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# Diet of the milk shark, *Rhizoprionodon acutus* (Chondrichthyes: Carcharhinidae), from the Senegalese coast

By A. Ba[1], M. S. Diop[2], Y. Diatta[3], D. Justine[2] and C. T. Ba[1]

[1]*Département de Biologie Animale, Faculté des Sciences et Techniques, Université Cheikh Anta Diop de Dakar, Dakar Fann, Senegal;* [2]*Commission Sous-Régionale des Pêches en Afrique de l'Ouest (CSRP), Dakar, Sénégal;* [3]*Laboratoire de Biologie Marine, LABEP–AO, IFAN–Ch. A. Diop, Dakar, Senegal*

## Summary

The diet of the milk shark, *Rhizoprionodon acutus*, from the Senegalese coast (12°30′N–14°45′N) was investigated in 3600 specimens with total lengths ranging from 44 to 113 cm for females and from 45 to 110 cm for males. Conducted from May 2010 to April 2011, the study revealed that of the 3600 stomachs examined, 577 contained food (16.03%). Cumulative prey diversity curves reached a stable level at 175 stomachs and thus the sample size was large enough to describe the overall milk shark diet. Relevant differences in the diet were found between sexes, maturity stages, sampling seasons and locations. The milk shark diet was composed of teleosts, crustaceans, mollucs, nematodes, annelids, and unidentified invertebrates. *R. acutus* seemed to have a preference for teleosts (98.75% in terms of IRI). The trophic level of milk shark calculated in this study was 4.2.

## Introduction

It has long been postulated that many species of sharks and other elasmobranchs are apex predators and, as such, are hypothesized as playing major roles in structuring marine communities through predation (Cortés, 1999; Stevens et al., 2000). Despite this, our understanding of the dynamics of prey consumption and processing of food in elasmobranchs remains rudimentary. Information on the dietary composition of a species is essential for understanding natural history, the role of elasmobranchs in marine ecosystems and the impact of elasmobranch predation on economically valuable or endangered prey (Rosecchi and Nouaze, 1987; Cortés, 1999). The diversity of prey that occurs within species has been attributed to many factors. There are examples of geographical differences in the diet of several species of sharks (Lowe et al., 1996; Simpfendorfer et al., 2001), ontogenetic shifts in shark feeding habits (Stillwell and Kohler, 1982; Lowe et al., 1996) and dietary shifts according to maturity stage (Lucifora et al., 2009). Several authors have also reported differences in the diet between sexes of sharks (Matallanas, 1982; Simpfendorfer et al., 2001) and seasons (Cortés et al., 1996). Therefore, it is important that life-stage specific biological and ecological information be gathered to aid in the assessment and monitoring of shark populations and their prey.

The milk shark, *Rhizoprionodon acutus* (Rüppell, 1837), the most widely distributed species of its genus, can be found all along the West African coasts, in the Indo-Pacific, in the northern part of the Indian Ocean, from the Indonesian to the Philippine archipelagos, and from Japan to Australia (Compagno, 1984). Milk shark is a pelagic shark commonly found up to 200 m-deep in tropical and sub-tropical estuarine and coastal waters (Compagno, 1984; Simpfendorfer, 2003) and is the most commonly and regularly landed small coastal shark on the Senegalese continental shelf (Capapé et al., 2006). Despite its wide distribution there is a paucity of information on milk shark feeding habits and diet (White et al., 2004; Patokina and Litvinov, 2005). Therefore, the objectives of this study were to: (i) describe the dietary composition and trophic level of the milk shark, (ii) identify the feeding strategy of this predator, and (iii) investigate whether there is a sexual, ontogenetic, seasonal and locational shift in the dietary composition of this species.

## Materials and methods

### Sampling

A total of 3600 stomachs were examined. Individuals were landed from May 2010 to April 2011 by artisanal fisheries in the Center West zone comprising Dakar, Mbour and Joal, and in Casamance (in the southwest), comprising Kafountine, Diogué, Elinkine and Cap Skiring (Fig. 1). Drift nets, surface longlines, sole gill nets and purse seines were the types of fishing gear used in all seasons. The milk shark has mostly been taken by longlines and gillnets in artisanal fisheries. Gillnets have been the only gear used in all capture sites, whereas longlines have been used at sites in the central west. Purse seine and sole nets were used only in the southwest. Sharks were measured for total length (TL in cm) and weighed (total weight, W in g). They were sexed and assessed for sexual maturity. The maturity stage was evaluated for males from the aspect of the testicles and the degree of calcification of the claspers. Three groups of males corresponding to three size classes were categorized in relation to the maturity stage: juveniles ($\leq$69 cm TL), sub-adults (70 $\leq$ TL $\leq$80 cm) and adults ($\geq$81 cm TL). Males were considered as 'juvenile' if the cartilage within the clasper was not calcified and the testicles were underdeveloped; they were considered as 'sub-adult' if their claspers were partially calcified and the testicles developed. Males were considered 'adult' if they had calcified claspers that rotated 180° in relation to their normal position and a freely opening rhipidion (Clarke and von Schmidt, 1965). The maturity stage of females was studied using the state of the ovary, the uterus and the oviducal glands with juveniles ($\leq$69 cm TL), sub-adults (70 $\leq$ TL $\leq$90 cm TL) and adults ($\geq$91 cm TL). Females were considered as 'juvenile' if the ovaries were small, the oocytes not differentiated and their uteri filiform; they were

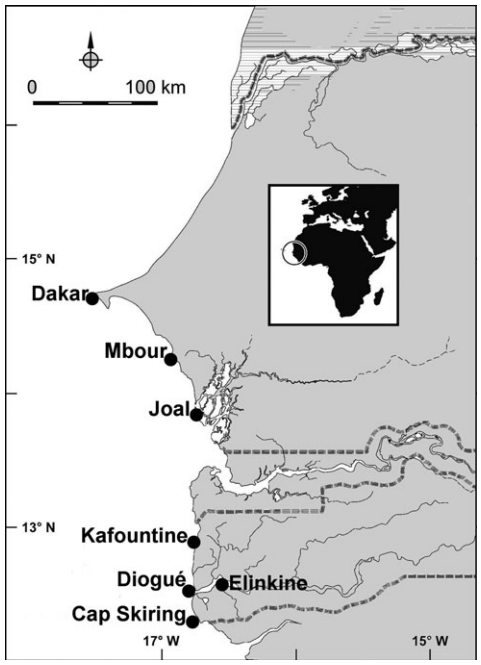


Fig. 1. Sampling sites, central and south coasts of Senegal

considered as 'sub-adults' when their ovaries were slightly enlarged, more transparent and the oocytes had become differentiated to one of various small sizes. Females were considered 'adult' if they were gravid or had a developed ovary (left side only; the right side being absent or rudimentary), enlarged oviducal glands and developed uteri (Castro, 1993). The presence of empty stomachs was also recorded.

### Diet analysis

Stomachs were excised from each individual and the inside flushed with 70% ethanol in order to collect any contents that may have been lodged or trapped inside the stomach (Cortés and Gruber, 1990). Samples were stored on ice in plastic bags and preserved in 70% ethanol. In the laboratory, the stomach contents of each shark were filtered through a sieve, rinsed with water and weighed (g) after draining off excess water. Prey items were identified to the smallest taxonomic level possible using various identification guides (Fischer et al., 1981; Séret and Opic, 1981; Bellemans et al., 1988), counted and weighed. Prey were identified where possible from external morphology or with the use of a dissecting microscope whenever necessary, depending on the digestion stage of each item. Unidentified prey were placed in with the unidentified teleosts or unidentified invertebrates.

### Data analysis

**Overall diet.** Prey were grouped into major categories for comparisons according to sex (male or female), maturity stage (juveniles, sub-adults and adults), season (hot season, May to October; cold season, November to April) and location (Center West zone and Casamance). Prey importance was evaluated by using the percentage by number (%N), mass (%W), frequency of occurrence (%F), and the index of relative importance (IRI) (Pinkas et al., 1971), expressed on a percentage basis (%IRI) (Cortés, 1997, 1998). These values were calculated for each prey item and the %IRI also calculated for higher taxa (e.g. teleosts, crustaceans and molluscs). The %IRI was calculated to facilitate comparisons between prey items (Saïdi et al., 2009) as:

$$\%\mathrm{IRI}_i = 100\,\mathrm{IRI}_i / \sum_{I=i}^{n} \mathrm{IRI}_i$$

Trophic diversity was calculated by Shannon–weiner (H') Index (Krebs, 1989).

$$H' = -\sum_{i=1}^{S} (P_i)\log_2(P_i)$$

where H' is diversity index of Shannon–Weiner, S is number previously assigned to the type of prey or groups, and $P_i$ the proportion of the total sample belonging to each group. In order to measure sample size sufficiency, the cumulative number of pooled stomachs is plotted against the cumulative prey diversity using the Shannon–Weiner diversity index with the asymptotic stabilization of the curve, indicating the minimum number of stomachs that have to be analysed to obtain precise, and thus more reliable, results (McElroy et al., 2006). Trophic level was calculated to determine the position of milk shark within the food web (Cortés, 1999) and to compare it to that of other regions. The trophic level was calculated as:

$$\mathrm{TL} = 1 + \left(\sum_{j=1}^{n} P_j \times \mathrm{TR}_j\right)$$

where $TR_j$ is the trophic level of each prey item and $P_j$ the proportion of each prey item in the diet of milk shark ($P_j$ value obtained from the %IRI of each prey item and trophic level of each prey obtained from Cortés (1999).

**Feeding strategy.** The prey importance (dominant or rare) and feeding strategy (specialist or generalist) were assessed by the method of Amundsen et al. (1996):

$$P_i = \left(\sum S_i / \sum S_{ti}\right) \times 100$$

where $P_i$ is the prey-specific abundance of prey i, $S_i$ is the stomach content or total number of the prey I, and $S_{ti}$ the total stomach content in those predators with prey in their stomach.

**Diet shifts.** The mean numbers of prey per stomach were calculated for each sex, each maturity stage, each season and each location. To determine if there were significant differences in stomach contents between sexes and between maturity stages, multivariate analysis of variance (MANOVA) was used (Moura et al., 2008). A similar analysis was performed to evaluate seasonal and locational variation in the diet of the sharks collected in this study. The dependent variable used was the Index of Relative Fullness (IRF). This index was derived by dividing the total weight (g) of the stomach contents for a given shark by the total weight (g) of that shark (Barry et al., 2008).

## Results

### Sample description

Composition was females 59.03% (2125) and males 40.97% (1475). Total length ranged from 44 to 113 cm TL for females and from 45 to 110 cm TL for males. Of the 3600 stomachs examined, 577 (16.03%) contained food and 3023

Table 1
Diet composition of *Rhizoprionodon acutus*, %N, %W, %F and %IRI = percentages by number, mass, frequency of occurrence and index of relative importance of prey, respectively

| Taxon of the items | %Ni | %Wi | %Fi | %IRI |
|---|---|---|---|---|
| Teleosts | 86.55 | 96.95 | 91.64 | 98.75 |
| Balistidae | | | | |
| *Cynoglossus monodi* | 0.16 | 0.42 | 0.17 | + |
| Carangidae | | | | |
| *Alectis alexandrinus* | 0.98 | 1.22 | 1.04 | 0.09 |
| *Dantex canariensis* | 0.33 | 0.22 | 0.35 | + |
| *Dantex sanctachelenae* | 0.16 | 0.28 | 0.17 | + |
| *Pseudocranx dantex* | 0.16 | 0.11 | 0.17 | + |
| *Selene dorsalis* | 1.47 | 2.47 | 1.56 | 0.25 |
| *Trachurus* sp. | 1.47 | 2.25 | 1.56 | 0.24 |
| Clupeidae | | | | |
| *Ethmalosa fimbriata* | 4.75 | 6.07 | 5.03 | 2.25 |
| *Sardina pilchardus* | 0.16 | 0.20 | 0.17 | + |
| *Sardinella aurita* | 7.36 | 9.58 | 7.80 | 5.46 |
| *Sardinella maderensis* | 6.06 | 7.07 | 6.41 | 3.48 |
| *Sardinella* sp. | 5.73 | 6.30 | 6.07 | 3.02 |
| Cynoglossidae | | | | |
| *Cynoglossus senegalensis* | 0.16 | 0.42 | 0.17 | + |
| Elopidae | | | | |
| *Elops senegalensis* | 0.16 | 0.14 | 0.17 | + |
| Eugraulidae | | | | |
| *Eugraulis eucrasiscolus* | 0.16 | 0.30 | 0.17 | + |
| Gerreidae | | | | |
| *Eucinostomus melanopterus* | 0.82 | 1.36 | 0.87 | 0.08 |
| Libridae | | | | |
| *Coris julis* | 0.16 | 0.15 | 0.17 | + |
| *Coris ruber* | 0.16 | 0.4 | 0.17 | 0.03 |
| Mugilidae | | | | |
| *Liza falcipinis* | 3.44 | 3.80 | 3.64 | 1.09 |
| Mullidae | | | | |
| *Pseudupeneus prayensis* | 3.27 | 3.75 | 3.47 | 1.01 |
| Muraenesocidae | | | | |
| *Cynoponticus ferox* | 0.49 | 0.51 | 0.52 | 0.02 |
| Muraenidae | | | | |
| *Echidna peli* | 0.49 | 0.58 | 0.52 | 0.02 |
| *Enchlycore nigricans* | 0.16 | 0.58 | 0.17 | 0.01 |
| *Liza mareii* | 0.33 | 1.14 | 0.35 | 0.02 |
| *Lycodontis afer* | 0.16 | 0.40 | 0.17 | + |
| *Lycodontis mareii* | 0.49 | 0.69 | 0.52 | 0.03 |
| *Muraena melanotis* | 0.16 | 0.30 | 0.17 | + |
| *Muraena robusta* | 0.49 | 0.52 | 0.52 | 0.02 |
| Polynemidae | | | | |
| *Pentanemus quinquarius* | 0.16 | 0.26 | 0.17 | + |
| Pomadasyidae | | | | |
| *Pomadasys incisus* | 2.13 | 3.52 | 2.25 | 0.53 |
| Pomatomidae | | | | |
| *Pomatomus saltator* | 0.16 | 0.33 | 0.17 | + |
| Sciaenidae | | | | |
| *Pseudotolithus senegalensis* | 0.16 | 0.57 | 0.17 | 0.01 |
| *Pseudotolithus* sp. | 1.96 | 2.71 | 2.08 | 0.40 |
| Serranidae | | | | |
| *Morone punctata* | 2.45 | 3.25 | 2.60 | 0.61 |
| Soleidae | | | | |
| *Pegusa triophthalmus* | 0.16 | 0.42 | 0.17 | + |
| Sparidae | | | | |
| *Dentex canariensis* | 0.16 | 0.17 | 0.17 | + |
| *Dentex congoensis* | 0.98 | 1.11 | 1.04 | 0.09 |
| *Dentex gibbosus* | 1.31 | 1.35 | 1.39 | 0.15 |
| *Pagellus bellottii* | 0.65 | 0.66 | 0.69 | 0.04 |
| *Sparus* sp. | 0.65 | 0.76 | 0.69 | 0.04 |
| Sphyraenidae | | | | |
| *Sphyraena guachancho* | 3.11 | 4.34 | 3.29 | 1.01 |
| Unidentified Fishes | 32.57 | 22.67 | 34.49 | 78.71 |
| Crustaceans | 6.2 | 2.33 | 6.58 | 0.63 |
| Aristeidae | 0.16 | 0.12 | 0.17 | + |
| *Aristeus varidens* | 0.16 | 0.12 | 0.17 | + |
| Copepods | 0.16 | + | 0.17 | + |
| Unidentified shrimps | 1.80 | 0.67 | 1.91 | 0.19 |
| Crabs | | | | |
| Portunidae | | | | |
| *Callinectes amnicola* | 0.16 | 0.14 | 0.17 | + |
| *Callinectes pallidus* | 0.16 | + | 0.17 | + |
| *Porturinus validis* | 1.96 | 0.95 | 2.08 | 0.25 |
| *Liocarcinus corrugatus* | 0.16 | + | 0.17 | + |
| Unidentified crabs | 1.80 | 0.45 | 1.91 | 0.18 |
| Molluscs | 4.88 | 4.22 | 5.18 | 0.53 |
| Lamellibranches | 0.16 | + | 0.17 | + |
| Gasteropods | | | | |
| Cymatiidae | | | | |
| *Charonia nidifera* | 0.16 | + | 0.17 | + |
| Nassariidae | | | | |
| *Bulia miran* | 0.49 | + | 0.52 | 0.01 |
| Strombidae | | | | |
| *Strombus latus* | 0.16 | + | 0.17 | + |
| Unidentified gasteropods | 0.65 | + | 0.69 | 0.02 |
| Cephalopoda | | | | |
| Octopodidae | | | | |
| *Octopus vulgaris* | 1.47 | 2.40 | 1.56 | 0.25 |
| Ommastreiphidae | | | | |
| *Ommastrephis pteropus* | 0.16 | + | 0.17 | + |
| Sepiidae | | | | |
| *Sepia* sp. | 1.63 | 1.82 | 1.73 | 0.25 |
| Annelides | 0.33 | + | 0.35 | + |
| Nematodes | 0.65 | + | 0.69 | 0.02 |
| Unidentified invertebrates | 1.15 | 0.14 | 1.21 | 0.06 |

+: <0.01.

were empty (vacuity index = 83.97%). Of the 1800 stomachs excised in the hot season, 320 (17, 18%) contained food, while in the 1800 stomachs excised in the cold season, 257 (14, 28%) contained food. The number of males with stomachs containing food was 224 (16.61%), and the number of females 353 (15.18%) (Table 1). The number of empty stomachs and those containing food was significantly different (test t = 46.163; d.f. = 6042; $P < 0.05$).

#### Overall diet and feeding strategy

Cumulative prey diversity reached a stable level at 175 stomachs for the six groups of prey (Fig. 2). Therefore, the sample size was considered large enough to describe the overall diet. The trophic level of *R. acutus* calculated in this study was 4.2. This species consumed a wide range of prey items belonging to six major groups: teleosts, crustaceans, molluscs, nematodes, annelids, and unidentified invertebrates (Table 1). Identified prey belonged to 21 families of teleosts, six families of mollucs and two families of crustaceans (Table 1). Among the six different prey categories found, teleosts were the most frequent prey in the both sexes, in all locations, in all seasons and all maturity stages (%IRI = 98.75% of the total; Fig. 3). The other categories had a much lower importance in the diet (%IRI <2%; Table 1) and were composed of crustaceans (%IRI = 0.62%), molluscs (%IRI = 0.53%) annelids, and unidentified invertebrates. Unidentified teleosts were the most common prey item in sharks analysed in this diet study and represented 34.4% (%F) and 78.71% (%IRI). Plotting prey-specific abundance against frequency of occurrence confirmed that teleosts were the dominant prey with a value of % F and $P_i$ higher than 80%, with this result suggesting a specialized feeding strategy for this species. Crustaceans,

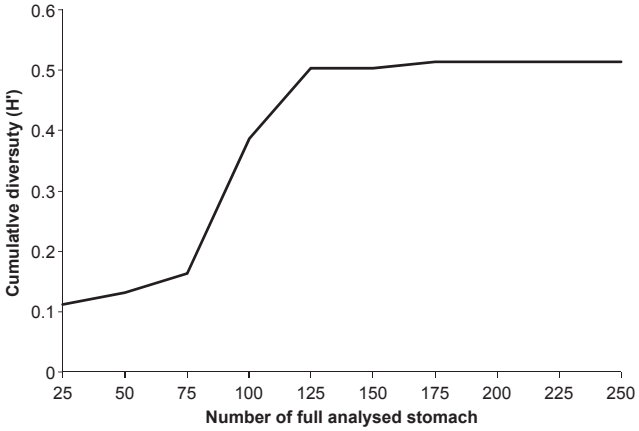


Fig. 2. Cumulative curve of prey diversity identified in *Rhizoprionodon acutus* stomachs derived by Shannon–Wiener (H') index

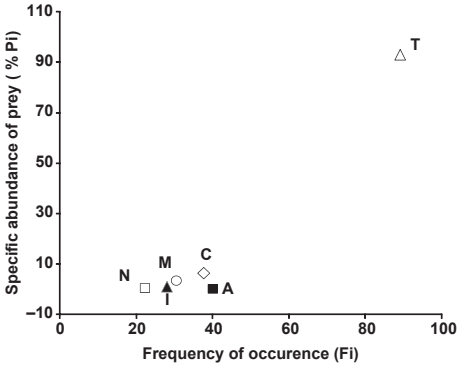


Fig. 4. Graphical representation of milk shark feeding strategy: prey-specific abundance (% P) plotted against percentage frequency of occurrence (%F) (T: teleosts; C: crustaceans; M: molluscs; N: nematodes; A: annelids; I: unidentified invertebrates)

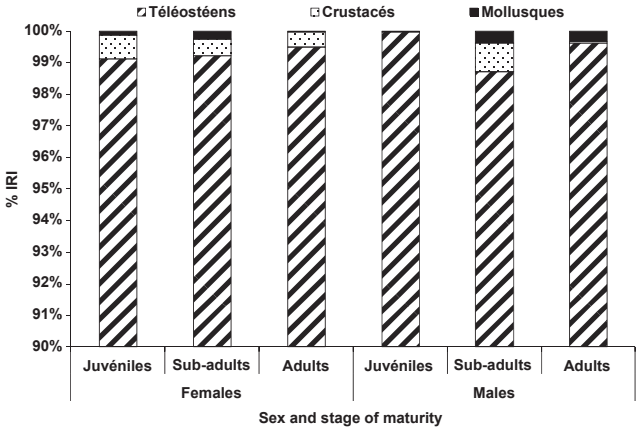


Fig. 3. Relative abundance by sex and stage of sexual maturity of teleosts, crustaceans and molluscs in the *Rhizoprionodon acutus* diet

Table 2
Variation according to sex and stage of sexual maturity of the number (N) and weight of prey in stomachs containing food (N), *Rhizoprionodon acutus*. %N, %W, %F and %IRI = percentage by number, mass, frequency of occurrence and index of relative importance of prey, respectively

| Sexes and maturity stage | N | N items | W items | %N | %W | %F | %IRI |
|---|---|---|---|---|---|---|---|
| Females | 353 | 373 | 10058.75 | | | | 71.39 |
| Juveniles | 129 | 137 | 3087.31 | 36.73 | 30.69 | 36.54 | 33.96 |
| Sub-adults | 70 | 76 | 2149.71 | 20.38 | 21.37 | 19.83 | 11.41 |
| Adults | 154 | 160 | 4821.73 | 42.90 | 47.94 | 43.63 | 54.62 |
| Males | 224 | 238 | 6221.25 | | | | 28.61 |
| Juveniles | 75 | 79 | 2058.12 | 33.19 | 33.08 | 33.48 | 30.00 |
| Sub-adults | 45 | 50 | 1129.01 | 21.01 | 18.15 | 20.09 | 10.64 |
| Adults | 104 | 109 | 3034.12 | 45.80 | 48.77 | 46.43 | 59.36 |
| Total | 577 | 611 | 16280 | | | | |

molluscs, nematodes, and unidentified invertebrates were included within the category of rare species (Fig. 4). The *Sardinella* genus was the most important among teleosts consumed and represented 20% (%F) and 12% (%IRI) (Table 1).

### Diet shifts

There were significant differences in the diets of males and females (MANOVA: $F = 3.896$, d.f. = 2; $P < 0.05$). Mean number of prey per stomach was 1.61 (±0.85) and 1.53 (±0.81), respectively, for females and males. Additionally, the value of %IRI was much higher for females (71.39%) than for males (28.61%) (Table 2).

The milk shark experienced an ontogenetic dietary shift, as evidenced by significant dietary differences between juveniles, sub-adults and adults in females (MANOVA: $F = 102.948$; d.f. = 2; $P < 0.05$) and in males (MANOVA: $F = 51.062$; d.f. = 2; $P < 0.05$). In females, the mean number of prey per stomach was 1.40 (±0.61), 1.62 (±0.81) and 1.68 (±0.83), respectively, for juveniles, sub-adults and adults while in males, this was estimated at 1.24 (±0.51), 1.88 (±0.90) and 1.74 (±1.12), respectively, for juveniles, sub-adults and adults. The value of % IRI was higher among adults in both sexes, accounting for 54.62 and 59.36%, respectively, for females (91–113 cm TL) and males (81–110 cm TL), followed by juveniles with 33.96 and 30%, respectively, for females and males (<70 cm TL). Sub-adults had the smallest % IRI values of 11.41% for females (70–90 cm TL) and (70–80 cm TL) and 10.44% for males (Table 2).

The milk shark showed a seasonal pattern in dietary composition. Mean prey number per stomach was $1.53 \pm 0.83$ and $1.68 \pm 0.85$, respectively, for warm and cold seasons. The %IRI value was higher in the hot season (77.71%) than in the cold season (22.29%) (Table 3). Both seasons showed significant differences in the diet composition (MANOVA: $F = 3.882$; d.f. = 1; $P < 0.05$).

The value of % IRI was higher in the Center West zone (82.74%) than in Casamance (17.26%) (Table 3). Casamance and the Center West zone revealed significant differences in the milk shark diet (MANOVA: $F = 30.468$; d.f. = 1; $P < 0.05$). Mean number of prey per stomach was 1.47 (±0.69) and 1.64 (±0.90), respectively, in Casamance and the Center West zone.

## Discussion

Small sample sizes and large variations in food categories greatly influence the dietary importance of prey items (Hyslop, 1980). Therefore, diversity curves according to the Shannon–Weiner have been used to determine the sample size for both *R. acutus* males and females, requiring at least

Table 3
Variation according to season and location of the number of individuals with stomachs containing food (N). %N, %W, %F and %IRI = percentage by number, mass, frequency of occurrence and index of relative importance of prey, respectively

| Parameters | N | %N | %W | %F | %IRI |
|---|---|---|---|---|---|
| Seasons | | | | | |
| Hot season | 399 | 65.03 | 64.59 | 69.15 | 77.71 |
| Cold season | 212 | 34.97 | 35.41 | 36.74 | 22.29 |
| Locations | | | | | |
| Casamance | 208 | 34.04 | 23.54 | 36.05 | 17.26 |
| Center zone | 403 | 65.96 | 76.46 | 69.84 | 82.74 |

175 stomachs. For many species of sharks, the cumulative prey curves reached a stable level in 200 stomachs (Morato et al., 2003; Bethea et al., 2004). No studies had previously determined the number of stomachs needed to describe the milk shark diet.

The proportion of empty stomachs, higher in this study, was generally important in shark populations (Wetherbee and Cortés, 2004). It was assessed at 59% for *R. taylori* (Simpfendorfer, 1998), and at 82.8%, 75.6% and 79.8%, respectively, for *Orectolobus ornatus, O. maculatus* and *O. halei* (Huveneers et al., 2007). We observed for the first time the presence of individuals in this species having empty stomachs. They were numerous throughout the year and represented 83.97% of the sample. The type of fishing gear appeared to have an impact on this high number of empty stomachs. Indeed, starving individuals tend to approach and be caught by baited fishing gear. This is because the sharks will evacuate their stomachs, turning them inside out in order to try to rid themselves of the hook.

The milk shark is a pelagic and coastal species that feeds mainly on pelagic prey. The presence of some demersal species in the diet showed that *R. acutus* could conduct vertical movements, like most shark species (White et al., 2004; Sims et al., 2008; Nakamura et al., 2011). These vertical movements allow them to meet a wider range of prey species (Simpfendorfer et al., 2001; Preti et al., 2004). Biotelemetry and tagging experiments could be undertaken to validate the movements of the milk shark along the Senegalese coasts. Analyses of *R. acutus* stomach contents showed that teleosts were generally the most abundant prey. Prey-specific abundance plotted against frequency of occurrence showed that *R. acutus* was a specialized feeder of teleosts. *R. acutus* seemed to correspond to the third case study presented by Amundsen et al. (1996) showing a population specialization toward one single prey type (teleosts). This is the case when most sharks feed on the dominant prey taxon, but small numbers of other prey types are occasionally included in the diet of some individuals. Thus, crustaceans, molluscs, nematodes, annelids, and other unidentified invertebrates are rare prey species. Among shark species of the genus *Carcharhinus*, *Sphyrna* and *Rhizoprionodon*, over 90% of stomachs contained teleosts (Stevens and Mcloughlin, 1991; Salini et al., 1992; Simpfendorfer, 1998; Gelsleichter et al., 1999; White et al., 2004). Our results confirm these previous observations on the diet of sharks. The largest prey families of teleosts in the diet of the milk shark varied in different localities. Especially on Australian shores there were Hemiramphidae, Mugilidae, Clupeidae, Athérinidae, Sillaginidae and Labridae. In this study, predation pressure was higher among Clupeidae, especially on *Sardinella*, Carangidae, Mugilidae, Mullidae, Muraenidae, Pomadasyidae, Sciaenidae, Sparidae and Serranidae. Differences in the diet between different geographic regions may have been the result of the types of habitat and prey groups that dominate these regions as well as the abundance of the different prey types within these habitats (Simpfendorfer, 1992; Lowe et al., 1996). The trophic level of *R. acutus* found in this study (4.2) made it a tertiary consumer. The TL we calculated for the milk shark was very similar to that of an earlier study (4.1; Cortés, 1999). The high TL of the milk shark indicated that it is top predator. Given this high TL, the removal of the top predators may have potential top-down effects on their prey and other lower-level consumers.

As reported in several studies (Klimley, 1987; Stillwell and Kohler, 1993; Simpfendorfer et al., 2001; McCord and Campana, 2003), sexual differences in the diet were shown in this study. These differences are related to either sexual segregation resulting from sex-specific preferences in the food-searching sites and the difference in the stomach size between males and females (Klimley, 1987; McCord and Campana, 2003; Capapé et al., 2006). Indeed, the increased consumption of large pelagic species was observed more often in females with a stomach larger than males, as that has been observed in scalloped hammerhead *Sphyrna lewini* (Klimley, 1987).

In our study, we evaluated differences in the diet among different maturity levels of the milk shark. These differences in the diet among juveniles, sub-adults and adults might be associated with the formation of schools segregated by size. Sharks might occupy habitats different from those of the larger sharks to avoid predation (Lowe et al., 1996). These conclusions agree with previously published studies on food habits of several shark species (Stillwell and Kohler, 1982; Cortés and Gruber, 1990; Lowe et al., 1996). Onset of sexual maturity and the related change in the energetic needs due to reproduction, such as gonad development, egg formation, and gestation increases, could trigger shifts in the feeding habits, which involve a change in habitat utilization. To match these increased energy requirements, a quantitative or qualitative change in diet is expected (Fishelson et al., 1987). The segregation of the milk shark by sex and stage of maturity could be an important component to reduce intraspecific competition.

The seasonal differences in the milk shark diet in this study might be related to changes in the abundance of the prey community or in the distributional differences among sharks according to the season. Seasonal migrations of sharks or of their prey and the changes in prey availability could explain seasonal shifts observed in the diet of the milk shark on the Senegalese coasts. Seasonal variation in diet has been reported for a number of other shark species (Matallanas, 1982; Stillwell and Kohler, 1982; Cortés et al., 1996).

Differences in the diet of the milk shark between Casamance and the Center West zone may have been the result of the types of habitat that dominate both of these locations, the abundance of the different prey types within these habitats, or some prey groups not being present in certain locations (Stillwell and Kohler, 1982). Unfortunately, data on the abundance of prey groups in each of these locations is lacking. The variation of diet according to locations is exemplified by many species of shark (Simpfendorfer, 1992; Lowe et al., 1996).

In summary, this study is the first to provide detailed information on the diet of *Rhizoprionodon acutus*. The

findings suggest the specialized feeding behaviour of this species in the center and south Senegalese coasts. *R. acutus* is a tertiary consumer with a diet changing according to sex, maturity stage, season and location.

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**References**

Amundsen, P. A.; Gabler, H. M.; Staldvik, F. J., 1996: A new approach to graphical analysis of feeding strategy from stomach contents data –modification of Costello (1990) method. J. Fish Biol. **48**, 607–614.

Barry, K. P.; Condrey, R. E.; Driggers, W. B.; Jones, C. M., 2008: Feeding ecology and growth of neonate and juvenile blacktip sharks *Carcharhinus limbatus* in the Timbalier–Terrebone Bay complex, LA, U.S.A. J. Fish Biol. **73**, 650–662.

Bellemans, M.; Sagna, A.; Fischer, W.; Scialabba, N., 1988: Guide des ressources halieutiques du Sénégal et de la Gambie. Espèces marines et d'eaux saumâtres. FAO, Rome.

Bethea, D. M.; Buckel, J. A.; Carlson, J. K., 2004: Foraging ecology of the early life stages of four sympatric shark species. Mar. Ecol. Prog. Ser. **268**, 245–264.

Capapé, C.; Diatta, Y.; Diop, M.; Guélorget, O.; Vergne, Y.; Quignard, J. P., 2006: Reproduction in the milk shark, *Rhizoprionodon acutus* (Rüppel, 1837) (Chondrichthyes: Carcharhinidae) from the coast of Senegal (eastern tropical Atlantic). Acta Adriat. **47**, 111–126.

Castro, J. I., 1993: The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Envir. Biol. Fish. **38**, 37–48.

Clarke, E.; von Schmidt, K., 1965: Sharks of the central gulf coast of Florida. Bull. Mar. Sci. **15**, 13–83.

Compagno, L. J. V., 1984: FAO Species Catalogue. 4. Requins du monde: un catalogue annoté et illustré des espèces de requins connues à ce jour. Partie 2. Carcharhiniformes. FAO Fish. Synop. **125**, 251–655.

Cortés, E., 1997: A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. Can. J. Fish. Aquat. Sci. **54**, 726–738.

Cortés, E., 1998: Methods of studying fish feeding: reply. Can. J. Fish. Aquat. Sci. **55**, 2708.

Cortés, E., 1999: Standardized diet compositions and trophic levels of sharks. ICES J. Mar. Sci. **56**, 707–717.

Cortés, E.; Gruber, S. H., 1990: Diet, feeding habits, and estimates of daily ration of young lemon sharks, *Negaprion brevirostris* (Poey). Copeia **20**, 4–218.

Cortés, E.; Manire, C. A.; Hueter, R. E., 1996: Diet, feeding habits, and diel feeding chronology of the bonnethead shark, *Sphyrna tiburo* in southwest Florida. Bull. Mar. Sci. **58**, 353–367.

Fischer, W.; Bianchi, G.; Scott, W. B., 1981: Fiches FAO d'identification des espèces pour les besoins de la pêche. Atlantique centre-est; zone de pêche 34, 47 (en partie). Canada Fonds de Dépôts. Ottawa, Ministère des Pêcheries et Océans Canada, en accord avec l'Organisation des Nations-Unies pour l'Alimentation et l'Agriculture, Vols. 1–7.

Fishelson, L.; Montgomery, L. W.; Myrberg, A. H., Jr, 1987: Biology of surgeonfish *Acanthurus nigrofuscus* with emphasis on changeover in diet and annual gonadal cycles. Mar. Ecol. Prog. Ser. **39**, 37–47.

Gelsleichter, J.; Musick, J. A.; Nichols, S., 1999: Food habits of the smooth dogfish, *Mustelus canis*, dusky shark, *Carcharhinus obscurus*, Atlantic sharpnose shark, *Rhizoprionodon terraenovae*, and the sand tiger, *Carcharias taurus*, from the northwest Atlantic Ocean. Envir. Biol. Fish. **54**, 205–217.

Huveneers, C.; Otway, N. M.; Gibbs, S. E.; Harcourt, R. G., 2007: Quantitative diet assessment of wobbegong sharks (genus *Orectolobus*) in New South Wales, Australia. ICES J. Mar. Sci. **64**, 1272–1281.

Hyslop, E. J., 1980: Stomach contents analysis: a review of methods and their application. J. Fish Biol. **17**, 411–429.

Klimley, A. P., 1987: The determinates of sexual segregation in the scalloped hammerhead sharks, *Sphyrna lewini*. Envir. Biol. Fish. **18**, 27–40.

Krebs, C. J., 1989: Ecological Methodology. Harper & Row, New York.

Lowe, C. G.; Wetherbee, B. M.; Crow, G. L.; Tester, A. L., 1996: Ontogenetic dietary shifts and feeding behavior of the tiger shark, *Galeocerdo cuvier*, in Hawaiian waters. Envir. Biol. Fish. **47**, 203–211.

Lucifora, L. O.; Garcia, V. B.; Menni, R. C.; Escalante, A. H.; Hozbor, N. M., 2009: Effects of body size, age and maturity stage on diet in a large shark: ecological and applied implications. Ecol. Res. **24**, 109–118.

Matallanas, J., 1982: Feeding habits of *Scymnorhinus licha* in Catalan waters. J. Fish Biol. **20**, 155–163.

McCord, M. E.; Campana, S. E., 2003: A quantitative assessment of the diet of the blue shark (*Prionace glauca*) off Nova Scotia, Canada. J. Northw. Atl. Fish. Sci. **32**, 57–63.

McElroy, D. W.; Wetherbee, B. M.; Mostello, C. S.; Lowe, C. G.; Crow, G. L.; Wass, R. C., 2006: Food habits and ontogenetic changes in the diet of the sandbar shark, *Carcharhinus plumbeus*, in Hawaii. Envir. Biol. Fish. **76**, 81–92.

Morato, T.; Sola, E.; Grós, M. P.; Menezes, G., 2003: Diets of thornback ray (*Raja clavata*) and tope shark (*Galeorhinus galeus*) in the bottom longline fishery of the Azores, northeastern Atlantic. Fish. Bull. **101**, 590–602.

Moura, T; Figueiredo, I.; Farias, I.; Serra-Pereira, B.; Neves, A.; Borges, M. F.; Gordo, L. S., 2008: Ontogenetic dietary shift and feeding strategy of *Raja undulata* Lacepède, 1802 (Chondrichthyes: Rajidae) on the Portuguese continental shelf. Sci. Mar. **72**, 311–318.

Nakamura, I.; Watanabe, Y. Y.; Papastamatiou, Y. P.; Sato, K.; Meyer, C. G., 2011: Yo-yo vertical movements suggest a foraging strategy for tiger sharks *Galeocerdo cuvier*. Mar. Ecol. Prog. Ser. **424**, 237–246.

Patokina, F. A.; Litvinov, F. F., 2005: Food composition and distribution of elasmobranches on the shelf and upper slope of the Eastern Central Atlantic. ICES CM, 26.

Pinkas, L.; Oliphant, M. S.; Iverson, I. L. K., 1971: Food habits of albacore, blue fin tuna and bonito in California waters. California Fish and Game. Fish. Bull. **152**, 1–105.

Preti, A.; Smith, S. E.; Ramon, D. A., 2004: Diet differences in the thresher shark (*Alopias vulpinus*) during transition from a warm-water regime to a cool-water regime off California–Oregon, 1998–2000. Reports of California Cooperative Oceanic Fisheries Investigations. **45**, 118–125.

Rosecchi, E.; Nouaze, Y., 1987: Comparaison de cinq indices utilisés dans l'analyse des contenus stomacaux. Revue des Travaux de l'Institut des Pêches Maritimes **49**, 111–123.

Saïdi, B.; Enajjar, S.; Bradaï, M. N.; Bouaïn, A., 2009: Diet composition of smooth-hound shark, *Mustelus mustelus* (Linnaeus, 1758), in the Gulf of Gabès, southern Tunisia. J. Appl. Ichthyol. **25**(Suppl. 1), 113–118.

Salini, J. P.; Blaber, S. J. M.; Brewer, D. T., 1992: Diets of sharks from estuaries and adjacent waters of the north-eastern Gulf of Carpentaria, Australia. Aust. J. Mar. Fresh. Res. **43**, 87–96.

Séret, B., Opic, P., 1981: Poissons de mer de l'ouest africain tropical. Initiations-documentations techniques N° 49. 455p.

Simpfendorfer, C. A., 1992: Biology of tiger sharks (*Galeocerdo cuvier*) caught by the Queensland shark meshing program off Townsville, Australia. Aust. J. Mar. Fresh. Res. **43**, 33–43.

Simpfendorfer, C. A., 1998: Diet of the Australian sharpnose shark, *Rhizoprionodon taylori*, from northern Queensland. Mar. and Freshwater Res. **49**, 757–761.

Simpfendorfer, C. A., 2003: *Rhizoprionodon acutus*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.1. Available at: http://www.iucnredlist.org (accessed on 24 August 2011).

Simpfendorfer, C. A.; Goodreid, A. B.; McAuley, R. B., 2001: Size, sex and geographic variation in the diet of the tiger shark, *Galeocerdo cuvier*, from Western Australian waters. Environ. Biol. Fish. **61**, 37–46.

Sims, D. W.; Southall, E. J.; Humphries, N. E.; Hays, G. C.; Bradshaw, C. J. A.; Pitchford, J. W.; James, A.; Ahmed, M. Z.; Brierley, A. S.; Hindell, M. A.; Morritt, D.; Musyl, M. K.; Righton, D.; Shepard, E. L. C.; Wearmouth, V. J.; Wilson,

R. P.; Witt, M. J.; Metcalfe, J. D., 2008: Scaling laws of marine predator search behaviour. Nature **451**, 1098–1102.

Stevens, J. D.; Bonfil, R.; Dulvy, N. K.; Walker, P. A., 2000: The effects of fishing onsharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES J. Mar. Sci. **57**, 476–494.

Stevens, J. D.; Mcloughlin, K. J., 1991: Distribution, size and sex composition, reproductive biology and diet of sharks from northern Australia. Aust. J. Mar. Fresh. Res. **42**, 151–199.

Stillwell, C. E.; Kohler, N. E., 1982: Food, feeding habits, and estimates of daily ration of the shortfin mako (*Isurus oxyrinchus*) in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **39**, 407–414.

Stillwell, C. E.; Kohler, N. E., 1993: Food habits of the sandbar shark *Carcharhinus plumbeus* off the U.S. northeast coast, with estimates of daily ration. Fish. Bull. **91**, 138–150.

Wetherbee, B. M.; Cortés, E., 2004: Food consumption and feeding habits. In: Biology of sharks and their relatives. J. A. Musick, J.C. Carrier, M. Heithaus (Eds). CRC Press, Boca Raton, FL, pp. 223–244.

White, W. T.; Platell, M. E.; Potter, C., 2004: Comparisons between the diets of four abundant species of elasmobranchs in a subtropical embayment: implications for resource partitioning. Mar. Biol. **144**, 439–448.

**Author's address:** Abdoulaye Ba, Département de Biologie Animale, Faculté des Sciences et Techniques, Université Cheikh Anta Diop de Dakar, B.P 5005, Dakar Fann, Senegal.
E-mail: balaye81@gmail.com