Tugela Banks in KwaZulu-Natal, South Africa. The netted region is currently composed of 38 individual net installations (see Dudley et al. 2005 for specific details on locations).



composition occurred between the two species. Individual ANOSIM tests were then undertaken to examine the diet of each species (male and female separately) by size. The ANOSIM test generates a global *R* statistic that provides a measure of the magnitude of difference among groups. The global *R* statistic ranges from –1 to +1, with 0 indicating no difference in groups, while +1 is complete separation.

Stable isotope analysis

All net-caught scalloped hammerhead (*n* = 38: size range: 52–223.4 cm PCL) and dusky (*n* = 63; size range: 70–280 cm PCL) sharks were sampled between 2005 and 2008. Trawl fishery-derived scalloped hammerhead (*n* = 5; size range: 38–58 cm PCL) were sampled in 2006. Baseline species, grooved mullet and devil ray – whale sharks were sampled between 2007 and 2009. White muscle tissue was excised from the muscle block anterior to the first dorsal fin adjacent to the vertebral column in sharks, from the wing-body cavity margin in rays, and from the anterior dorsal section in teleost fish. All samples were stored frozen (–20 °C). The muscle tissue was then freeze-dried and homogenized. Lipid extraction of all samples was undertaken by agitating the dried powdered muscle tissue in a 2:1 chloroform–methanol solution for 24 h. The tissue and solvent were then filtered and the resulting residue–filter paper dried at 60 °C for 48 h to evaporate the remaining solvent. Lipid extraction was undertaken because of the bias of soluble urea in shark muscle tissue (Hussey et al. 2010*a*; N.E. Hussey, unpublished data). Between 400 and 600 µg of lipid extraction tissue was weighed into tin capsules, and stable carbon and nitrogen isotope ratios were provided from a continuous flow isotope ratio mass spectrometer (Finnigan MAT Delta$^{\text{plus}}$, Thermo Finnigan, San Jose, California, USA).

Stable isotope abundances are expressed in delta (δ) values as the deviation from standards in parts per thousand (‰) using the following equation:

$$(1) \qquad \delta X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where X is ^{15}N or ^{13}C and R is the ratio ^{15}N/^{14}N or ^{13}C/^{12}C. The standard reference material was Pee Dee Belemnite carbonate for CO_2 and atmospheric nitrogen for N_2. The analytical precision for δ^{15}N was <0.22‰ and for δ^{13}C was <0.24‰ based on more than 100 analyses of a NIST standard 8414 (bovine muscle) across multiple runs and was 0.14‰ for δ^{15}N and 0.05‰ for δ^{13}C based on a single run of NIST standard sucrose (n = 13) and ammonium sulphate (n = 13).

Small scalloped hammerhead and dusky sharks with umbilical scar data were excluded from the following analyses because of maternal influence on stable isotope signatures (Olin et al. 2011). Size-based δ^{15}N profiles for each species were plotted and regression models fitted to the data by species and sex.

TP estimation from stomach contents and δ^{15}N

To facilitate a comparison between methods of calculating TP, calculations were based on stomach contents (TP_{SCA}) and δ^{15}N (TP_{SIA}). Dietary samples for each shark species in conjunction with the estimated TP of functional prey groups were used to calculate TP_{SCA} using the following equation (Cortés 1999):

$$(2) \qquad TP_{SCA} = 1 + \left(\sum_{i=1}^{7} p_i \times TP_i\right)$$

where TP_{SCA} is the trophic position of the species in question, p_i is the proportion of each functional prey group i in the total diet (expressed as % mass), and TP_i is the trophic position for each functional prey category. TP of functional prey groups were taken directly from Cortés (1999), who assessed the TP of a wide range of shark species using stomach contents, and were defined as follows: elasmobranch (3.65), teleost (3.24), cephalopod (3.2), crustacean (2.52), mollusc (2.1), bird (3.87), and mammal (4.02). The miscellaneous functional prey group (Appendix A) was excluded from all trophic-level calculations.

To determine a measure of shark TP using δ^{15}N (TP_{SIA}) and accepting that large sharks are highly mobile and move between both coastal and offshore environments, we used a two-source food web model according to Post (2002):

$$(3) \qquad TP_{SIA} = \lambda + \{\delta^{15}N_{\text{shark}} - [\delta^{15}N_{\text{base1}} \times \alpha + \delta^{15}N_{\text{base2}} \times (1 - \alpha)]\}/\Delta^{15}N$$

where λ is the TP of the selected base consumers (TP = 3, zooplanktivorous fish), $\delta^{15}N_{\text{base1}}$ is the value of the coastal base consumer (the grooved mullet (mean ± standard deviation, SD): 12.63‰ ± 1.47‰; n = 5), $\delta^{15}N_{\text{base2}}$ is the value of the pelagic base consumer (the whale shark – devil ray (mean ± SD): 9.86‰ ± 0.45‰; n = 10), and α is the calculated proportion of the nitrogen in the consumer derived from the base of the coastal food web ($\delta^{15}N_{\text{base1}}$):

$$(4) \qquad \alpha = (\delta^{13}C_{\text{shark}} - \delta^{13}C_{\text{base2}})/(\delta^{13}C_{\text{base1}} - \delta^{13}C_{\text{base2}})$$

The $\delta^{13}C_{\text{base1}}$ of the grooved mullet was –13.23‰ ± 1.02‰ and $\delta^{13}C_{\text{base2}}$ of the whale shark – devil rays was –17.14‰ ± 0.3‰, which provide the expected negative δ^{13}C gradient between coastal and pelagic food webs (Post 2002; Hill et al. 2006). The grooved mullet inhabits shallow coastal areas, while devil rays and whale sharks are predominantly pelagic. To enable accurate inferences on TP within food webs requires knowledge of species-specific diet tissue discrimination factors ($\Delta^{15}N = \delta^{15}N_{\text{shark}} - \delta^{15}N_{\text{food}}$). A Δ^{15}N value of 2.3‰ for large sharks was used according to Hussey et al. (2010*a*, 2010*b*). A general linear model (GLM) with adjusted Bonferroni pairwise comparisons was used to examine the effects and interactions of sex, size, and method of calculating TP (TP_{SCA} and TP_{SIA}) on derived TP values for both shark species.

Habitat: size-based δ^{13}C profiles

To interpret regional δ^{13}C movement or residency patterns of the two shark species over ontogeny, the following assumptions were made: (*i*) The range of expected $\delta^{13}C_{\text{shark}}$ values in coastal waters were predicted using the mean (±1 SD) δ^{13}C values for small scalloped hammerhead (~60–100 cm PCL) and dusky (~100–140 cm PCL) sharks that have known nursery grounds on the continental shelf in KZN (Fennessy 1994; Hussey et al. 2009) and are regularly caught in beach protection nets (Dudley et al. 2005; de Bruyn et al. 2005). These animals therefore spend the majority of this life stage, over the tissue integration period, on the continental shelf. (*ii*) Distinct systematic latitudinal and inshore–offshore gradients in δ^{13}C occur off South Africa. With increasing distance from KZN to the Western Cape, there is a marked increase in δ^{13}C in coastal waters (Fig. 1; Hill et al. 2006; Hill and McQuaid 2008). Measurements of suspended particulate matter in offshore waters were substantially depleted in δ^{13}C compared with coastal waters (Hill et al. 2006).

Size-based δ^{13}C profiles were plotted for each species. Large sharks may be highly mobile, undertaking large unidirectional migrations but also rapid return migrations (Bonfil et al. 2005). Considering estimated turnover on carbon isotope ratios in muscle tissue (390–540 days; MacNeil et al. 2006), the identification of distinct size-based δ^{13}C profiles would only be expected if sharks remained resident in core isotopically distinct environments for extended periods of time.

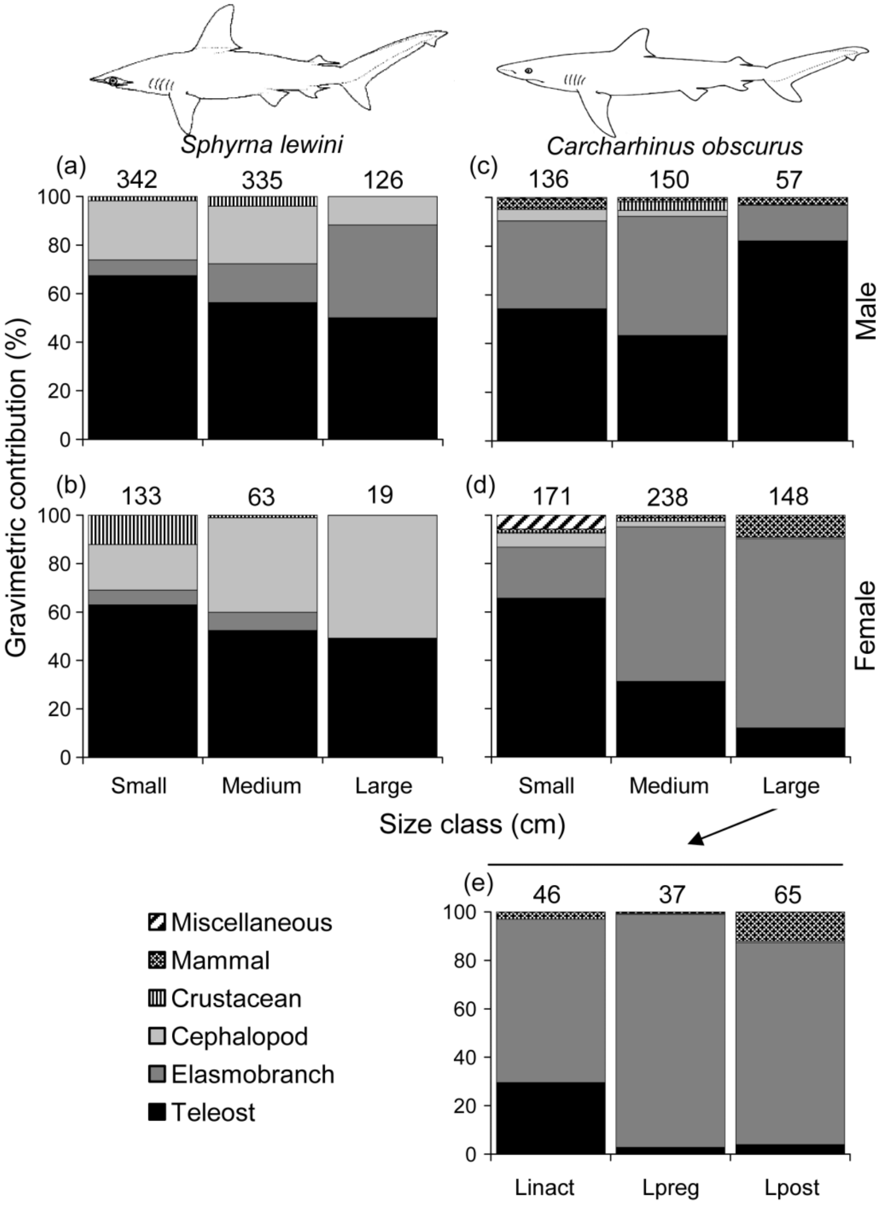
Results

Multivariate analysis of stomach content data

The overall % mass diet composition of the scalloped hammerhead shark was significantly different from that of the dusky shark (R statistic = 0.611; p = 0.001). Additionally, size-based shifts in diet were observed for male and female sharks of both species (Figs. 2 and 3; see Appendix A for detail of stomach contents).

For scalloped hammerhead sharks, small sharks of both sexes fed predominantly on teleosts. With increasing size, males included more elasmobranchs in the diet, while cepha-

Fig. 2. Percent mass (% mass) contribution of functional prey categories defined by Cortés (1999) to the diet of scalloped hammerhead (*a*, *b*) and dusky (*c*, *d*) sharks by size class and sex. (*e*) Large female dusky sharks are further subdivided into inactive (Linact), pregnant (Lpreg), and postpartum animals (Lpost). Numbers indicate sample sizes per size class.



lopods dominated the diet of large females (Fig. 2; Appendix A, Table A1). MDS ordination of the male diet data found that several dietary samples of large animals were located to the right of the plot frame, identifying the importance of elasmobranchs (Fig. 3; Appendix A, Table A1). For females, medium and large sharks were more highly clustered within the MDS plot, indicating a transition to a cephalopod- and teleost-dominated diet (Fig. 3; Appendix A, Table A1).

The diet of small male and female dusky sharks was also dominated by teleosts but included an elasmobranch component (Fig. 2; Appendix A, Table A2). In contrast with scalloped hammerhead sharks, large male dusky sharks fed on teleosts, while the diet of large female sharks, particularly pregnant and postpartum animals, consisted of elasmobranchs (Fig. 2; Appendix A, Table A2). MDS ordination of the male dusky shark dietary samples found a clear transition in diet between the three size classes (Fig. 3). For female dusky sharks, MDS ordination found that data points were located further to the right of the plot frame with increasing size, highlighting the importance of elasmobranchs in the diet (Fig. 3). Pregnant–postpartum female data were highly clustered to the right, while nonactive–immature females exhibited a high degree of overlap with all size classes (Fig. 3). ANOSIM pairwise comparisons for each sex found that the diet of different size class male and female dusky sharks were significantly different (Fig. 3).

Size-based $\delta^{15}N$ profiles

For scalloped hammerhead sharks, males showed a significant increase in $\delta^{15}N$ with increasing PCL; accepting the small sample, the female increase was not significant (Fig. 4; $F_{[1,23]} = 56.84$, $p < 0.0001$ and $F_{[1,6]} = 4.71$, $p = 0.073$;

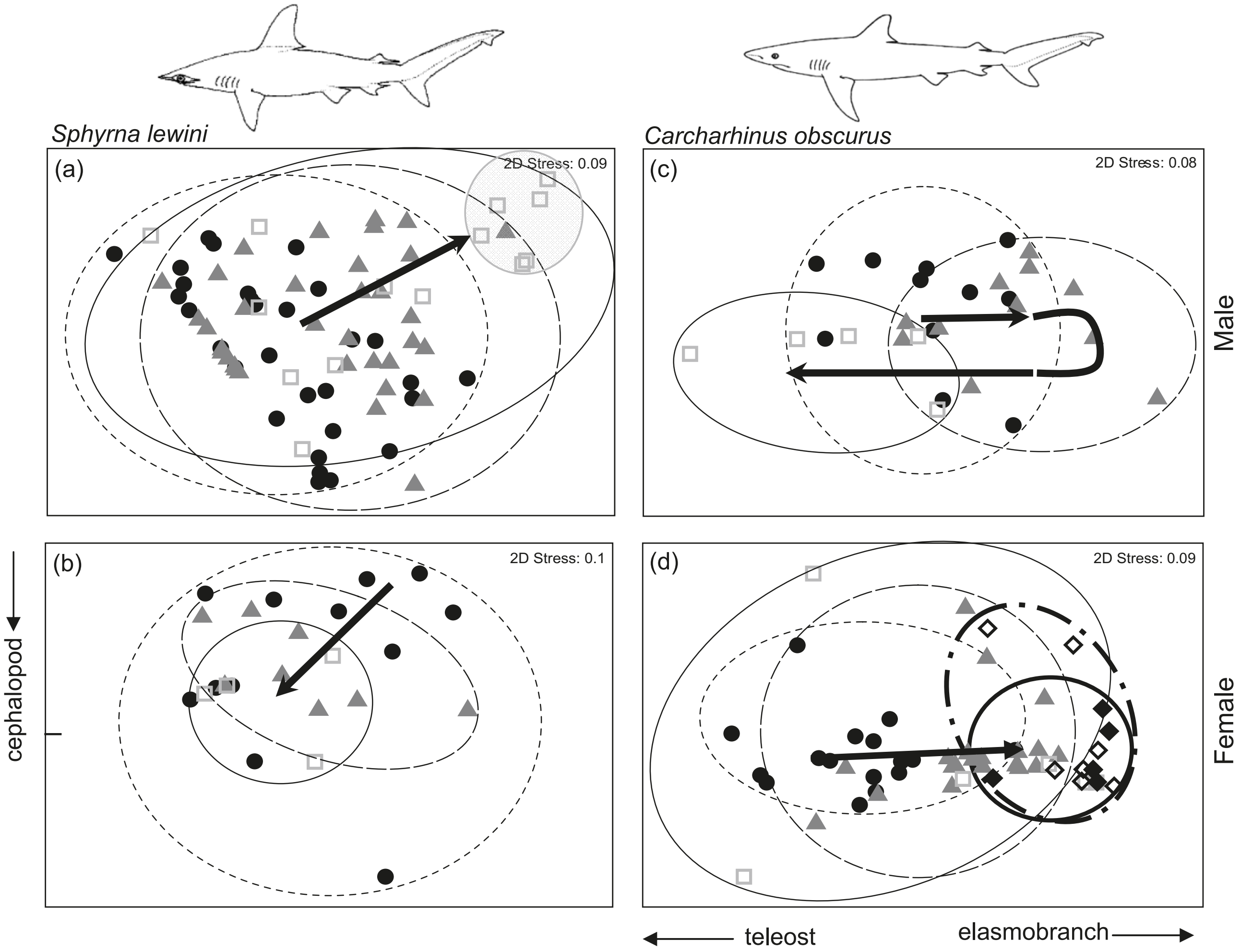


Fig. 3. Nonmetric multidimensional scaling (MDS) ordination of the percent mass (% mass) dietary samples of scalloped hammerhead (*a*, *b*) and dusky (*c*, *d*) sharks for each sex, by size class. For scalloped hammerhead and dusky sharks, black circles indicate small, grey triangles are medium, and open squares are large reproductively inactive sharks. For female dusky sharks, black diamonds indicate pregnant and open diamonds show postpartum sharks. Ellipses mark the outer bounds of dietary samples for small (thin short dashed lines), medium (thin long dashed lines), large–inactive (thin solid lines), pregnant (thick solid lines), and postpartum (thick dot-dashed lines) size classes. Arrows within the MDS indicate the size-based trends in diet. The arrows associated with functional prey groups (*x* and *y* axes) identify major components in the diet. For male scalloped hammerhead sharks, the shaded grey circle highlights large sharks focused on an elasmobranch diet. Significant ANOSIM pairwise comparisons for each species and sex by size are shown with the global *R* value and level of significance (***, $p < 0.001$; **, $p < 0.01$; and *, $p < 0.05$).

Male scalloped hammerhead:
Small vs. Large – 0.334 ***
Medium vs. Large – 0.223 **

Male dusky:
Medium vs. Large – 0.434 **

Female dusky:
Small vs. Medium – 0.381 ***
Small vs. Linact – 0.639 ***
Small vs. Lpreg. – 0.798 ***
Small vs. Lpost – 0.866 ***
Medium vs. Linact – 0.325*
Medium vs. Lpreg – 0.256*
Medium vs. Lpost – 0.329*

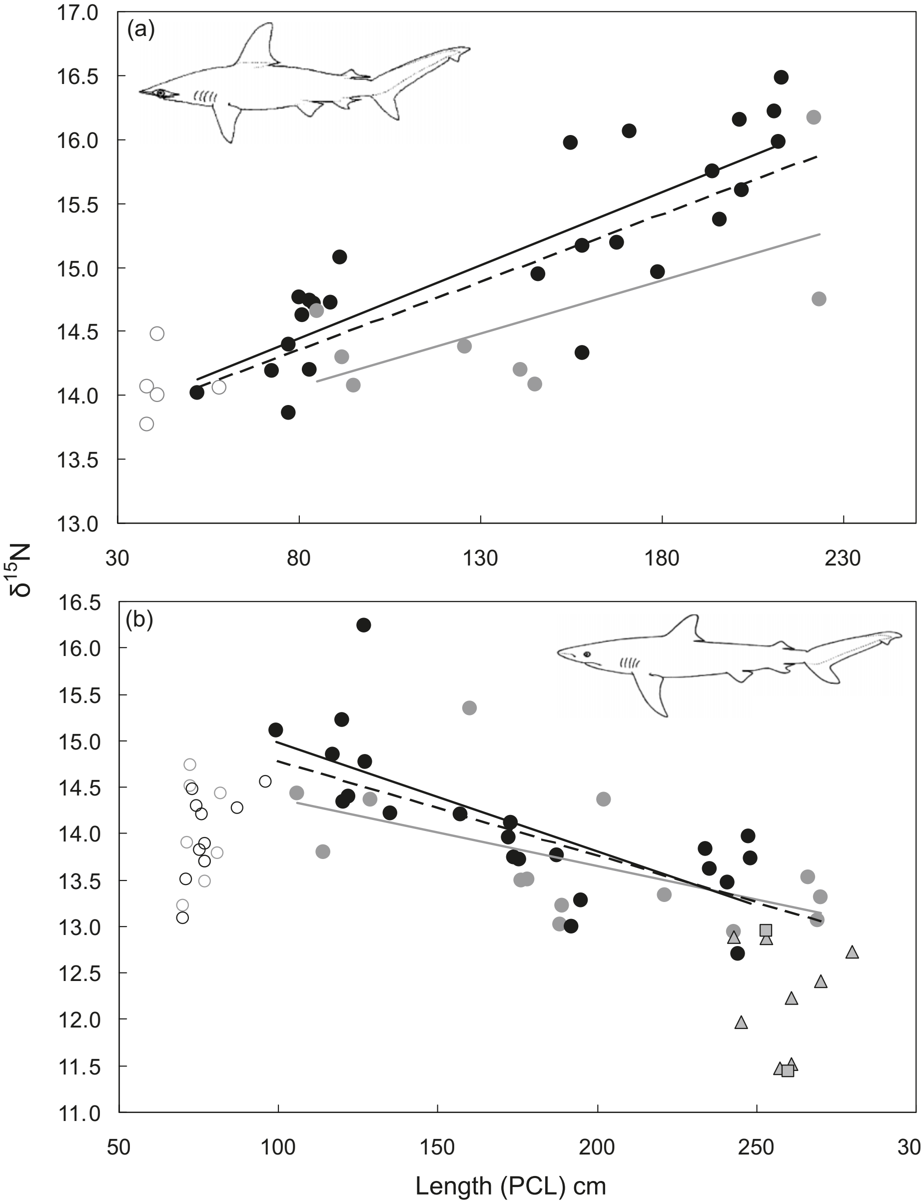
male and female, respectively). Excluding pregnant and postpartum animals from the analysis, a significant negative linear relationship between $\delta^{15}N$ and PCL was observed for both sexes of dusky shark ($F_{[1,20]} = 23.90$, $p < 0.0001$ and $F_{[1,12]} = 6.16$, $p = 0.029$; male and female, respectively). Pregnant and postpartum dusky sharks had lower $\delta^{15}N$ values than inactive large sharks ($t_{[11]} = -4.11$, $p = 0.002$; Fig. 4), but exhibited a degree of variability, with $\delta^{15}N$ values ranging from 11.4‰ to 13.0‰.

Trophic-level estimation: stomach contents and $\delta^{15}N$

Mean TP_{SCA} (±1 standard error, SE) of scalloped hammerhead and dusky sharks for both sexes and all size class combined were 4.3 ± 0.01 and 4.5 ± 0.02, respectively. Mean TP_{SIA} of all scalloped hammerhead and dusky sharks were 4.7 ± 0.05 and 4.3 ± 0.04, respectively.

For male scalloped hammerhead sharks, TP_{SCA} and TP_{SIA} increased with increasing animal size, whereas the TP_{SCA} value for female sharks was similar across size classes, but

Fig. 4. δ^{15}N ontogenetic profiles of (*a*) scalloped hammerhead and (*b*) dusky sharks by sex (black circles represent males, grey circles represent females); for dusky sharks, triangles represent pregnant sharks, squares represent postpartum sharks, and open circles represent neonatal animals with umbilical scar. Linear regression models were fitted to both scalloped hammerhead and dusky sharks by sex (solid black line: male; solid grey line: female) and for sex data combined (broken line).



TP_{SIA} increased with size (Fig. 5). Intrasize class variability between calculated TP_{SCA} and TP_{SIA} of both sexes of scalloped hammerhead sharks was evident (Fig. 5). A GLM on the scalloped hammerhead TP data (size class 1 and 3 animals) found that size and TP method had a significant effect (variance explained: 71.2%; Table 1; Fig. 5). The trend of calculated TP_{SCA} for male dusky sharks was similar across size classes, while TP_{SIA} showed a minor decline with increasing size class (Table 1; Fig. 5). For female dusky sharks, clear differences in estimated TP by TP_{SCA} and TP_{SIA} were observed among the Linact, Lpreg, and Lpost sharks (Fig. 5). A GLM testing only medium and Linact sharks found there was no significant effect of sex, size, or TP method on calculated TP (variance explained: 10.3%; Table 1).

Size-based δ^{13}C profiles

The δ^{13}C values of small scalloped hammerhead sharks between 70 and 100 cm, which were primarily males, were highly clustered with minimal variability (range: –15.69‰ to –15.21‰; mean ± SE: –15.41‰ ± 0.16‰; Fig. 6). Accepting the small sample size, the δ^{13}C values of male and female scalloped hammerhead sharks between 120 and 160 cm PCL indicated sexual segregation with a difference of ~2.5‰ (Fig. 6). The δ^{13}C signatures of male scalloped hammerheads >160 cm PCL then declined to a point where the signatures of both sexes >200 cm were similar (Fig. 6). For dusky sharks <160 cm PCL, δ^{13}C values were similar to those of small scalloped hammerhead sharks but were more variable. Most dusky sharks >200 cm PCL of both sexes were depleted in ^{13}C relative to predicted KZN continental shelf signatures (Fig. 6). Preg-

Fig. 5. Mean calculated trophic position (±1 standard error, SE) by diet (TP_{SCA}, striped bars) and $\delta^{15}N$ (TP_{SIA}, solid bars) for each sex and size class of the scalloped hammerhead shark (black bars; *a*, *b*) and dusky shark (grey bars; *c*, *d*).

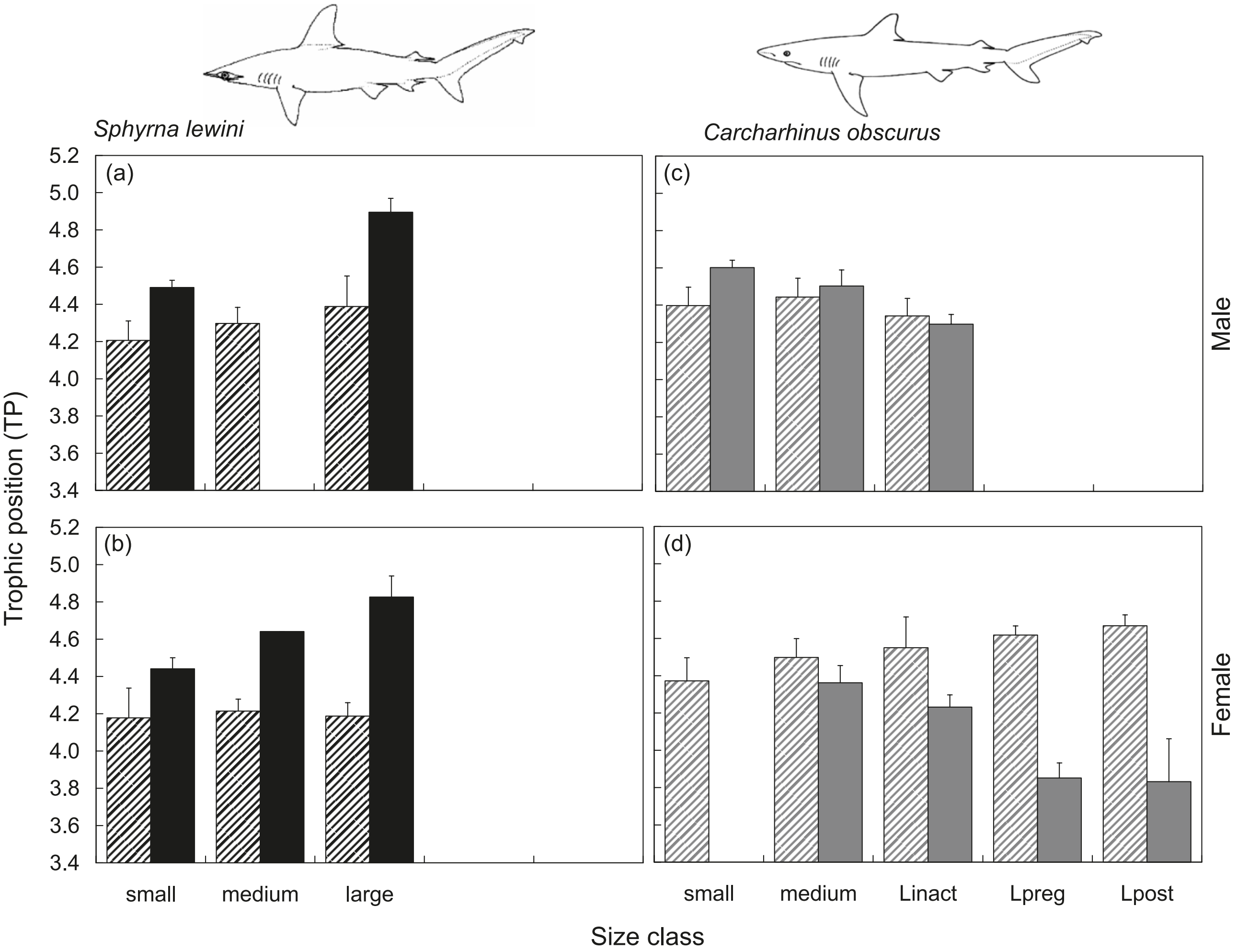


Table 1. General linear models (GLMs) testing the effects of size, sex, method of calculating trophic position (TP_{SCA} and TP_{SIA}), and associated interactions on estimated TP for the scalloped hammerhead and dusky shark.

	Scalloped hammerhead				Dusky			
Source	df	MS	*F*	*p*	df	MS	*F*	*p*
Size	1	0.865	33.83	**<0.0001**	1	0.140	3.45	0.067
Sex	1	0.116	4.52	0.036	1	0.003	0.08	0.782
Method	1	2.586	101.09	**<0.0001**	1	0.183	4.51	0.037
Size × sex	1	0.032	1.23	0.270	1	0.050	1.23	0.271
Size × method	1	0.335	13.10	**<0.0001**	1	0.078	1.93	0.169
Sex × method	1	0.013	0.49	0.484	1	0.210	5.18	0.026
Size × sex × method	1	0.019	0.75	0.388	1	0.006	0.15	0.702
Residual	86	0.026			69	0.041		

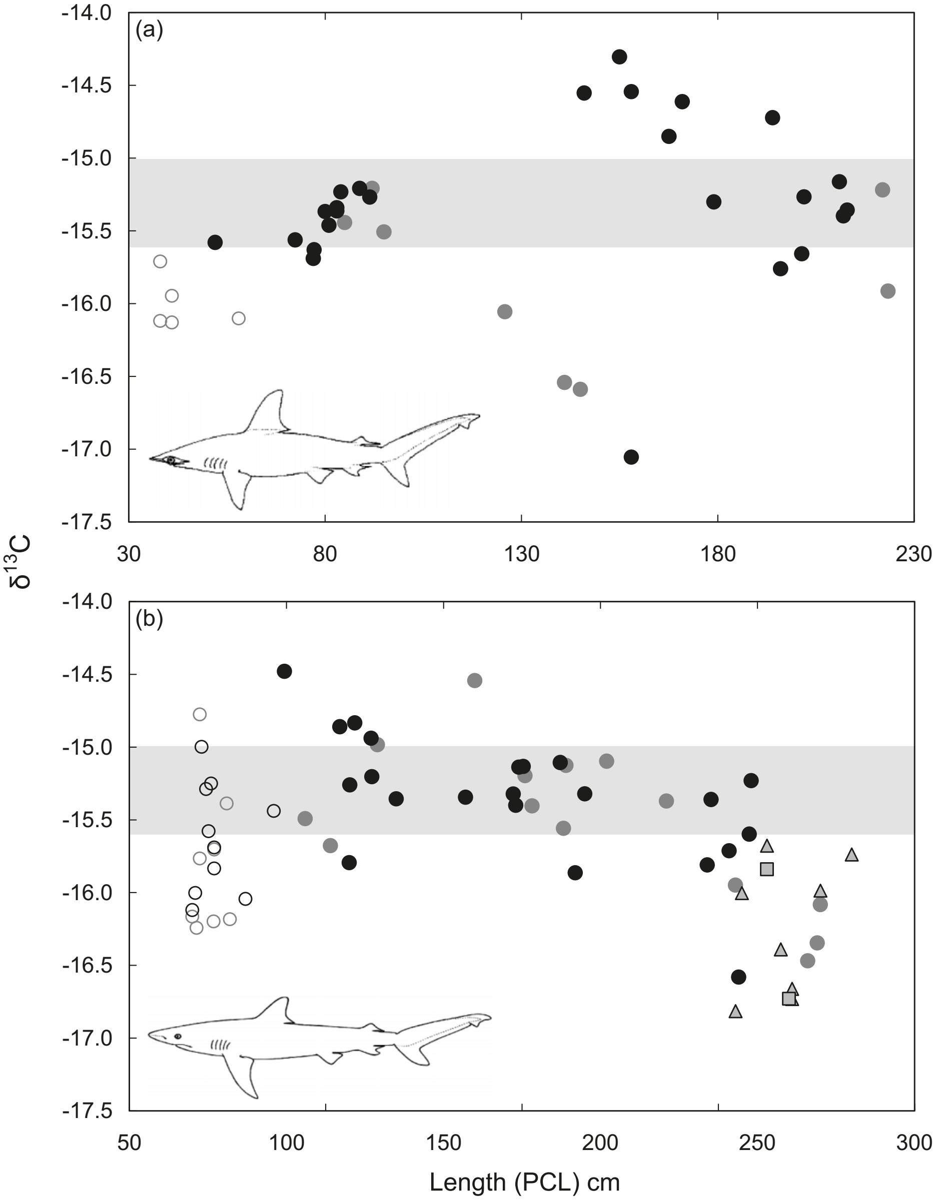
Note: A criterion for significance of $p < 0.01$ was set for all tests; bold font indicates significant factors and interactions.

nant and postpartum *C. obscurus* $\delta^{13}C$ values were more depleted than large inactive male and female sharks (min.: –16.8‰ and max.: –15.7‰).

Discussion

Knowledge of size-based effects of large marine predators is vital to our understanding of ecosystem structure and function and to predict the effects of species removal. To date, our principal understanding of the TP of sharks has stemmed from stomach content analysis as a stand alone proxy (Cortés 1999) and initial work investigating the application of stable isotopes (Fisk et al. 2002; Estrada et al. 2003, 2006). These data provide a comparative analysis of stomach content analysis and $\delta^{15}N$ and $\delta^{13}C$ data for two large sharks and provide empirical evidence for size-based and gender driven variations in diet, TP, and habitat use. Accepting the complexities of calculating TP using both TP_{SCA} and TP_{SIA}, a combined

Fig. 6. $\delta^{13}C$ ontogenetic profiles of (*a*) scalloped hammerhead and (*b*) dusky sharks by sex (black circles represent males, grey circles are females, and open circles are neonatal animals with umbilical scar); for dusky shark, triangles are pregnant sharks, and squares are postpartum sharks. Grey bar depicts the predicted $\delta^{13}C$ range of the KwaZulu-Natal (KZN) coastal habitat of scalloped hammerhead and dusky sharks.



method approach was required to better understand these size-based interactions.

Size-based trophic profiles: stomach content data and $\delta^{15}N$–$\delta^{13}C$

Inter- and intra-specific differences in calculated TP by size class were evident and would be expected considering size, diet, and habitat–movement characteristics of the two species. For example, the slightly higher TP, calculated by TP_{SIA} and $TP_{SCA,}$ of small dusky relative to small scalloped hammerhead sharks, reflected the contribution of elasmobranchs to the diet of the dusky shark. Body size of sympatric elasmobranch species at birth influences TP through associated differences in gape size and manoeuvrability. These factors may enable the larger juvenile dusky sharks to exploit seasonally abundant prey resources (Hussey et al. 2009) that juvenile scalloped hammerheads cannot, resulting in resource partitioning via habitat expansion.

Large scalloped hammerhead sharks fed at a higher TP than dusky sharks based on TP_{SIA}, while TP_{SCA} of male scalloped hammerheads was similar and female TP_{SCA} was lower. Differences in the diet of small and large scalloped hammerhead sharks have been attributed to a switch in resource base driven by a move from coastal to pelagic environments (Klimley 1987). In agreement with our diet data, neritic and pelagic cephalopods have been reported as an important component of the diet of large female sharks (Clarke 1971; Klimley 1987). When considering reported $\delta^{15}N$ data for pelagic ommastrephid squids (10‰–15‰: Parry 2008; Cherel et al. 2009) and a diet discrimination factor of 2.3‰ (Hussey et al. 2010*a*), the $\delta^{15}N$ values of large female scalloped hammerhead sharks and associated TP_{SIA}, in conjunction with both diet data and the shift in $\delta^{13}C$ (see discussion on habitat below), indicate a switch in both habitat and resource use. For large female scalloped hammerheads, TP_{SCA} was underestimated by the broad functional prey group of cephalopods, encompassing both large voracious pelagic species and small coastal species. This highlights the complexity of using broad, functional, trophic-level prey categories in the calculation of TP of large predators and suggests that published TP_{SCA} values are likely underestimated in certain cases. For large male scalloped hammerhead sharks, the importance of elasmobranchs in the diet was unusual (Klimley 1987, Stevens and Lyle 1989) but supported the observed increase in $\delta^{15}N$ and $TP_{SIA.}$ The marginal discrepancy between TP_{SIA} of large male and female scalloped hammerhead sharks may have been a result of the elasmobranch diet component of male sharks and (or) variable $\delta^{13}C$ profiles between sexes.

The marked difference in magnitude between TP_{SCA} and TP_{SIA} for inactive, pregnant, and postpartum dusky sharks was a result of the different integrative periods of the two TP methods. Dudley et al. (2005) reported a scarcity of pregnant dusky sharks other than those at or near term in KZNSB net catches, suggesting individuals are only present in the coastal region at the point of parturition. In addition, KZN coastal waters constitute known nursery grounds for several elasmobranch species (Bass et al. 1973, 1975), and elasmobranchs commonly occur in the diet of large sharks (Cliff and Dudley 1991*a*, 1991*b*). The higher TP_{SCA} of pregnant–postpartum dusky sharks was therefore a result of the snapshot sampling of stomach content analysis (possibly 2–3 weeks) compared with the long-term integrated signature of $TP_{SIA.}$ It is important to note that the observed low $\delta^{15}N$ values and calculated TP_{SIA} of pregnant and postpartum females may also be slightly biased by two possible factors. Corresponding $\delta^{13}C$ values of these sharks were depleted relative to reproductively inactive sharks. Based on the assumption that pelagic food webs are more depleted in $\delta^{13}C$ than coastal food webs (Hill et al. 2006), and associated shifts in $\delta^{15}N$ are reported (Sherwood and Rose 2005), these sharks may either be feeding offshore or migrating to KZN for parturition from other geographic localities (i.e., movement from isotopically distinct food webs at different latitudes). Considering we accounted for the base $\delta^{13}C$ of both inshore and offshore food webs in KZN in our two-source TP_{SIA} model, latitude effects may be the driving factor. Alternatively, the low $\delta^{15}N$ and calculated TP_{SIA} may be a result of preferential ^{15}N excretion from the mother to near-term young through the placental connection. Enriched $\delta^{15}N$ values in near-term pups relative to mothers have been observed for both carcharhinid and lamnid sharks (McMeans et al. 2009; N.E. Hussey and A.T. Fisk, unpublished data).

With the exception of large female dusky sharks, the overall ontogenetic TP_{SCA} and TP_{SIA} trends for each species were similar, although the magnitudes differed in the case of the scalloped hammerhead sharks and TP_{SCA} declined in male dusky sharks. Ontogenetic shifts in diet have been reported for several elasmobranchs (see review by Wetherbee and Cortés 2004), and a corresponding increase in $\delta^{15}N$ with size of animal has been shown for several marine taxa (e.g., Graham et al. 2007; Cherel et al. 2009; Newsome et al. 2009). This is in general agreement with our scalloped hammerhead shark data but contrasts the results in the dusky shark, where $\delta^{15}N$ and TP_{SIA} decreased with size and TP_{SCA} remained relatively constant (excluding pregnant and postpartum females). Low TP_{SCA} estimates of the large inactive male and female dusky sharks may be explained by a bias to sampling this size class during the annual sardine run, the principal period when these sharks are present in coastal waters (Dudley et al. 2005). For TP_{SIA}, the ontogenetic profile in the dusky shark is more puzzling. Compared with scalloped hammerheads, large dusky sharks are equipped with a substantially larger gape size and serrated teeth form, typically associated with predators feeding and (or) scavenging on large prey. Spear fishermen in northern KZN report frequent sightings of large dusky sharks throughout the year on or near the edge of the continental shelf (A. Heydorn, Richards Bay, KZN, personal communication, 2009). Two possibilities are therefore proposed for the observed TP_{SIA} ontogenetic trend in dusky sharks: (*i*) Small schooling fish are abundant in the region, the resulting predator–prey encounter rates are high, and energetic costs of foraging (prey chase down and manipulation) are minimal, providing large dusky sharks with an adequate prey base of lower trophic-level species. Small dusky sharks incorporate an elasmobranch component in their diet because of the abundance of elasmobranch prey in the coastal environment, and therefore overall TP values are similar between life stages. (*ii*) Large dusky sharks are incorporating larger pelagic prey in their diet on the edge of the continental shelf where system $\delta^{15}N$ values are lower, and the two-source TP model or selected base species were ineffective at accounting for this. The degree of variation between the small and large inactive dusky shark $\delta^{13}C$ signatures (more pronounced for pregnant and postpartum females) would suggest a combination of the above two possibilities, which results in dilution of the observed $\delta^{13}C$ and $\delta^{15}N$ values.

Coarse resolution size-based habitat profiles: $\delta^{13}C$

Small male scalloped hammerhead shark $\delta^{13}C$ values were highly clustered. Fennessy (1994) and de Bruyn et al. (2005) reported high catches of small scalloped hammerheads in the prawn trawl fishery on the Tugela Banks and in KZNSB beach protection nets, respectively. These observations, in conjunction with the $\delta^{13}C$ data, indicate that the home range for this size class of male scalloped hammerhead is restricted. For female scalloped hammerhead sharks of 120–160 cm PCL, $\delta^{13}C$ values were depleted relative to predicted continental shelf values, indicating prolonged residence in offshore–pelagic waters. Klimley (1987) documented that schools of scalloped hammerhead sharks on a seamount in the Gulf of Mexico consisted of predominantly female animals of 140–180 cm total length, in agreement with our data.

For male scalloped hammerhead sharks of ~80 cm PCL, $\delta^{13}C$ values followed a trend of enrichment with increasing size. Male sharks of ~140–160 cm PCL were enriched ~1‰ to predicted continental shelf values and 2.5‰ to corresponding female sharks of the same size. When considering the known $\delta^{13}C$ gradient in secondary consumers in South African waters (Hill et al. 2006), these enriched $\delta^{13}C$ values suggest that male sharks remain on the continental shelf but undertake southerly movement with a period of residency in the Eastern Cape – Transkei region. These movement and residency patterns are supported by tag–recapture data (Diemer et al. 2011). The high catch rate of male scalloped hammerhead sharks relative to females in KZNSB net installations further supports sexual segregation in this species (de Bruyn et al. 2005). Surprisingly, the $\delta^{13}C$ signatures of large individuals of both sexes were similar to signatures of small animals residing in nursery habitat in KZN. Our current knowledge of the ecology of large scalloped hammerheads is limited. Bass et al. (1975) reported that adult females were rare in KZN waters, while large males were common during summer. Clarke (1971), Branstetter (1987), and Stevens and Lyle (1989) reported that large female scalloped hammerheads were rare in coastal waters of Hawaii (except at the time of parturition), northwestern Gulf of Mexico, and off Northern Australia, respectively. In schools of hammerhead sharks in the Gulf of California, Klimley (1987) reported that few animals larger than 200 cm total length were present. Clarke (1971) suggested that large hammerheads may remain offshore, but our data do not confirm this. The observed $\delta^{13}C$ signatures may suggest these animals are highly migratory both by latitude and between inshore and offshore environments, incorporating $\delta^{13}C$ signatures from various isotopically distinct regions.

For dusky sharks, $\delta^{13}C$ values of small animals were more variable, with some individuals up to ~130 cm PCL enriched in $\delta^{13}C$ relative to small scalloped hammerhead sharks. These enriched $\delta^{13}C$ values may reflect the southern migration of small dusky sharks to the Eastern Cape region and a period of residency in Eastern Cape waters (Bass et al. 1973; Hussey et al. 2009). Variable $\delta^{13}C$ values may also indicate that small dusky sharks adopt different life strategies, with some "nomadic" individuals undertaking migrations, while others remain resident in KZN throughout the year (Hussey et al. 2009). The overall trend of decreasing $\delta^{13}C$ with increasing size would suggest larger animals of both sexes are spending periods of time foraging in shelf edge – offshore waters, which are typically depleted in ^{13}C (Sherwood and Rose 2005). Compagno (1984) documented that large dusky sharks occupy an intermediate offshore coastal habitat. The more depleted $\delta^{13}C$ values and larger $\delta^{13}C$ variability of pregnant and postpartum dusky sharks could be a result of a reproductive separation within the large female size class, with pregnant females spending proportionally more time in offshore waters or at higher latitudes. Alternatively, it may be indicative of the immigration of pregnant females to KZN for parturition from multiple geographic localities and (or), as previously discussed, a result of a physiological process of isotope transfer between mother and pups.

Stable isotopes as a tool to examine TP and habitat use of large sharks

Understanding both TP_{SCA} and TP_{SIA} ontogenetic profiles of large predators in the marine environment is complex. Parameters affecting calculated TP_{SCA} are documented, but the complexities associated with stable isotope trophic profiling are less well understood. Multiple factors may influence our calculations and interpretations of data, including (*i*) movement between isotopically distinct food webs (coastal–pelagic–latitude: Weng et al. 2005; Queiroz et al. 2010), (*ii*) knowledge that sharks undertake variable movement strategies (diel movement: Klimley and Nelson 1984; seasonal migrations: Domeier and Nasby-Lucas 2008; Hussey et al. 2009; large-scale movement and transoceanic migrations: Bonfil et al. 2005), (*iii*) ontogenetic–gender physiological changes (growth rate: Natanson et al. 2002), (*iv*) mother × developing young interactions (McMeans et al. 2009), and (*v*) diverse diets within a single food web (coastal (demersal–midwater), offshore (shallow pelagic – mesopelagic); Wetherbee and Cortés 2004). Accurate interpretation of stable isotope data of large mobile predators therefore requires the disentangling of the connectivity and interplay between the $\delta^{15}N$ and $\delta^{13}C$ ontogenetic profiles (Layman et al. 2007). For sharks, our lack of understanding of their movement among and residency within multiple isotopically distinct environments and the limited availability of accurate isoscapes may confound or limit the potential of two-source TP_{SIA} models. In many instances, the importance of variable $\delta^{13}C$ values on observed $\delta^{15}N$ trends and hence trophic profiles are overlooked (France et al. 1998; Parry 2008). By adopting a multifaceted approach encompassing stomach content data and $\delta^{15}N$ and $\delta^{13}C$ ontogenetic profiles, we increased the level of confidence in the conclusions drawn from the data. Future work could include sampling multiple tissues with different metabolic turnover rates to better understand diet and movement effects on ontogenetic TP profiles (MacNeil et al. 2005, 2006).

Where discrete geographical gradients in baseline $\delta^{13}C$ values occur, $\delta^{13}C$ profiles of long-term integrative muscle tissue of large predatory sharks provide accurate insights into coarse resolution ontogenetic movement patterns as previously described for marine mammals (e.g., Best and Schell 1996). Understanding movement and defining migration corridors of large marine vertebrates is critical for species protection and management (Weng et al. 2005). Stable isotope data of large mobile predators can therefore provide an important platform for the development of a priori hypotheses for the efficient design and implementation of species-specific satellite tagging programs and for validating population-level movement–residency patterns. It is important to note, however, that this is dependent on the availability of established baseline isotope data for the study region.

Our study indicates that sharks as top predators interact within multiple components of the marine system and raises important questions over the proportional influence exerted on single food web components by species, gender, and (or) size class effects. Furthermore, when considering community-based stable isotope approaches, if only large individuals are sampled, TP estimates for predators may be biased by associated $\delta^{13}C$ values. With the recent advancement of isoscapes (Bearhop et al. 2005), and through directed satellite tagging programs, future work will advance the development of multisource productivity – baseline consumer models in conjunction with movement–residency time periods of large sharks to improve isotopic predictions of TP.

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Appendix A

Tables A1 and A2 appear on the following pages.

Table A1. The diet of the scalloped hammerhead shark (*Sphyrna lewini*) off KwaZulu-Natal, South Africa, from archived stomach content data (1983–2006).

	Small				Medium				Large			
	% Mass		% IRI		% Mass		% IRI		% Mass		% IRI	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Teleost	**62.98**	**67.37**	**55.63**	**83.87**	**52.35**	**56.28**	**54.80**	**57.56**	**49.24**	**49.76**	**64.21**	**68.37**
Acantheridae	0.56		0.03									
Anguillidae	4.37	2.17	0.33	0.21	1.82	0.24	0.29	0.01		0.90		0.21
Ariidae	0.72	0.77	0.07	0.04	0.49	2.25	0.15	0.33		1.91		0.53
Balistidae												
Belonidae						0.07		0.00				
Carangidae	0.73	1.88	0.07	0.34		0.08		0.04		0.05		0.01
Cheilodactyleidae					3.57	0.58	0.22	0.01				
Chirocentridae												
Chloropthalmidae												
Cichlidae												
Clupeidae	1.58	0.24	0.24	0.01		1.22		0.16		1.37		0.37
Congridae	0.26		0.01									
Cynoglossidae												
Dactylopteridae									0.75		0.15	
Elopidae												
Engraulidae		0.09		0.00						0.04		0.03
Ephippidae												
Exocetidae		1.57		0.06		0.32		0.01				
Exocoetidae												
Gempylidae												
Gerreidae												
Haemulidae	0.39	3.75	0.04	2.95	2.54	1.31	1.40	1.30		15.81		13.66
Istiophoridae												
Leiognathidae	0.06	1.30	0.02	0.15		0.26		0.01		0.06		0.01
Mugilidae						0.22		0.01		0.15		0.02
Mullidae	2.89	1.39	0.12	0.02		1.05		0.02				
Muraenidae												
Myctophidae					0.06		0.03					
Oplegnathidae						0.14		0.00		1.74		0.63
Ostraciidae	0.52		0.02			0.21		0.01				
Ostraciidae		0.09		0.00								
Peristediidae									1.94		0.26	
Platycephalidae		0.14		0.01		2.38		0.08				
Pleuronectidae												
Plotosidae	1.36	1.05	0.13	0.17		3.70		0.52		4.46		0.65
Pomacentriidae	0.19		0.03									
Pomatomidae												
Priancathidae		1.28		0.02								
Sciaenidae	2.31	5.19	0.43	0.77	1.85	8.52	0.30	6.23		1.81		1.89
Scombridae	6.22	4.13	0.87	0.45	10.66	1.70	3.16	0.37		8.36		1.13
Scorpididae												
Serranidae		0.91		0.07		0.18		0.00		0.35		0.03
Sparidae	3.21	12.16	1.59	8.89	4.16	9.56	1.84	10.49	7.50	0.81	2.38	1.63
Sphyraenidae		0.84		0.09	0.42	0.10	0.14	0.01	0.50		0.21	
Sygnathidae		0.04		0.00		0.01		0.00				
Synodontidae	13.37	2.71	3.31	0.16	0.49	0.20	0.15	0.02	0.60		0.14	
Teraponidae	3.37	4.57	0.42	0.73	3.86	2.11	1.31	0.53	6.38	0.13	0.68	0.02
Trichiuridae	4.40	4.10	0.31	0.65	4.69	8.11	2.58	5.91		0.79		0.16
Triglidae	0.04		0.01									
Unidentified teleost	16.43	17.03	47.58	68.08	17.74	11.77	43.23	31.47	31.56	11.01	60.38	47.39
Elasmobranch	**6.05**	**6.52**	**1.28**	**0.58**	**7.56**	**16.01**	**1.34**	**5.43**	**0.00**	**37.96**	**0.00**	**9.74**
Carcharhinidae										1.25		0.14
Dasyatidae						1.27		0.02		2.56		0.24
Gymnuridae						2.76		0.09		2.25		0.22
Lamnidae												
Mobulidae												
Myliobatidae												
Odontaspididae												
Rajidae	1.88		0.14		3.02		0.65					
Rhinobatidae	0.44	2.76	0.02	0.11	1.63	5.34	0.18	2.12		11.54		1.42
Rhinopeteridae												

Table A1 (*concluded*).

	Small				Medium				Large			
	% Mass		% IRI		% Mass		% IRI		% Mass		% IRI	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Scyliorhinidae	3.51	2.39	1.09	0.28	1.11	6.64	0.12	3.19		8.01		3.59
Sphyrnidae												
Squalidae					1.80		0.39					
Squatinidae										4.80		0.19
Unidentified batoid		0.29		0.01								
Unidentified shark										6.96		2.98
Unidentified elasmobranch	0.21	1.07	0.03	0.17						0.58		0.95
Cephalopod	**18.87**	**24.34**	**29.00**	**15.23**	**39.07**	**23.71**	**43.53**	**33.83**	**50.69**	**11.72**	**35.62**	**21.82**
Coleoidae	1.79	1.65	0.18	0.38		0.37		0.08				
Enoploteuthidae					1.41	1.24	0.15	0.20	31.56	0.09	3.35	0.03
Loligo spp.												
Lycoteuthidae		0.18		0.01								
Octopodidae	10.40	7.59	25.03	7.81	2.93	4.69	1.58	3.72	4.89	0.43	6.10	0.08
Octopoteuthidae	0.41	4.63	0.10	1.13	16.44	0.20	3.55	0.03	13.22	9.71	25.91	12.83
Ommastrephidae												
Sepiidae (cuttlefish)	6.28	10.20	3.70	5.90	2.11	3.09	2.64	3.58	1.02	1.50	0.26	8.88
Teuthoidea (squids)						13.90		26.22				
Unidentified cephalopod		0.07		0.00	16.17	0.22	35.60	0.01				
Crustacean	**12.10**	**1.75**	**14.09**	**0.32**	**0.99**	**4.01**	**0.25**	**3.17**	**0.06**	**0.00**	**0.09**	**0.00**
Anomura (hermit crab)												
Brachyura (crabs)	0.11		0.03		0.09	2.05	0.02	2.55				
Macrura (rock lobsters)		1.17		0.22	0.48	0.04	0.10	0.01	0.06		0.09	
Mantis shrimp	11.90		14.06			1.56		0.51				
Unidentified prawn		0.37		0.09	0.36	0.27	0.12	0.08				
Unidentified crustacean	0.09	0.21	0.01	0.01	0.06	0.09	0.01	0.02				
Mammal	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Tursiops aduncus												
Unidentified dolphin												
Unidentified cetacean												
Unidentified mammal												
Unidentified Mysticeti												
Unidentified seal												
Bird	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.01**	**0.00**	**0.08**	**0.00**
Unidentified bird						0.00		0.00	0.01		0.08	
Miscellaneous	**0.00**	**0.03**	**0.00**	**0.00**	**0.04**	**0.00**	**0.07**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Bivalve					0.04		0.07					
Gastropod		0.03		0.00								
Fisherman's bait												

Note: % Mass, percent gravimetric mass; % IRI, percent index of relative importance. For sample sizes, see Fig. 2.

Table A2. The diet of the dusky shark (*Carcharhinus obscurus*) off KwaZulu-Natal, South Africa, from archived stomach content data (1983–2006).

	Small				Medium				Large			
	% Mass		% IRI		% Mass		% IRI		% Mass		% IRI	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Teleost	**65.67**	**54.27**	**91.80**	**82.46**	**31.98**	**43.28**	**64.64**	**67.93**	**12.06**	**78.95**	**78.13**	**99.06**
Acantheridae												
Anguillidae	1.44		0.12		0.21		0.01					
Ariidae					0.19		0.02					
Balistidae	0.16		0.02		0.35	0.09	0.01	0.00				
Belonidae												
Carangidae	0.31	0.97	0.16	0.11	2.16	0.92	0.17	0.05	0.01		0.00	
Cheilodactyleidae					0.34	0.24	0.02	0.01				
Chirocentridae												
Chloropthalmidae	0.39		0.02									
Cichlidae					0.22	0.15	0.01	0.00				
Clupeidae	2.23	1.99	0.17	1.01	11.88	32.84	36.10	60.67	10.39	78.74	77.08	99.03
Congridae												
Cynoglossidae	0.04		0.01									
Dactylopteridae												
Elopidae												
Engraulidae	0.03		0.01		1.57	0.06	5.25	0.01				
Ephippidae					1.25		0.03					
Exocetidae												
Exocoetidae						0.59		0.02				
Gempylidae		1.67		0.06								
Gerreidae	0.97		0.05									
Haemulidae	0.41	0.44	0.35	0.63	0.24	0.24	0.13	0.03	0.57		0.02	
Istiophoridae									0.23		0.01	
Leiognathidae	3.97		0.11			0.14		0.01				
Mugilidae	1.58	1.11	0.12	0.46		0.38		0.01				
Mullidae						0.04		0.00				
Muraenidae		0.91		0.04	2.16							
Myctophidae												
Oplegnathidae					0.55	0.04	0.01	0.00				
Ostraciidae					0.02		0.00					
Ostraciidae												
Peristediidae												
Platycephalidae												
Pleuronectidae		0.27		0.02		0.05		0.01				
Plotosidae		1.54		0.14					0.21		0.01	
Pomacentriidae												
Pomatomidae	2.28	0.73	0.31	0.10	0.11		0.00		0.11		0.00	
Priancathidae												
Sciaenidae	1.15	7.53	0.19	1.01	0.49	0.13	0.10	0.00	0.17		0.02	
Scombridae	18.40	11.08	5.58	1.79	4.22	3.91	1.75	0.86	0.02	0.09	0.00	0.00
Scorpididae	0.11		0.01									
Serranidae												
Sparidae	5.74	1.17	3.21	0.15	0.32	0.06	0.13	0.00	0.14		0.02	
Sphyraenidae					0.08		0.00					
Sygnathidae												
Synodontidae		0.08		0.02								
Teraponidae												
Trichiuridae					0.01		0.00					
Triglidae												
Unidentified teleost	26.46	24.79	81.37	76.93	5.63	3.40	20.90	6.22	0.21	0.11	0.97	0.03
Elasmobranch	**21.11**	**36.14**	**2.19**	**14.79**	**65.26**	**48.97**	**32.65**	**24.35**	**78.25**	**14.26**	**20.92**	**0.85**
Carcharhinidae	1.20	1.66	0.04	0.06	17.74	4.84	8.34	0.51	29.91	8.12	9.50	0.55
Dasyatidae	4.70	11.04	0.86	3.77	10.03	3.38	4.79	0.55	0.85	0.23	0.05	0.00
Gymnuridae						0.86		0.02				
Lamnidae									5.58		0.29	
Mobulidae	0.68		0.08		0.85		0.05					
Myliobatidae					1.85		0.15		1.75		0.05	
Odontaspididae									6.76		0.54	
Rajidae									0.00		0.00	
Rhinobatidae		0.80		0.04	1.77		0.05		0.23		0.01	
Rhinopeteridae	2.89		0.08						0.39		0.01	

Table A2 (*concluded*).

	Small				Medium				Large			
	% Mass		% IRI		% Mass		% IRI		% Mass		% IRI	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Scyliorhinidae					0.14		0.01		6.62		0.17	
Sphyrnidae	5.27	2.86	0.30	0.21	16.96	6.51	4.35	0.50	7.18	0.52	0.96	0.01
Squalidae												
Squatinidae					0.76	0.73	0.02	0.02	0.00		0.00	
Unidentified batoid	0.62	0.24	0.08	0.02	0.08	1.71	0.01	0.04				
Unidentified elasmobranch	0.01	0.90	0.01	0.14	1.22	0.30	0.21	0.03	0.01		0.00	
Unidentified shark	5.74	18.65	0.74	10.56	13.86	30.64	14.69	22.66	18.98	5.39	9.34	0.29
Cephalopod	**5.78**	**4.68**	**1.99**	**1.97**	**2.29**	**2.37**	**1.76**	**0.84**	**0.47**	**0.01**	**0.17**	**0.00**
Coleoidae												
Enoploteuthidae												
Loligo spp.	0.05	0.01	0.01	0.02								
Lycoteuthidae												
Octopodidae	0.41	1.82	0.09	0.28	1.52	1.49	0.72	0.27	0.42		0.03	
Octopoteuthidae												
Ommastrephidae	0.02		0.01									
Sepiidae (cuttlefish)	1.71	1.32	0.68	1.26	0.65	0.62	1.01	0.55	0.05	0.01	0.14	0.00
Teuthoidea (squids)	0.41	0.01	0.23	0.02	0.09	0.09	0.03	0.00				
Unidentified cephalopod	3.17	1.52	0.96	0.40	0.02	0.17	0.00	0.02				
Crustacean	**0.43**	**0.68**	**0.13**	**0.06**	**1.47**	**3.57**	**0.87**	**6.68**	**0.01**	**0.00**	**0.01**	**0.00**
Anomura (hermit crab)												
Brachyura (crabs)	0.07		0.05		0.63	1.10	0.35	0.48	0.01		0.01	
Macrura (rock lobsters)	0.12	0.60	0.05	0.03	0.08	0.18	0.03	0.04				
Mantis shrimp					0.75	2.29	0.49	6.16				
Unidentified prawn	0.17	0.06	0.02	0.02	0.02		0.00					
Unidentified crustacean	0.07	0.02	0.01	0.02	0.00	0.00	0.00	0.00				
Mammal	**1.33**	**3.73**	**0.11**	**0.42**	**1.12**	**1.82**	**0.06**	**0.20**	**9.20**	**2.98**	**0.77**	**0.04**
Tursiops aduncus									3.27	2.98	0.17	0.04
Unidentified dolphin	1.33	3.73	0.11	0.42	0.46	1.82	0.03	0.20	0.27		0.01	
Unidentified Mysticeti									5.36		0.58	
Unidentified seal									0.30		0.01	
Unidentified cetacean												
Unidentified mammal					0.65		0.04					
Bird	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Unidentified bird												
Miscellaneous	**5.69**	**0.50**	**3.78**	**0.30**	**0.04**	**0.00**	**0.01**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**
Bivalve												
Gastropod					0.01		0.01					
Fisherman's bait	5.69	0.50	3.78	0.30	0.03		0.00					

Note: % Mass, percent gravimetric mass; % IRI, percent index of relative importance. For sample sizes, see Fig. 2.