

The food and feeding habits of the Delagoa threadfin bream, *Nemipterus bipunctatus* (Valenciennes, 1830), from the coastal waters around Dar es Salaam, Tanzania

Joseph S. Sululu^{1,*}, Simon G. Ndaró², Simon J. Kangwe¹

¹ Tanzania Fisheries Research Institute, P.O. Box 78850, Dar es Salaam, Tanzania.

² Department of Aquatic Sciences and Fisheries Technology, University of Dar es Salaam, P.O. Box 35064, Dar es Salaam, Tanzania.

* corresponding author: jsululu02@gmail.com

Abstract

Nemipterus bipunctatus is among the Nemipterids that support artisanal fisheries throughout most of the Western Indian Ocean (WIO) region. Despite its economic importance, information on food and feeding habits is poorly known in the region. Feeding habit was examined with respect to size, sex, maturity stages of the predator, and season. The food preference for *N. bipunctatus* was determined using Index of Relative Importance (IRI). Crustaceans were the main prey group accounting for more than 40% IRI of the total food ingested with crabs being the most dominant prey item in the group. Fish ranked as the second prey group accounting for 32.1 % IRI of the total food consumed. Meiofauna, bivalves, miscellaneous and cephalopods made up the rest of the diet. Significantly higher mean number of major prey categories were encountered in *N. bipunctatus* stomachs during the southeast monsoon as compared to during the northeast monsoon (two way contingency table analysis test, χ^2 -test, $df=3$, $p < 0.001$). An ontogenic diet shift study revealed that meiofauna, cephalopods, and bivalves groups had higher contributions in the diet of smaller *N. bipunctatus* of total length (TL) 9.5-11.5 cm, to 13.6- 15.5cm; the values for this group ranged from 49.7% IRI to 0.4% IRI respectively. Fish prey contributed significantly to the diet of larger individuals of this species, ranging from 0% in small fish (9.6-11.5cm TL) to 77.0% in large fish (> 21.5cm TL). Crustaceans contributed a small proportion to the diet of this species in the upper size classes with this category almost constant in the middle and lower size classes. It was therefore concluded that the main food of *N. bipunctatus* is crustaceans. However, an ontogenic shift in diet occurs, with meiofauna, bivalves and cephalopods preferred by smaller size classes, and fish by larger size classes.

Keywords: *Nemipterus bipunctatus*, Main prey groups, fish size, diet composition, IRI

Introduction

Feeding is one of the most important activities of organisms. Basic functions such as growth, development and reproduction of an organism take place at the expense of the energy acquired through food (Nikolsky, 1963). Studies of feeding behavior of fishes are very important whenever fish stock assessment and ecosystem modeling are required. For instance, approaches for multi-species virtual population analysis (Sparre, 1991; Bulgakova *et al.*, 2001) and the ECOPATH II ecosystem model (Christensen & Pauly, 1992) require information on the dietary composition of fishes. Besides, information on feeding ecology is

important to understand the functional role of the fish within their ecosystems (Hajisamae *et al.*, 2003; Abdel-Aziz & Gharib, 2007).

Fishes show diverse adaptations in their feeding behaviour and are therefore classified into different trophic categories. One of these behaviours is predation, being an essential part of interaction among species, which has a profound influence on population dynamics and is a basic element of biological competition (Sainsbury, 1982). Without knowledge of the food requirements, feeding behaviour pattern, and predator-prey relationships, it is not possible to

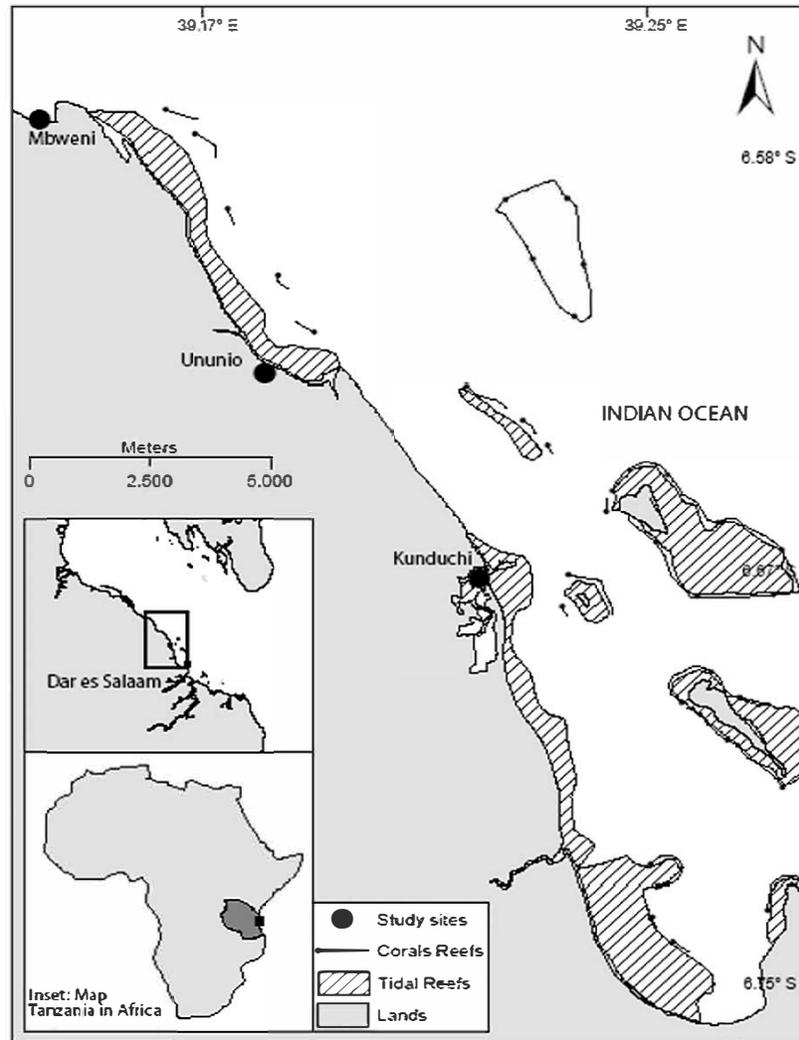


Figure 1. Location of the study sites along the Dar-es-Salaam coast.

understand the predicted changes that can result from any natural or anthropogenic intervention (Hajisamae *et al.*, 2006). Different sizes of fish belonging to the same species may feed on similar diets, however they tend to choose or prefer particular dietary items depending on size, sex stage of maturity, and prey availability. The dietary preferences among individuals of the same species often occur due to differential prey capture abilities to take diverse morphological and behavioural variations of prey (Sudheesan *et al.*, 2009). The 'where', 'when' and 'what' of dietary choice is subject to feeding habits based on foraging theory (Hyslop, 1980), where a fish always chooses the most profitable prey (Gerking, 1994). Stomach content analysis can be a useful method to use when investigating what food a predator mainly depends on, its ecology and foraging behaviour (Clarke & Kristensen, 1980).

Several studies have investigated the food and feeding habits of large pelagic fishes from the Western Indian

Ocean (WIO). For instance, Potier *et al.* (2007), Malone *et al.* (2011) and Roger (1994) studied the diet of large pelagics (lancetfish, swordfish, yellowfin tuna, Wahoo, Skipjack tuna, dolphin fish) from the WIO. However, very little is known about the feeding habits and diet shifts of small demersal species in the WIO. Ndaro & Olafsson (1995) studied the feeding habits of *Gerres oyena* in a tropical lagoon in Zanzibar; this is among the few studies that have been conducted in the region. The present study aims at determining the diet composition (major trophic groups) of *N. bipunctatus* and its intra-population variation. This species belongs to the family Nemipteridae, distributed throughout the Indian Ocean and abundant in coastal waters (Russell, 1990). The species support a large artisanal fishery in Tanzania and the WIO region as a whole. Findings of this study will allow for better understanding of the feeding behaviour and diet shifts of this species, and may be useful for stock and ecosystem-level analyses.

Materials and methods

Study sites

The fieldwork was conducted at three fish landing sites (Kunduchi, Ununio, Mbwani) located on the eastern coast of Tanzania (Fig. 1). These landing sites were chosen because they are some of the most active in Tanzania and have high fish landings. Landings from these sites were considered more representative and likely to capture different sizes of *N. bipunctatus*. Fishing activities at these landing sites are normally concentrated within the near shore reef lagoons as fishermen infrequently venture beyond the outer reef due to unsuitable fishing crafts.

Sampling methodology

Monthly fish samples were randomly collected from the artisanal hand-line fishery from January to December, 2012. The fishers used hand-lines (with hooks of sizes ranging between number 12 and 14) to catch this species. Upon arrival of the fishers at the landing sites after 4 to 5 fishing hours, Nemipterids were collected from the catches and identified to species level using Bianchi (1985). Identified specimens were kept chilled in boxes to slow down the bacterial digestion process until further analysis.

Diet

The stomachs of fish of different sizes were split open using scissors to remove all food items. Food items were identified following the description given in the FAO species identification key (Bianchi, 1985). Various food items were separated, identified to genus level, and whenever possible to the species level, and later counted under their respective groups. Methods defined by Hyslop (1980) were used to determine: (i) percentage numerical abundance (% N), indicated by the number of individuals of each prey category recorded for all stomachs expressed as a percentage of the total number recorded in all food categories; (ii) percentage weight (% W), indicated by the volume of individuals of each prey type in all stomachs expressed as a percentage of the total volume of food items measured in all stomachs; and (iii) percentage frequency of occurrence (% FO), indicated by the number of stomachs in which each prey item had occurred and expressed as a percentage of the total number of stomachs examined. The Index of Relative Importance (IRI) was determined by linear combination of % N, % W and % FO as single numerical values expressed according to Pinkas *et al.* (1971), Cailliet & Ebeling (1990) and Vivekanandan (2001) as follows:

$$IRI = (C_N + C_W) \times FO$$

The index was expressed as a percentage for each food group as follows:

$$\%IRI = (IRI / \sum IRI) \times 100$$

Sex determination and classification of maturity class

The ventricle of the fishes was split open using a pair of scissors to determine the sex and maturity stages as described by Ntiba & Jaccarini (1990). The maturity class for both male and female *N. bipunctatus* was determined macroscopically. The classification of maturity stages in male specimens was mainly based on the shape of the testes and colour of the milt from testes. In females, maturity stages were classified based on the shape of the ovary, and size and colour of the oocytes. For both sexes maturity stages were classified (IIa = developing virgin, IIb = resting and recovering, III = early developing, IV = late developing, V = ripe and running, and VI = spent). Stages IIa were IIb were considered immature, and stages III, IV and V were considered mature and most important in reproduction.

Determination of the quantity of prey ingested by *N. bipunctatus*

The threadfin breams are known to feed on a variety of food categories, therefore determination of the quantity of prey items ingested was done by counting individual items for each prey category encountered in the fish stomach. Multiple fragments of individual items (for instance fish bones and scales) were counted as different individuals per stomach each time they were encountered regardless of being in the same prey category.

Comparison of diet according to size, maturity class and sex of fish

The mean number of prey items in each size class was calculated to determine the relationship between *N. bipunctatus* size and the quantity of prey items ingested. However, to test for the differences in the quantity of prey items consumed between mature and immature, male and female *N. bipunctatus*, the mean number of prey items encountered in their stomachs was used in statistical comparison.

Statistical analysis

Spearman rank correlation (r_s) was used to test for the relationship between fish size and the mean number of food items ingested. The Mann-Whitney *U*-test (MWU) was used to test for difference in mean number of food items in the diet of immature and mature fishes. The difference in the mean number of food items consumed by mature male and female

Table 1. Percentage IRI (% IRI), Index of Relative Importance (IRI), and percentages of Number (NO), Frequency (FO) and Weight (WO) of different prey groups and items encountered in *N. bipunctatus* stomachs.

| Prey items | %NO | %FO | %WO | IRI | % IRI |
|-------------------------------|-------|-------|-------|--------|-------|
| Crustaceans | | | | | |
| Penaeid prawns | 6.92 | 7.15 | 8.98 | 113.74 | 12.06 |
| Crabs | 10.50 | 8.90 | 14.71 | 224.37 | 23.79 |
| Squilla | 3.67 | 8.72 | 5.90 | 83.48 | 8.85 |
| Crustaceans total | 21.10 | 24.77 | 29.59 | 421.59 | 44.69 |
| Fish | | | | | |
| <i>Sardinella</i> spp. | 8.28 | 4.43 | 8.50 | 74.29 | 7.88 |
| <i>Triachurus</i> spp. | 0.68 | 0.82 | 1.45 | 1.75 | 0.19 |
| <i>Stolephorus</i> spp. | 11.02 | 5.84 | 10.91 | 128.12 | 13.58 |
| <i>Cynoglossus</i> spp. | 5.01 | 4.80 | 6.95 | 57.48 | 6.09 |
| <i>Caranx</i> spp. | 1.04 | 1.48 | 1.93 | 4.41 | 0.47 |
| <i>Thrysa</i> spp. | 3.58 | 3.76 | 5.70 | 34.91 | 3.70 |
| Nemipteridae | 0.17 | 0.22 | 0.63 | 0.18 | 0.02 |
| <i>Siganus</i> spp. | 0.02 | 0.02 | 0.12 | 0.00 | 0.00 |
| <i>Trachinocephalus myops</i> | 0.62 | 0.86 | 1.03 | 1.43 | 0.15 |
| <i>R. kanagurta</i> | 0.05 | 0.04 | 0.11 | 0.01 | 0.00 |
| Balistidae | 0.20 | 0.27 | 0.34 | 0.14 | 0.02 |
| <i>Lethrinus</i> spp. | 0.11 | 0.15 | 0.29 | 0.06 | 0.01 |
| Fish total | 30.78 | 22.71 | 37.96 | 302.77 | 32.10 |
| Meiofauna | | | | | |
| Nematodes | 0.06 | 0.29 | 0.19 | 0.07 | 0.01 |
| Annelids | 4.68 | 5.53 | 3.88 | 47.40 | 5.03 |
| Copepods | 1.09 | 0.11 | 0.32 | 0.16 | 0.02 |
| Small shrimps | 2.05 | 14.97 | 1.83 | 58.13 | 6.16 |
| Meiofauna total | 7.89 | 20.90 | 6.23 | 105.76 | 11.21 |
| Bivalves | | | | | |
| Mussels | 6.11 | 5.87 | 9.71 | 92.84 | 9.84 |
| Bivalves total | 6.1 | 5.9 | 9.7 | 92.8 | 9.84 |
| Miscellaneous | | | | | |
| Fish scales | 2.75 | 2.15 | 3.56 | 13.56 | 1.44 |
| Fish bones | 0.17 | 0.24 | 0.64 | 0.20 | 0.02 |
| Miscellaneous total | 2.93 | 2.39 | 4.20 | 13.76 | 1.46 |
| Cephalopods | | | | | |
| Squids | 0.31 | 10.14 | 0.13 | 4.50 | 0.48 |
| Octopus | 0.34 | 4.05 | 0.16 | 2.05 | 0.22 |
| Cephalopods total | 0.65 | 14.19 | 0.30 | 6.55 | 0.69 |

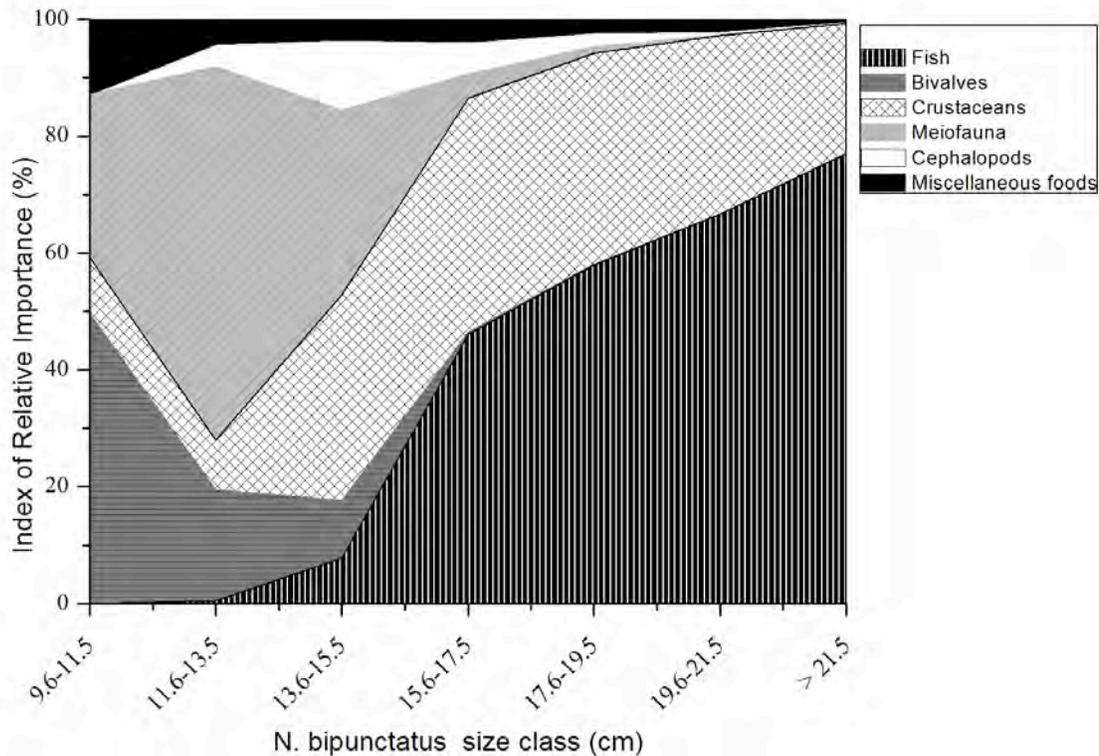


Figure 2. The percentage Index of Relative Importance (% IRI) of food items in the diet of *N. bipunctatus* by length class.

N. bipunctatus was examined using the *t*-test. Two-way contingency table analyses using the Chi-square test were used to test the difference in the mean number of major prey categories between seasons. All statistical data analyses were performed using SPSS analytical software. A 0.05 significance level was used for all tests.

Results

Diet composition

Six principal food groups were observed in the diet of *N. bipunctatus*. These included 12 fish species (*Stolephorus* spp, *Triuchurus* spp, *Sardinella* spp, *Cynoglossus* spp, *Caranx* spp, *Thryssa* spp, *Nemipterid* spp, *Rastrelliger kanagurta*, Balistidae, *Lethrinus* spp, *Siganus* spp, *Trachinocephalus myops*), 2 cephalopods (Squid and Octopus), 3 crustaceans (penaeid prawns, crabs and Squilla), 1 bivalve (mussels), 4 meiofauna (free living nematodes, annelids, copepods and small shrimps) and miscellaneous foods (fish scales and bones).

A total of 1367 *N. bipunctatus* specimens of 9.5-21.5 cm were examined; 20.5% of these specimens had empty stomachs. Prey groups and food items were encountered in 1087 stomachs of *N. bipunctatus* and are shown in Table 1. Crustaceans were the main prey group accounting for more than 40% IRI of the total food ingested. In this group, crabs were the main prey item

with 23.8 % IRI, followed by penaeid prawns accounting for 12.1 % IRI. The penaeid prawns were represented by *Penaeus indicus* and *Penaeus semisulcatus*. Fish ranked as the second prey group accounting for 32.1 % IRI of the total food consumed, and *Stolephorus* spp. was the most dominant prey in the group with 13.6 % IRI. Meiofauna formed the third most important food element of *N. bipunctatus*. The composition of this prey category to the total food ingested was 11.2% IRI, with annelids being the main prey items (5% IRI) in the group. Although bivalves were represented by only mussels, they made a remarkable contribution to the diet of this species and were ranked fourth after Meiofauna. Mussels were the only prey item in this category accounting for 9.8% IRI of the total amount of foods encountered in stomachs of *N. bipunctatus*. Miscellaneous food and cephalopods contributed very minor proportions; they formed only 1.5% IRI and 0.7% IRI of all prey categories encountered in stomachs of *N. bipunctatus*, respectively. Moreover, the *t*-test showed variation among the four key prey categories contained in the stomachs of male and female *N. bipunctatus*. There was a significant difference in consumption of crustacean prey category ($t= 4.0$, $df= 45$, $p<0.05$) and bivalve prey category ($t=2.4$, $df=45$, $p<0.05$) between males and females. On the other hand, there was no significant difference in consumption of the fish prey

Table 2. Monthly percentage Index of Relative Importance (% IRI) of different food items of *N. bipunctatus* during 2012.

| Prey items | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec |
|-------------------------|-------|-------|------|------|-------|------|------|-------|-------|-------|-------|-------|
| Fishes | | | | | | | | | | | | |
| <i>Sardinella</i> spp. | 9.53 | 9.01 | 17.4 | 12.4 | 13.52 | 12.3 | 14.7 | 14.1 | 11.90 | 10.96 | 7.25 | 12.20 |
| <i>Triachurus</i> spp. | 2.20 | 0.01 | 0.12 | 0.11 | 0.15 | - | - | - | 0.19 | 0.15 | 0.06 | 0.03 |
| <i>Stolephorus</i> spp. | 16.37 | 20.12 | 26.9 | 21.6 | 15.53 | 21.8 | 22 | 21.5 | 19.44 | 22.25 | 26.5 | 22.29 |
| <i>Cynoglossus</i> spp. | 4.00 | 0.26 | 2.03 | 1.45 | 2.46 | 0.21 | 5.86 | 1.29 | 0.88 | 2.69 | 0.64 | 4.14 |
| <i>Caranx</i> spp. | - | 0.49 | 0.12 | 0.51 | 0.1 | 0.04 | 0.14 | 1.43 | 0.14 | 0.40 | 0.01 | 0.04 |
| <i>Thrysa</i> spp. | 5.97 | 3.72 | 0.71 | 0.32 | 2.29 | 2.83 | 2.05 | 0.92 | 0.31 | 1.12 | 0.16 | 1.94 |
| Nemipteridae | - | 0.01 | 0.02 | - | 0.00 | - | - | 0.00 | 0.04 | 0.46 | | 0.02 |
| <i>Siganus</i> spp. | - | - | - | - | - | - | - | - | 0.53 | - | - | - |
| T. myops | - | 2.01 | - | 0.95 | 0.88 | 0 | 0.24 | 0.07 | 0.04 | 0.12 | | 0.11 |
| R. kanagurta | - | | - | - | - | - | - | - | 0.01 | - | - | - |
| Balistidae | - | 0.02 | - | 0.03 | 0 | 0.21 | - | 0.00 | 0.02 | 0.00 | - | - |
| <i>Lethrinus</i> spp. | - | 0.01 | - | 0.04 | 0.01 | 0.00 | - | - | 0.00 | 0.00 | - | - |
| Total | 38.07 | 35.7 | 47.3 | 37.4 | 34.94 | 37.4 | 45 | 39.3 | 33.5 | 38.15 | 34.6 | 40.77 |
| Crustaceans | | | | | | | | | | | | |
| Penaeid prawns | 2.19 | 1.03 | 0.02 | 0.56 | 0.95 | 0.36 | 0.5 | 0.06 | 0.47 | 0.66 | 0.22 | 1.21 |
| Crabs | 46.1 | 56.8 | 47.4 | 56.4 | 56.96 | 56.8 | 51.6 | 52.5 | 61.42 | 57.8 | 42.10 | 55.1 |
| Squilla | 1.04 | 0.16 | 0.26 | 0.08 | 0.16 | 0.2 | 0.02 | 0.00 | 0.59 | 0.42 | 0.09 | 0.17 |
| Total | 49.4 | 58 | 47.6 | 57 | 58.07 | 57.3 | 52.1 | 52.58 | 62.48 | 58.9 | 42.40 | 56.5 |
| Meiofauna | | | | | | | | | | | | |
| Nematodes | 0.6 | - | 0.04 | - | 0.02 | 0.02 | - | - | - | - | - | - |
| Annelids | 3.76 | | 0.13 | 0.58 | 0.65 | 0.54 | 0.27 | 1.55 | 0.38 | 0.44 | 0.47 | 0.01 |
| Copepods | 0.52 | - | - | - | - | - | - | - | - | - | - | - |
| Small shrimps | 0.69 | 0.01 | 0.7 | 1.66 | 0.32 | 0.92 | 0.31 | 3.28 | 0.91 | 0.03 | 15.4 | 0.74 |
| Total | 5.57 | 0.01 | 0.87 | 2.24 | 0.99 | 1.48 | 0.58 | 4.83 | 1.29 | 0.47 | 15.9 | 0.75 |
| Bivalves | | | | | | | | | | | | |
| Mussels | 3.21 | 5.30 | 3.37 | 1.94 | 4.95 | 3.27 | 1.87 | 2.13 | 1.87 | 2.1 | 2.43 | 1.66 |
| Total | 3.21 | 5.30 | 3.37 | 1.94 | 4.95 | 3.27 | 1.87 | 2.13 | 1.87 | 2.1 | 2.43 | 1.66 |
| Miscellaneous | | | | | | | | | | | | |
| Fish scale | - | 0.14 | 0.12 | 0.18 | 0.03 | 0.18 | 0.04 | 0.67 | 0.23 | - | - | 0.34 |
| Bones | 1.18 | 0.32 | 0.08 | 0.37 | | 0.09 | - | - | 0.08 | - | 4.69 | |
| Total | 1.18 | 0.46 | 0.2 | 0.55 | 0.03 | 0.27 | 0.04 | 0.67 | 0.31 | - | 4.69 | 0.34 |
| Cephalopods | | | | | | | | | | | | |
| Squid | 2.2 | 0.55 | 0.65 | 0.81 | 1.02 | 0.23 | 0.4 | 0.49 | 0.53 | 0.41 | - | - |
| Octopus | 0.41 | 0.01 | 0.01 | 0.04 | 0 | - | - | - | 0.02 | - | 0.01 | 0.02 |
| Total | 2.61 | 0.56 | 0.66 | 0.85 | 1.02 | 0.23 | 0.4 | 0.49 | 0.55 | 0.41 | 0.01 | 0.02 |

Table 3. Two way contingency table analysis and the Chi-square test of seasonal variation of major prey categories of *N. bipunctatus*.

| Prey group | Season | | | χ ² |
|----------------|--------|-----|-----|----------------|
| | NE | SE | Nj | |
| Crustaceans | 105 | 162 | 267 | 0.1 |
| Fish | 64 | 118 | 182 | 8.8 |
| Meiofauna | 73 | 88 | 161 | 13.5 |
| Bivalves | 30 | 47 | 77 | 0.0 |
| χ ² | | | | 22.4 |

Nj= Mean numbers of preys by seasons **, P < 0.001, df= 3

category ($t = -1.5$, $df=45$, $p=0.2$) and meiofauna ($t=0.9$, $df=45$, $p=0.4$) between sexes.

Ontogenic diet shifts

Various prey categories in the diet of *N. bipunctatus* of different size classes are shown in Fig. 2. The percentage (% IRI) for fish prey increased while that of meiofauna, bivalves and cephalopods decreased with size of the predator. The % IRI of fish ranged from 0% in *N. bipunctatus* of 9.6-11.5 cm (TL) to 77.0% in *N. bipunctatus* of > 21.5 cm (Fig. 3), while that of meiofauna, bivalves and cephalopods ranged from 49.7% in *N. bipunctatus* of 9.6-11.5 cm to 0.4% in *N. bipunctatus* of > 21.5 cm. The % IRI for crustaceans did not change much with size of *N. bipunctatus*, with their values ranging from 9.6% in fish of 9.6-11.5 cm to 22.3% in fish of > 21.5 cm. It was therefore apparent that *N. bipunctatus* mainly feeds on meiofauna, cephalopods and bivalves at smaller sizes (from 9.5-11.5 cm to 13.6-15.5 cm), and on crustaceans

throughout its life cycle at all size classes. However, fishes were observed to be more important in the diet of larger individuals of this species.

Seasonal variation in feeding activity pattern

Analysis of the monthly variation in IRI of prey items in the diet of *N. bipunctatus* is shown in Table 2. Crustaceans were the most important prey category, occurring in the stomach of *N. bipunctatus* in the highest proportions (> 50%) almost every month. Within the crustacean group, crabs formed the main food item of the species in all months. The highest value for crabs was in September (% IRI=61.42) and lowest in November (% IRI= 42.10). Fishes formed the second most important food element of *N. bipunctatus* and were observed throughout the year. *Stolephorus* spp. (*S. commersonii* and *S. indicus*) were the most dominant species in the stomachs of *N. bipunctatus*, with % IRI value ranging from 16.37 (January) to 26.9 (March). Meiofauna

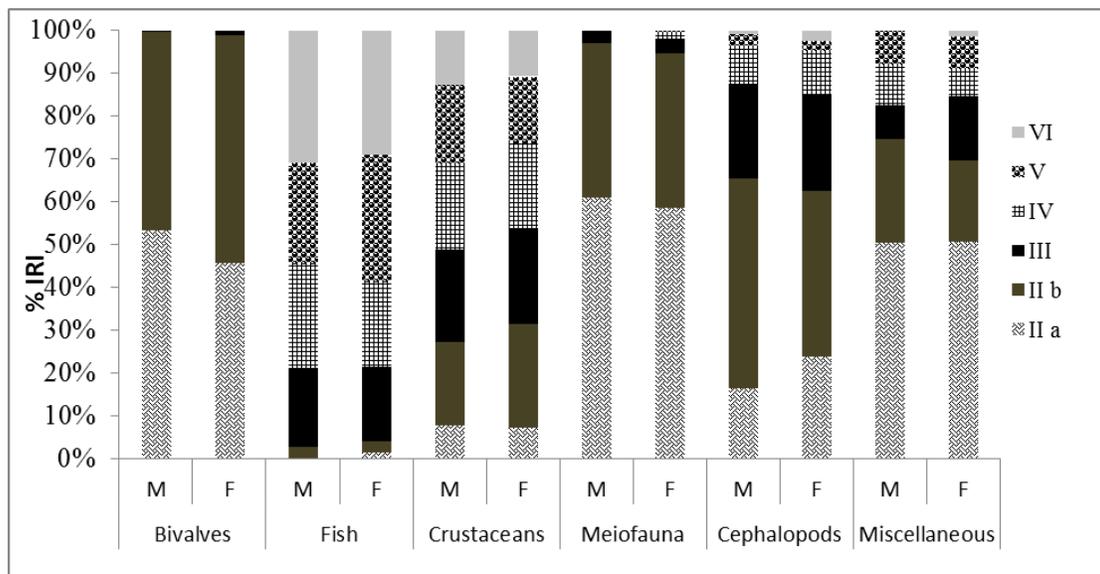


Figure 3. Feeding of *N. bipunctatus* on different prey groups in relation to sex and maturity stage. (M=Male, F= Female)

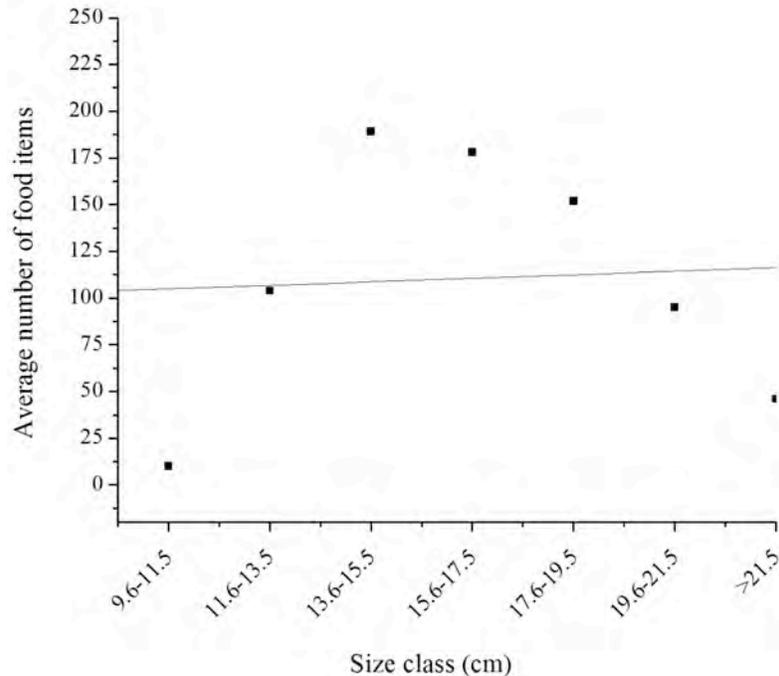


Figure 4. Relationship between body length and mean number of food items in the stomach of *N. bipunctatus*.

ranked third among the food organisms with small shrimps being dominant recording the highest % IRI of 15.40 in November and lowest % IRI of 0.01 in February.

Bivalves ranked as the fourth most important prey category, and were encountered in the diet of *N. bipunctatus* in all months. The group was represented by mussels only and the peak period for this food item was in February (% IRI = 5.30), and the least amount was recorded in December (% IRI = 1.66). Although miscellaneous foods and cephalopods were found in the diet of *N. bipunctatus*, their contributions were very minor, and they were considered as a secondary inclusion in the diet. The highest % IRI in both groups was observed in January, and lowest proportion of diet consumed was recorded in May for meiofauna, and November for cephalopods. Generally, four major prey groups were encountered in the stomach of *N. bipunctatus* as shown in Table 2.

Analysis performed on specimens collected during the northeast (NE) and southeast (SE) monsoon revealed that there was significant seasonal variation in the diet of *N. bipunctatus*. Fishes were the most dominant prey group in both seasons (NE - from November-April, SE - from May-October). Higher proportions of all key prey groups were encountered in *N. bipunctatus* stomachs during the SE monsoon as compared to NE monsoon. Two-way contingency table analysis using

the Chi-square test showed that there is a significant difference in the mean number of major prey categories in the stomach of fish between seasons (χ^2 -test, $df=3$, $p<0.001$, Table 2).

Comparison of diet between sexes and maturity stages

Meiofauna, cephalopods, miscellaneous and bivalves were the main dietary items of immature (stages IIa and II b) male and female *N. bipunctatus*. Mature individuals (stages III-VI) of this species consumed a low variety of prey items as compared to immature ones. However, there was no significant difference in consumption of different prey items between males and females in immature and mature individuals (paired sample t = test, $p>0.05$). Exceptional results were noted for the fish prey category in mature individuals where male *N. bipunctatus* were observed to feed on a larger proportion (% IR) of fish prey than females (t -test, $p>0.05$) (Fig. 3).

Comparison of diet between size, maturity class and sex

No significant correlation was found between the mean number of food items and size among different size classes of *N. bipunctatus* (Spearman rank correlation (r_s), $r = 0.036$, $N=1,367$, $p>0.05$; Fig. 4). Mature fish had significantly higher mean numbers of food items in their stomachs ($n=4$) compared to the immature ones ($n=2$),

(Mann-Whitney *U*-test = 11.0, $p < 0.01$). However, there was no significant difference between the mean number of food items consumed by mature male ($n=4$) and female ($n=4$) *N. bipunctatus* (*t*-test, $t=0.6$, $p=0.57$).

Discussion

Diet composition and feeding strategy

Generally, *N. bipunctatus* exhibited a benthic carnivorous and opportunistic feeding habit, with crustaceans, particularly crabs, forming the main diet. Other prey groups in the diet included fishes, meiofauna, bivalves, miscellaneous items, and cephalopods. Similar results on the diet composition of *N. bipunctatus* have been reported by Madan & Velayudhan (1984). Sudheesan *et al.*, (2009), Raje (2002), Acharya *et al.*, (1994) and Manojkumar *et al.*, (2015) studied the feeding habit and stomach contents of *Nemipterus japonicus* and concluded that this species is a benthic carnivore mainly feeding on crabs. Although *N. bipunctatus* seemed to prefer most benthic crustaceans as has been reported for other nemipterids, it also consumes a broad spectrum of fishes (Manojkumar *et al.*, 2015). The importance of fishes in the diet of *N. bipunctatus* could not be overlooked as they ranked second after crustaceans and more than 12 species were encountered in the stomach of this nemipteridae spp. While the range of prey consumed by *N. bipunctatus* was large, comparatively few prey groups; for instance crustaceans (crabs) and fish (*Stolephorus* spp.) dominated the diet (% IRI) in all months. This indicated that *N. bipunctatus* was either selecting prey or that some prey items were found more frequently than others throughout the year, probably due to seasonal variations which determines their abundance (Manojkumar *et al.*, 2015). Similar findings have been reported by Vivekanandan (2001), Acharya *et al.* (1994) and Rao & Rao (1991), who studied the trophic status of *N. japonicus* in India. Cannibalistic behaviour was also commonly observed in this species as in the case of *N. mersoprion* (Raje, 1996) and *N. japonicus* (Manojkumar *et al.*, 2015; Kuthalingam, 1965).

Ontogenic diet shifts

A comparison of prey groups consumed by different size classes of *N. bipunctatus* showed ontogenic diet shifts. Small sized prey such as meiofauna (copepods, shrimps etc), and bivalves (mussels) were the main prey categories for sub-adult *N. bipunctatus*, later being replaced by different fish species, the secondary prey for larger individuals of this species. On the other hand crustaceans were consumed throughout the life cycle of *N. bipunctatus*. These results signify an important change in feeding strategy in which the diet of smaller

individuals comprised a large number of smaller prey while those of larger individuals consisted of fewer, larger prey. As the mouth size severely limits the size of prey which can be ingested (Stickney, 1976), the diet of fish is related to their digestive morphology and mouth structure. As the fish grow the size of the mouth increases proportionately, their swimming capacity is modified, and their energy requirements vary (Stergiou & Fourtouni, 1991; Platell *et al.*, 1998). Thus larger fish have different diet requirements to smaller ones, and attempt to satisfy this by consuming larger prey types. Similar findings on members of the Nemipteridae have been reported elsewhere. For instance, Vivekanandan (2001) reported that *N. japonicus* primarily feeds on crustaceans, diversifies its feeding as it grows, and relies on fish as a secondary prey group when attaining a larger size. Manojkumar (2008) also found the same trend in the feeding habit of *Nemipterus mesoprion* from the Malabar coast.

A change in diet as fish grow is related to complex feeding habits of various fish species. Species may feed at different levels in the food chain at different stages of their life cycle, or change feeding behaviour with age. Similar observations have been also reported in other species; for instance Landry (1997) found that fully adult cod fish are predators on herring but when they are small (< 50 cm) they feed on copepods and other planktonic crustaceans. The observation of changes in feeding habit with age in *Nemipterus* species has been reported previously (Vivekanandan, 2001; Rao & Rao, 1991).

Although the present study revealed that food preference of *N. bipunctatus* changes with size, it should also be kept in mind that food preference of fish is very complex and is subjective to a number of factors including prey or food accessibility and mobility, food abundance, food energy content, food size selection and seasonal changes (Hart & Ison, 1991; Stergiou & Fourtouni, 1991).

Seasonal variation in feeding activity pattern

Monthly variation of prey items in the diet of *N. bipunctatus* showed that crabs from the crustaceans group was the most dominant prey item in every month. An existence of such a wide range of crustaceans, particularly crabs in the stomach of this species has been also reported by Afshari *et al.* (2013), Bakhsh (1994), and Manojkumar (2004) in *N. japonicus*. The dominance or presence of any prey in the diet of fish depends, among other factors, on its frequent availability in the environment. Nikolsky (1963) revealed that the reason for the difference in frequency of food

types in the stomach is related to its frequent availability in the environment. Presumably, this could be a reason for higher contribution of crabs/crustaceans found throughout the year in the diet of *N. bipunctatus*.

Seasonal differences in consumption of the key prey groups were also significant in the present study. Higher preference of crustaceans was observed in both seasons (NE and SE), hence signifying its importance as the main diet for this species (Table 3). Following these observations, presumably *N. bipunctatus* is a selective feeder or tends to capture whatever prey it finds most frequently in its surroundings. Such behaviour is also exhibited in other teleost fishes (Wootton, 1995). The seasonal dominance of crustacean prey in the diet has been reported elsewhere in other *Nemipterus* species; for instance Afshari *et al.* (2013) found this prey group to be the most dominant in the diet of *Nemipterus japonicus* in three seasons (spring, summer and autumn). Higher proportions of all key prey in the stomachs of *N. bipunctatus* recorded in the SE monsoon could be related to seasonal variation which is known to determine their abundance (Manojkumar *et al.*, 2015). Most of the fish collected during the NE monsoon were in advanced stages of sexual maturity with the body cavity fully occupied by ripe mature gonads (personal observation). The reduced feeding activity on the four key prey groups during this time could be an indication of intense spawning along Dar es Salaam coast. It is important to emphasize that the effect of seasonality should always be considered in fish feeding studies, because the temporal changes of biotic and abiotic factors alters the structure of the food web through the year, and as a result the fish often show seasonal diet shifts (Kariman *et al.*, 2009).

This study found that *N. bipunctatus* feeds on a variety of foods in its life cycle, and mainly on crustaceans. However, it exhibited an ontogenic diet shift and consume meiofauna, cephalopods and bivalves at small sizes, and then prefers fish prey at a larger size. Crustaceans are fed on throughout its life cycle at all sizes. Most of what was found in the diet of individuals during this study was of animal origin (fishes, crustaceans and cephalopods) confirming that *N. bipunctatus* is a carnivore.

Acknowledgements

The authors would like to thank the Marine and Coastal Environment Management Project (MACEMP) for funding this study. Thanks are extended to the Tanzania Fisheries Research Institute for logistic help and provision of space for laboratory work.

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