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# Feeding ecology of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) incidentally caught in the gillnet fisheries off Zanzibar, Tanzania

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**Abstract**

The stomach contents of 26 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) incidentally caught in gillnet fisheries around Unguja Island (Zanzibar) between February 2000 and August 2002 were examined. The relative importance of each prey species was assessed through indices of relative importance. In total, 1403 prey items comprising 50 species of bony fish and three species of squid were identified from food remains. Five species of fish, *Uroconger lepturus*, *Synaphobranchus kaupii*, *Apogon apogonides*, *Lethrinus crocineus*, *Lutjanus fulvus*, and three species of squid, *Sepioteuthis lessoniana*, *Sepia latimanus* and *Loligo duvauceli*, were the most important prey species. Based on an index that included frequency of occurrence, percentage by number and by weight, *Uroconger lepturus* proved to be the most important prey species of mature dolphins whereas *Apogon apogonides* was the preferred prey of immature dolphins. These results indicate that Indo-Pacific bottlenose dolphins off the coast of Zanzibar forage on a relatively large number of prey species, but that only a few small- and medium-sized neritic fish and cephalopods contribute substantially to the diet. Further, the ecology and behavior of the preferred fish prey species indicate that the dolphins forage over reef or soft bottom substrata and near the shore.
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*Keywords:* Indo-Pacific bottlenose dolphin; *Tursiops aduncus*; stomach contents; feeding ecology; diet; Zanzibar

## 1. Introduction

The distribution of many cetaceans is closely linked to that of their preferred prey (Gaskin, 1982). For example, the seasonal abundance of common dolphins (*Delphinus delphis*) off the southeast coast of Africa closely parallels the annual sardine run (Young and Cockcroft, 1994). Similarly, the winter distribution of killer whales (*Orcinus orca*) in Norwegian waters underwent major changes following the distributional shift in spring-spawning herring during the late 1980s (Similää et al., 1996). Therefore, reliable information on the diet and feeding habits contributes important information for the elaboration of the distribution and abundance of small cetaceans. Analyses of stomach contents of dolphins and other marine mammal predators can also be useful in many other investigations; such as indicating what food a predator depends on, the predator's diving prowess, foraging behavior and ecology (Clarke and Kristensen, 1980).

It is known that the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) feeds on a wide variety of fish and

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cephalopods (Cockcroft and Ross, 1990). In their study, Cockcroft and Ross (1990) concluded that bottlenose dolphins off Natal, South Africa, feed primarily on fish, *Pomadasys olivaceum* and *Pagellus bellotti*, and cephalopods, *Loligo* spp. and *Sepia officinalis*, all of which are common inshore. However, very little information is available on the feeding ecology of this species in other parts of its distribution range and, in particular, no studies have been conducted in the East African region (Mozambique, Tanzania and Kenya).

*Tursiops aduncus* is one of the most common incidentally caught dolphins in Tanzanian waters (Amir et al., 2002). In the present study, samples of dolphins incidentally caught in gillnet fisheries around Zanzibar were used to conduct the first investigation of the feeding ecology of a small cetacean in Tanzania.

## 2. Materials and methods

### 2.1. Study area

The study was conducted in the coastal waters off Unguja Island, which is part of Zanzibar. Zanzibar consists of two sister islands, Unguja and Pemba, located about 60 km off the coast of Tanzania, East Africa. Unguja Island is situated at approximately 6° South and 39° East (Fig. 1).

### 2.2. Sample collection

Stomach contents were examined of 35 Indo-Pacific bottlenose dolphins incidentally caught in gillnets between February 2000 and August 2002. Twenty-six of the stomachs contained prey remains, thus forming the basis of this study. The remaining nine were from calves and contained only milk and these were excluded from further analyses. The approximate positions where the dolphins were caught are shown in Fig. 1.

### 2.3. Examination of stomach contents

During the necropsy of the dolphins, intact stomachs were ligated, excised, and weighed full and stored in polyurethane bags at about −20 °C until further analysis. During later examination, the thawed stomachs were opened along a midline incision that followed its curvature. The prey items were emptied and rinsed in a plastic tray, and then sieved through a 1 mm mesh size sieve. Prey items were subsequently sorted and preserved. Intact or partially digested prey items were identified and measured (length and weight) where possible. Cephalopod beaks were removed and preserved in 10% buffered formalin whilst fish otoliths were removed and stored dry in glass vials to await species identification.

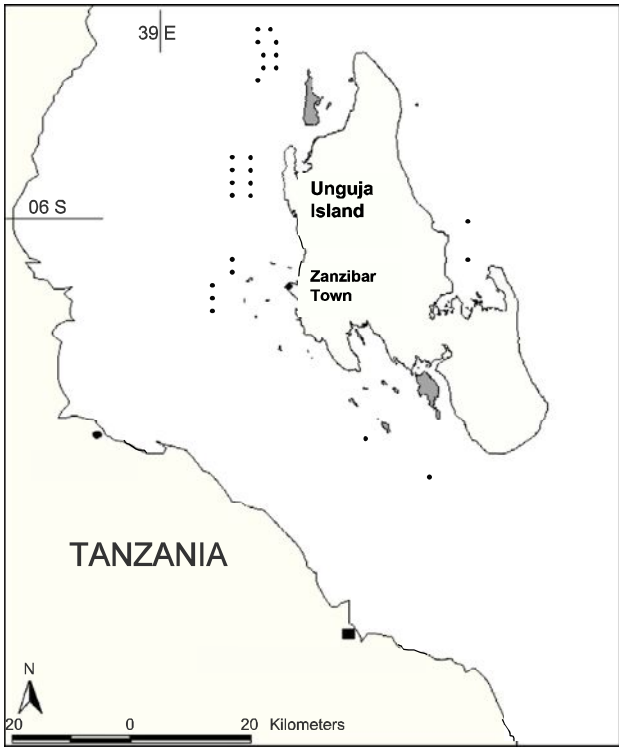



Fig. 1. Map of Unguja Island showing the location (indicated by •) where each Indo-Pacific bottlenose dolphin specimen was incidentally caught in gillnets fisheries ($n = 26$).

All prey remains were identified to the lowest possible taxonomic level. A binocular microscope was used to examine the fish sagittal otoliths. Fish otoliths were identified using a published guide (Smale et al., 1995) and whole fish according to Smith and Heemstra (1986). Cephalopod beaks were identified using a reference collection from specimens bought in the local fish market. Fish nomenclature and details on fish habitat were derived from Smith and Heemstra (1986). Details on cephalopod habitat were derived from Roper et al. (1984). The minimum number of prey consumed by each dolphin was estimated by counting the lower or upper beaks for cephalopods and the otoliths for bony fish. For otoliths and cephalopod beaks, it was assumed that the number of prey was equal to half the number of the remains paired by size, or by the greatest number of left or right otoliths and upper or lower cephalopod beaks, respectively.

Otolith length (from the rostrum to the posterior edge of the otolith, parallel to the sulcus) in fish and lower rostral length (LRL; tip of the rostrum to the jaw angle) or lower hood length (LHL) of cephalopod beaks were measured to the nearest 0.02 mm with an optical micrometer and vernier calipers. The total length and reconstructed weight of some fish were estimated from a direct measurement of intact prey for each prey item or from the relationships of otolith length and fish length or fish weight given by Smale et al. (1995). For

fish species where sample sizes were too small to calculate reliable regressions, length and weight were estimated indirectly, either from similar species or from the measurements of the available specimens. Cephalopod mantle length and reconstituted weight were computed from the beak measurements, using appropriate regressions derived from the reference collection.

### 2.4. Calculation of prey importance

Four different indices were used to investigate the occurrence and relative importance of the prey found in the stomachs; percentage by number (% $N$), percentage frequency of occurrence (% FO), percentage by weight (% $W$) and an index of relative importance (IRI).

Percentage by number (% $N$), is a measure of the numerical abundance of each prey species (% $N_i$) in the diet which was calculated as:

$$\% N_i = N_{ij}/N_j \times 100$$

where $N_{ij}$ is the number of prey species $i$ in stomach $j$ and $N_j$ is the total number of prey in stomach $j$.

Percentage frequency of occurrence (% FO), is a measure of the frequency of occurrence of each prey species (% $FO_i$) which was calculated as:

$$\% FO_i = F_{ij}/F_j \times 100$$

where $F_{ij}$ is the number of stomachs $i$ containing prey $j$ and $F_j$ is the total number of stomachs containing prey remains.

Percentage by weight (% $W$), is the weight of each prey (% $W_i$) in the diet calculated as:

$$\% W_i = W_{ij}/W_j \times 100$$

where $W_{ij}$ is the estimated weight of prey $i$ in stomach $j$ and $W_j$ is the estimated weight of all prey in stomach $j$.

Index of relative importance (IRI) of each prey is a combination of the previous three parameters calculated according to Pinkas et al. (1971) as:

$$IRI_i = (\% N_i + \% W_i) \times \% FO_i$$

### 2.5. Comparison of diet between sex and maturity class

Most previous investigations on the feeding ecology of marine mammals have generated an average weight value for each prey species, based on the pooled information from all stomachs (e.g. length of all collected otoliths of a particular fish species), this value then being used for comparisons of different subsets of the data. To avoid pseudo-replication when calculating mean prey size, estimated individual prey lengths and weights should first be averaged within each stomach, and these averages then used to estimate mean prey length and weight consumed by all dolphins in the sample. Therefore, the $n$ used to calculate mean prey size should be related to the number of dolphins whose stomachs contained measured otoliths, not to the total number of otoliths measured. However, in order to make the present study comparable to previous studies, the problem with pseudo-replication was ignored for the overall results presented in Table 1.

In the comparisons between male and female dolphins as well as immature and mature groups the eight most important prey species were used and the mean lengths of the prey species were calculated according to the logic presented above. However, to test for differences in prey size consumed between mature male and female, and immature and mature dolphins, length data for only three prey species (*Synaphobranchus kaupii*, *Uroconger lepturus* and *Apogon apogonides*) were used as they were found in numbers large enough to allow statistical comparison.

### 2.6. Classification of dolphin maturity classes

Dolphins were classified as immature or mature based on their reproductive condition. Sexual maturity in females was determined from evidence of ovulation (presence of a *corpus luteum* or a *corpus albicans*) on either ovary following Perrin and Donovan (1984), unless the female was obviously sexually mature at the time of capture (i.e., pregnant or lactating). Histological analyses of the testes were used for the determination of sexual maturity in males following Collet and Saint Girons (1984). Standard histological slides were prepared after the testis tissue had been sectioned in 3 μm sections, dried in a hot air oven, stained with Harris hematoxylin and counterstained by eosin, dehydrated with alcohol and cleared with xylene. The sections were then mounted and coverslipped with DPX and examined for the presence and abundance of spermatogonia, spermatocytes and spermatozoa. On each slide the diameter of 20 circular seminiferous tubules was measured at a magnification of 125, using an ocular micrometer. The arithmetic mean diameter was calculated and used as an index of tubule diameter. Specimens were classified as immature if seminiferous tubules were small, round and narrow and densely packed in interstitial tissue, and if the tubules were without lumen, contained primary spermatogonia and no cells of later stages. The seminiferous tubules of pubertal animals were slightly elongated, with small diameter, little interstitial tissue between the tubules and with small and empty lumen. Further, spermatogonia and spermatocytes were found in the tubules, with spermatids rarely present and no spermatozoa present. For sexually mature animals, the seminiferous tubules contained spermatogonia, spermatocytes, spermatids and often spermatozoa. The presence of spermatozoa indicated

Table 1
Number ($N$), percentage number (% $N$), frequency of occurrence (FO), percentage of frequency (% FO), weight, percentage weight (% $W$) and index of relative importance (IRI) of prey taxa found in the stomach contents of Indo-Pacific bottlenose dolphins

| Prey species | $N$ | % $N$ | FO | % FO | Weight | % $W$ | IRI |
|---|---|---|---|---|---|---|---|
| Fish | | | | | | | |
| Apogonidae | | | | | | | |
| *Apogon apogonides* | 138 | 9.8 | 14 | 53.8 | 3556 | 4.6 | 779.2 |
| *A. aureus* | 11 | 0.8 | 4 | 15.4 | 91.3 | 0.1 | 13.9 |
| *A. angustatus* | 4 | 0.3 | 2 | 7.7 | 23.8 | 0.0 | 2.4 |
| Argentinidae | | | | | | | |
| *Glossanodon* sp. | 2 | 0.1 | 1 | 3.8 | 350 | 0.5 | 2.3 |
| Carangidae | | | | | | | |
| *Decapterus macarellus* | 3 | 0.2 | 2 | 7.7 | 750 | 1.0 | 9.2 |
| *Alepes djedaba* | 17 | 1.2 | 2 | 7.7 | 450 | 0.6 | 13.8 |
| *Carangoides* sp. | 21 | 1.5 | 2 | 7.7 | 120 | 0.2 | 12.7 |
| Chlorophthalmidae | | | | | | | |
| *Chlorophthalmus punctatus* | 2 | 0.1 | 1 | 3.8 | 240 | 0.3 | 1.8 |
| Citharoidae | | | | | | | |
| *Citharoides* sp. | 10 | 0.7 | 2 | 7.7 | 560 | 0.7 | 11.1 |
| Clupeidae | | | | | | | |
| *Sardinops* sp. | 1 | 0.1 | 1 | 3.8 | 60 | 0.1 | 0.6 |
| Congridae | | | | | | | |
| *Uroconger lepturus* | 399 | 28.4 | 14 | 53.8 | 13700.2 | 17.9 | 2492.8 |
| *Conger cinereus* | 2 | 0.1 | 2 | 7.7 | 1235 | 1.6 | 13.5 |
| *Rechias wallacei* | 1 | 0.1 | 1 | 3.8 | 589 | 0.8 | 3.2 |
| Cynoglossidae | | | | | | | |
| *Cynoglossus* sp. | 3 | 0.2 | 1 | 3.8 | 220 | 0.3 | 1.9 |
| Dactylopteridae | | | | | | | |
| *Dactyloptena peterseni* | 4 | 0.3 | 3 | 11.5 | 328 | 0.4 | 8.2 |
| Gerreidae | | | | | | | |
| *Gerres* sp. | 1 | 0.1 | 1 | 3.8 | 23 | 0.0 | 0.4 |
| Gempylidae | | | | | | | |
| *Thyrsitoides marleyi* | 36 | 2.6 | 3 | 11.5 | 1080 | 1.4 | 45.8 |
| Gobiidae | | | | | | | |
| *Istigobius decoratus* | 5 | 0.4 | 3 | 11.5 | 201 | 0.3 | 7.1 |
| Haemulidae | | | | | | | |
| *Pomadasys stridens* | 3 | 0.2 | 2 | 7.7 | 168 | 0.2 | 3.3 |
| Holocentridae | | | | | | | |
| *Sargocentron* sp. 1 | 17 | 1.2 | 2 | 7.7 | 680 | 0.9 | 16.1 |
| *Sargocentron* sp. 2 | 4 | 0.3 | 1 | 3.8 | 160 | 0.2 | 1.9 |
| Leiognathidae | | | | | | | |
| *Leiognathus equula* | 10 | 0.7 | 4 | 15.4 | 275 | 0.4 | 16.5 |
| Lethrinidae | | | | | | | |
| *Lethrinus crocineus* | 39 | 2.8 | 10 | 38.5 | 4990 | 6.5 | 357.1 |
| Lutjanidae | | | | | | | |
| *Pristipomoides filamentosus* | 12 | 0.9 | 3 | 11.5 | 720 | 0.9 | 20.7 |
| *Lutjanus fulvus* | 33 | 2.4 | 4 | 15.4 | 4010.5 | 5.2 | 116.6 |
| *Lutjanus lutjanus* | 31 | 2.2 | 3 | 11.5 | 3210 | 4.2 | 73.8 |
| Monacanthidae | | | | | | | |
| *Aluterus monoceros* | 8 | 0.6 | 3 | 11.5 | 2021 | 2.6 | 37.0 |
| Mugiloididae | | | | | | | |
| *Parapercis robinsoni* | 2 | 0.1 | 1 | 3.8 | 142 | 0.2 | 1.3 |
| Muraenesidae | | | | | | | |
| *Muraenesox bagio* | 7 | 0.5 | 1 | 3.8 | 6360 | 8.3 | 33.8 |
| Muraenidae | | | | | | | |
| *Gymnothorax* sp. | 24 | 1.7 | 3 | 11.5 | 2300 | 3.0 | 54.3 |
| *Uropterygius* sp. | 8 | 0.6 | 4 | 15.4 | 867 | 1.1 | 26.2 |
| Myctophidae | | | | | | | |
| *Diaphus lucidus* | 13 | 0.9 | 1 | 3.8 | 20 | 0.0 | 3.4 |
| *Diaphus perspicillatus* | 1 | 0.1 | 1 | 3.8 | 1.9 | 0.0 | 0.3 |
| *Benthosema fibulatum* | 1 | 0.1 | 1 | 3.8 | 2.1 | 0.0 | 0.3 |
| *Taaningichthys bathyphilus* | 1 | 0.1 | 1 | 3.8 | 2.4 | 0.0 | 0.3 |
| Nemipteridae | | | | | | | |
| *Nemipterus* sp. | 9 | 0.6 | 2 | 7.7 | 370.7 | 0.5 | 8.7 |
| Opichthidae | | | | | | | |
| *Opichthus apicalis* | 14 | 1.0 | 1 | 3.8 | 26 | 0.0 | 4.0 |

Table 1 (*continued*)

| Prey species | *N* | % *N* | FO | % FO | Weight | % *W* | IRI |
|---|---|---|---|---|---|---|---|
| *Muraenichthys gymnotus* | 28 | 2.0 | 2 | 7.7 | 15 | 0.0 | 15.5 |
| *Brachysomophis crocodilinus* | 1 | 0.1 | 1 | 3.8 | 303 | 0.4 | 1.8 |
| Ophidiidae | | | | | | | |
| *Brotula multibarbata* | 4 | 0.3 | 2 | 7.7 | 80 | 0.1 | 3.0 |
| Platycephalidae | | | | | | | |
| *Cociella crocodila* | 1 | 0.1 | 1 | 3.8 | 12 | 0.0 | 0.3 |
| Pomacanthidae | | | | | | | |
| *Centopyge multispinis* | 9 | 0.6 | 6 | 23.1 | 203 | 0.3 | 20.9 |
| Pomacentridae | | | | | | | |
| *Pomacentrus trichourus* | 1 | 0.1 | 1 | 3.8 | 87 | 0.1 | 0.7 |
| Scorpaenidae | | | | | | | |
| *Parascorpaena* sp. | 2 | 0.1 | 1 | 3.8 | 334 | 0.4 | 2.2 |
| Serranidae | | | | | | | |
| *Cephalopholis sonnerati* | 4 | 0.3 | 2 | 7.7 | 226 | 0.3 | 4.5 |
| Sparidae | | | | | | | |
| *Chrysoblephus puniceus* | 1 | 0.1 | 1 | 3.8 | 170 | 0.2 | 1.1 |
| Sternoptychidae | | | | | | | |
| *Polyipnus indicus* | 1 | 0.1 | 1 | 3.8 | 138 | 0.2 | 1.0 |
| Synaphobranchidae | | | | | | | |
| *Synaphobranchus kaupii* | 205 | 14.6 | 16 | 66.7 | 10845.3 | 14.2 | 1879.6 |
| Synodontidae | | | | | | | |
| *Saurida gracilis* | 3 | 0.2 | 2 | 7.7 | 240.1 | 0.3 | 4.1 |
| Trichiuridae | | | | | | | |
| *Benthodesmus* sp. | 1 | 0.1 | 1 | 3.8 | 55 | 0.1 | 0.5 |
| Unidentified fish | 62 | 4.4 | 8 | 30.8 | 1456.15 | 1.9 | 194.4 |
| Group Total (bony fishes) | 1220 | 86.9 | 24 | 92.3 | 64070.5 | 83.5 | 15735.1 |
| Cephalopods | | | | | | | |
| Loliginidae | | | | | | | |
| *Loligo duvauceli* | 51 | 3.7 | 4 | 15.4 | 4213.8 | 5.5 | 140.4 |
| *Sepioteuthis lessoniana* | 97 | 6.9 | 9 | 37.5 | 6085.7 | 7.9 | 513.9 |
| Sepiidae | | | | | | | |
| *Sepia latimanus* | 35 | 2.5 | 7 | 26.9 | 2354.5 | 3.1 | 149.8 |
| Group totals (cephalopods) | 183 | 13.1 | 13 | 50.0 | 12654 | 16.5 | 1476.8 |
| Totals | 1403 | 100.0 | 26 | | 76724.5 | 100.0 | |

sexual maturity, but some specimens with no spermatozoa could also be classified as sexually mature, if the seminiferous tubules showed distinct elongation, with a large diameter and lumen and very little interstitial tissue. Of the 26 dolphins that had prey remains in their stomachs, 15 were classified as mature (7 males and 8 females) and 11 as immature (7 males and 4 females; Table 4).

### 2.7. Statistical analyses

Homogeneity of the immature and mature dolphin samples with respect to sex ratio was examined using Fisher's exact test. Contingency table analyses (Fisher–Freeman–Hamilton exact tests) were used to investigate the abundance of the eight most important prey species in male and female, and immature and mature dolphins. The *t*-test or Mann–Whitney *U*-test (MWU) was used to test for differences in prey size and number of prey species in the diet of male and female, and immature and mature dolphins. Spearman rank correlation ($r_s$) was used to test for the relationship between dolphin size and the number of prey species and individuals ingested. The statistical tests were performed using Stat Exact (Cytel Software Corp., 2001) and Statistica (Statsoft, Inc., 1999). A 0.05 significance level was used for all tests.

## 3. Results

### 3.1. Prey species

A total of 1403 prey items comprising 50 species of bony fish and three species of squid were found in the stomach contents of the Indo-Pacific bottlenose dolphins investigated (Table 1). Of the fish remains, 37 were identified to species level and 13 to genus level from a total 35 families. All unidentified fish were pooled in a single category. All the cephalopod beaks in the diet were from squid and comprised three species from two families (Table 1). Fish constituted the most important prey group, accounting for 87% of the total number of prey items consumed and occurring in 24 (92.3%) of the

26 stomachs examined. Cephalopods comprised 13% by number of the prey taken and were found in 13 (50%) of the 26 stomachs that contained prey items. Fish were also the most important prey group according to their weight, constituting 83.5% of the mass of all prey consumed. *Uroconger lepturus* was the most important fish consumed, representing 28.4% by number, 53.8% by occurrence and 17.9% by mass. *Synaphobranchus kaupii* was the second most important fish prey, representing 14.6% by number, 66.7% by occurrence and 14.1% by mass of all the prey eaten. *Sepioteuthis lessoniana* was the most abundant squid consumed, accounting for 6.9% by number, occurring in 37.5% of the stomachs and contributing 7.9% of the total mass of the prey (Table 1). In addition to the identified prey taxa, remains of crustaceans were found in some stomachs of dolphins. However, it is likely that some of the crustaceans were consumed secondarily since a number were found intact in the fish prey stomachs and hence were not included in the diet analysis.

### 3.2. Prey importance

The eight most important prey species in the diet based on the calculated index of relative importance (IRI) values were, in order of importance: *Uroconger lepturus*, *Synaphobranchus kaupii*, *Apogon apogonides*, *Sepioteuthis lessoniana*, *Lethrinus crocineus*, *Sepia latimanus*, *Loligo duvauceli* and *Lutjanus fulvus*. These eight species contributed about 64.8% of the measured total weight of prey. The eight most important prey species identified by the IRI calculation also had the highest percentage number, percentage frequency of occurrence and percentage weight, supporting their selection for the comparison between the mature male and female, and the immature and mature dolphin diets. Twenty-one prey species occurred only once in the stomachs examined and most of these had very low IRI values.

### 3.3. Comparison of diet between sex and maturity class

The immature and mature dolphins were homogenous in sex ratio (Fisher's exact test = 1.69, $p = 0.25$). There was no significant difference in choice of prey species between mature male and female dolphins or between immature and mature animals (Fisher–Freeman–Hamilton exact test, FI = 6.54, $p = 0.48$ and FI = 5.3, $p = 0.62$, respectively). Ranking the importance of prey species based on the IRI showed that *Uroconger lepturus* was the most important prey species in both mature male and female animals whereas *Apogon apogonides* was the preferred prey of immature dolphins (Tables 2 and 3).

No significant differences were found in the mean lengths of the three most important prey species eaten by mature male and female dolphins (*t*-tests, *U. lepturus*: $t = -0.05$, $p = 0.96$; *S. kaupii*: $t = 0.56$, $p = 0.59$; *A. apogonides*: $t = -0.29$, $p = 0.79$). However, significant differences were found in the mean lengths of the three most important prey species eaten by immature and mature dolphins, where the prey of the immature dolphins were smaller (*t*-tests, *U. lepturus*: $t = -2.63$, $p = 0.025$; *S. kaupii*: $t = -4.86$, $p < 0.001$; Mann–Whitney *U*-test, *A. apogonides*, $Z = -2.16$, $p = 0.03$).

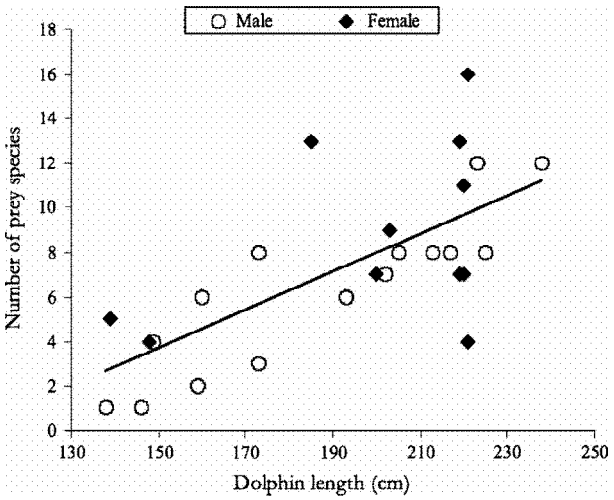



Fig. 2. Relationship between body length and number of prey species in the stomach of Indo-Pacific bottlenose dolphins.

The number of prey species found per bottlenose dolphin stomach varied between 1 and 16 ($\bar{x}=7$; Table 4), with a highly significant correlation between the length of the dolphin and the number of prey species consumed ($r = 0.68$, $N = 26$, $p < 0.001$; Fig. 2). No significant difference was found between the number of prey species consumed by mature male and female dolphins (*t*-test, $t = -0.152$, $p = 0.882$). However, there was a significant difference between the number of prey species consumed by mature and immature dolphins, where immature animals had eaten fewer prey species (*t*-test, $t = -3.346$, $p = 0.03$).

The number of prey items per bottlenose dolphin stomach varied between 3 and 105 ($\bar{x}=42$; Table 4), with a significant correlation between the number of prey items per stomach and dolphin length ($r = 0.49$, $N = 26$, $p < 0.01$; Fig. 3). Immature dolphins had fewer prey items in their stomachs compared to the mature animals, although this was not statistically significant (Mann–Whitney *U*-test, $Z = -1.95$, $p = 0.052$). There was no significant difference between the number of prey items consumed by mature male and female bottlenose dolphins (Mann–Whitney *U*-test, $Z = 1.35$, $p > 0.10$).

## 4. Discussion

The results of the present study show that bony fishes are the most important food source for Indo-Pacific bottlenose dolphins in waters around Zanzibar. Our

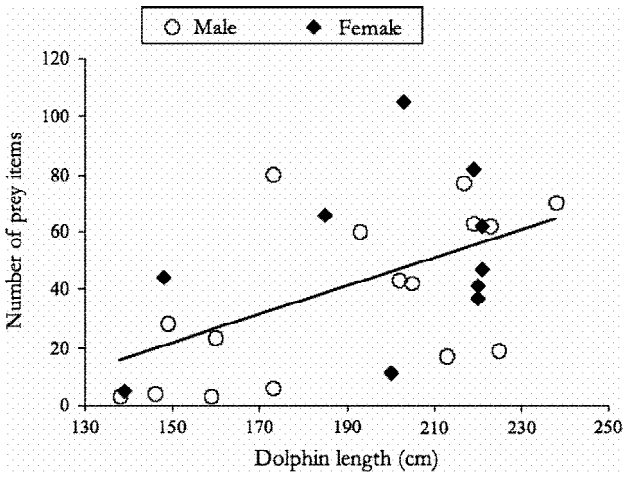



Fig. 3. Relationship between body length and number of prey items in the stomach of Indo-Pacific bottlenose dolphins.

results confirm the predominance of fish in the diet of this species as previously observed by Cockcroft and Ross (1990) who examined stomach contents of 165 bottlenose dolphins caught in shark nets along the Natal coast of South Africa. Cockcroft and Ross (1990) found that fish accounted for 75% and squid 25% of the prey mass. The corresponding values in the present study were 84% and 16%, respectively.

*Uroconger lepturus* and *Synaphobranchus kaupii* were the most important prey species found followed by *Apogon apogonides* and *Sepioteuthis lessoniana*. In general, these species are classified as having a distribution that is near shore and benthic or bathydemersal and they are often associated with coastal reefs or soft substrata (Smith and Heemstra, 1986). *Uroconger lepturus* occurs in coastal areas with sandy bottoms and, offshore, on soft sandy mud in a depth range of 18–760 m. *Synaphobranchus kaupii* lives mostly on the bottom and is found on the continental slope near the upper limit of the abyssal zone. It is probably most common in waters between 800 and 2000 m deep. *Apogon apogonides* inhabits shallow waters, mostly coastal reefs 3–30 m in depth, and is found in aggregations among branching corals and sometimes in mangroves. *Lethrinus crocineus* is found in coastal waters mostly over coral reefs and rocky areas, but can also be found over soft substrata at depths of 150 m. *L. crocineus* is a slow swimmer that stays close to the bottom and usually forms small schools. *Lutjanus fulvus* inhabits coral reefs and rubble to depths of 80 m and is usually solitary (Smith and Heemstra, 1986). With the exceptions of *U. lepturus* and *S. kaupii* that also occur in deep water, all the fish prey species have inshore distributions. Of the cephalopods, *Sepioteuthis lessoniana* is a neritic species found to depths of 100 m, *Sepia latimanus* is a shallow water species found on coral reefs down to depths of 30 m, and *Loligo duvauceli* is a neritic species, which occurs in shallow waters in depths of 30–170 m (Roper et al., 1984). The ecology and behavior of the preferred prey species thus indicate that the dolphins forage over reef and soft bottom substrata and near shore.

The prey spectrum in the diet of dolphins is usually related to the most abundant and readily available prey (Cockcroft and Ross, 1990; Young and Cockcroft, 1994). The results of the present study show that bottlenose dolphins around Zanzibar consume a wide variety of prey. However, little information is available on the abundance of fish species round Zanzibar and it is therefore not possible to draw any conclusions on whether the prey species chosen by the dolphins are also the most abundant and easily captured.

In general, it can be observed that the eight most important prey species in the dolphin diet, viz. five fish and three squid species, which accounted for over 51% in number and 64% of the mass of all the prey consumed, appear to form the basis of the diet of the Indo-Pacific bottlenose dolphins in waters round Zanzibar. The results of this study agree with previous findings that relatively few prey species form the basis of the diet of dolphins. For example, Cockcroft and Ross (1990) reported that, of the 72 prey species taken by bottlenose dolphins off southern Natal in South Africa, six prey species had IRI values that were considerably higher than the others and contributed approximately 60% of the mass of all the prey taken. Young and Cockcroft (1994) observed that five of the 40 prey species contributed about 86.9% by mass of the diet of common dolphins off the south east coast of southern Africa. Silva (1999) reported that six of the 35 prey species accounted for over 75% in number and mass of all the prey taken by common dolphins off the Portuguese coast.

Table 2
Index of relative importance, rank of importance and mean length of the eight main prey species consumed by male and female mature Indo-Pacific bottlenose dolphins

| Species | Mature males ($N = 7$) | | | Mature females ($N = 8$) | | |
|---|---|---|---|---|---|---|
| | IRI | Rank | Mean length (mm) | IRI | Rank | Mean length (mm) |
| Fish | | | | | | |
| *Uroconger lepturus* | 4018.5 | 1 | 286 | 5397.3 | 1 | 315 |
| *Synaphobranchus kaupii* | 1161.3 | 3 | 980 | 1856.8 | 2 | 941 |
| *Apogon apogonides* | 2676.2 | 2 | 95 | 617.5 | 4 | 87 |
| *Lethrinus crocineus* | 291.2 | 6 | 229 | 349.1 | 6 | 252 |
| *Lutjanus fulvus* | 450.3 | 5 | 195 | 12.5 | 8 | 164 |
| Cephalopods | | | | | | |
| *Sepioteuthis lessoniana* | 243.1 | 7 | 112 | 761.9 | 3 | 103 |
| *Sepia latimanus* | 602.7 | 4 | 113 | 50.9 | 7 | 104 |
| *Loligo duvauceli* | | | | 395.2 | 5 | 149 |
| Total number of species | 37 | | | 44 | | |

Table 3
Index of relative importance, rank of importance and mean length of the eight main prey species consumed by immature and mature Indo-Pacific bottlenose dolphins

| Species | Immature dolphins ($N = 11$) | | | Mature dolphins ($N = 15$) | | |
|---|---|---|---|---|---|---|
| | IRI | Rank | Mean length (mm) | IRI | Rank | Mean length (mm) |
| Fish | | | | | | |
| *Uroconger lepturus* | 2125.8 | 2 | 273 | 3959.4 | 1 | 305 |
| *Synaphobranchus kaupii* | 567.8 | 3 | 467 | 3799.7 | 2 | 955 |
| *Apogon apogonides* | 6547.5 | 1 | 84 | 647.3 | 5 | 94 |
| *Lethrinus crocineus* | 325.5 | 4 | 200 | 672.8 | 4 | 245 |
| *Lutjanus fulvus* | 27.7 | 6 | 151 | 252.1 | 8 | 195 |
| Cephalopods | | | | | | |
| *Sepioteuthis lessoniana* | 319.6 | 5 | 100 | 946.4 | 3 | 110 |
| *Sepia latimanus* | | | | 450.6 | 6 | 109 |
| *Loligo duvauceli* | | | | 422.4 | 7 | 149 |
| Total number of species | 25 | | | 53 | | |

Although the results show an increase in the number of prey species relative to increasing dolphin size, the same group of fish and squid species made up the bulk of the diet of both sexes and maturity classes. However, some variations were observed in the relative importance of the most important prey species. Mature male dolphins ate mainly *U. lepturus* followed by *A. apogonides* and *S. kaupii*, whereas mature females fed primarily on *U. lepturus* followed by *S. kaupii* and *S. lessoniana* (Table 2). In contrast, immature dolphins were found to prey more frequently on *A. apogonides* followed by *U. lepturus* and *S. kaupii* (Table 3). In addition, *L. duvauceli* was found only in the stomach contents of mature females, while *S. latimanus* and *L. duvauceli* were not found in the stomach contents of immature dolphins. The reasons for these variations are unclear, though they may reflect changes in the dietary needs of dolphins with respect to size, sex and reproductive state (Young and Cockcroft, 1994).

There were no differences in the sizes of prey taken by mature male and female dolphins. In contrast, Cockcroft and Ross (1990) observed significant differences in

Table 4
Length, sex, maturity stage, number of prey species and prey items of the 26 specimens of Indo-Pacific bottlenose dolphins

| Specimen number | Body length (cm) | Sex | Maturity stage | Number of prey species | Number of prey items |
|---|---|---|---|---|---|
| TA011 | 138 | Male | Immature | 1 | 3 |
| TA040 | 139 | Female | Immature | 5 | 5 |
| TA015 | 146 | Male | Immature | 1 | 4 |
| TA038 | 148 | Female | Immature | 4 | 44 |
| TA021 | 149 | Male | Immature | 4 | 28 |
| TA044 | 159 | Male | Immature | 2 | 3 |
| TA023 | 160 | Male | Immature | 6 | 23 |
| TA042 | 173 | Male | Immature | 3 | 6 |
| TA043 | 173 | Male | Immature | 8 | 80 |
| TA032 | 185 | Female | Immature | 13 | 66 |
| TA036 | 193 | Male | Immature | 6 | 60 |
| TA031 | 200 | Female | Mature | 7 | 11 |
| TA027 | 202 | Male | Mature | 7 | 43 |
| TA037 | 203 | Female | Mature | 9 | 105 |
| TA013 | 205 | Male | Mature | 8 | 42 |
| TA008 | 213 | Male | Mature | 8 | 17 |
| TA034 | 217 | Male | Mature | 8 | 77 |
| TA024 | 219 | Female | Mature | 7 | 63 |
| TA028 | 219 | Female | Mature | 13 | 82 |
| TA035 | 220 | Female | Mature | 11 | 37 |
| TA041 | 220 | Female | Mature | 7 | 41 |
| TA010 | 221 | Female | Mature | 4 | 47 |
| TA026 | 221 | Female | Mature | 16 | 62 |
| TA030 | 223 | Male | Mature | 12 | 62 |
| TA020 | 225 | Male | Mature | 8 | 19 |
| TA025 | 238 | Male | Mature | 12 | 70 |

prey sizes and to some degree different species taken by calves, adolescents, lactating females, non-lactating females and mature males. This difference between the two studies could be the result of the smaller sample size of 26 stomachs used in our study compared to that of Cockcroft and Ross (1990) who examined the stomach contents of 165 bottlenose dolphins.

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