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Predatory diversity of finfish species inhabiting the same ecological niche

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ABSTRACT

A total of 211 specimens of *Nemipterus japonicus* (Bloch, 1791) and 169 specimens of *Saurida tumbil* (Bloch, 1795) were examined for different morphological traits and stomach contents. *N. japonicus* has a laterally compressed and deep body, small mouth opening and villiform teeth only on the jaws, soft gill rakers with bristles, small stomach and long intestine. These adaptations are suited for predation on small preys. *S. tumbil* has an elongated cylindrical body, with wide mouth opening, different types of sharp depressible teeth, small spine-like gill rakers, well developed stomach and short intestine, which are again the adaptations to feed on larger preys. Both the fishes are cannibalistic and asynchronous feeders. However, *N. japonicus* seems to be an opportunistic feeder, predating on crustaceans (80%), fishes, cephalopods, gastropods and polychaetes while *S. tumbil* is more like a selective feeder, predating on fishes (90%), crustaceans and cephalopods. The study reveals that though these predators inhabit the same ecological niche of demersal waters and have the opportunity to utilize similar food resources, they are entirely different in morphology which is attributed to the difference in their diet.

Keywords: Feeding habits, Index of relative importance (IRI), Morphological diversity, Predation

Introduction

Feeding is one of the most important activities of organisms. The basic functions like growth, development and reproduction of an organism take place at the expense of the energy acquired through food (Nikolsky, 1963). Fishes show varied adaptations in their feeding habits and accordingly classified into different trophic categories. One such feeding habit is predation in which an animal or organism, the predator, hunts and kills other organism, the prey, for food. It is an important part of interaction among species, which has profound influence on population dynamics, and is a key element on biological competition (Sainsbury, 1982). Moreover, different species of fishes have evolved individual predatory strategies so that they could avoid direct competition with each other (Cailliet and Ebeling, 1990). Hence, the dietary differences among species have often been claimed to be due to differential prey capture abilities that bring about diverse morphological and behavioural variations. Hence the facial structure, mouth, bucco-pharynx, oesophagus, stomach and intestine are indices of feeding adaptability. Further, the food habit and trophic morphology studies of fishes are important to understand the role they play in the trophic food web (Gerking, 1994; Luczkovich *et al*., 1995) and these data can be integrated into conceptual models that allow a better understanding of the structure and function of diverse aquatic ecosystems (Pauly and Christensen, 2000).

The greater lizardfish, *Saurida tumbil* (Bloch, 1795) and the Japanese threadfin bream, *Nemipterus japonicus* (Bloch, 1791) are two demersal predatory species that share the same habitat, living on muddy bottoms upto depths of 60 m. Both the species are distributed in the Indian Ocean and they are major contributors in the demersal fish catch of India. Although both the species have equal opportunities to feed upon similar prey items, as they inhabit the same ecological niche, the demersal zone of sea, they exhibit high degree of variation in their morphological characteristics and feeding habits. The present study is an attempt to compare the food and feeding habits of the two species found along the Mumbai coast, in relation to their body morphology especially mouth, role of dentition and gill rakers in its feeding mechanism. The findings may be useful to understand the complex trophic behaviour and ultimately for fishery management of these resources.

Materials and methods

The study was conducted on fresh specimens of 211 numbers of *Nemipterus japonicus* (total length: 84-282 mm) and 169 *Saurida tumbil* (total length: 162-389 mm), collected randomly from the morning trawl catches landed at New Ferry Wharf, Sasoon Dock and Versova fish landing centre of Mumbai, India, during September 2005 to April 2006. Total length, standard length, head length, body depth and the length of lower and upper jaws, vertical and horizontal mouth openings were measured with the help of digital calipers after opening the mouth to about an angle of 90° between the upper and lower jaws. The first gill arch of left side of the fish was dissected out and the length of different parts of gill arch was measured. Weight of each specimen was also recorded using a digital balance.

PROC MEANS procedure was used to estimate the descriptive statistics of morphometric traits applying SAS computer-based program (SAS user's guide, 2000).

Predator mouth area (M_A) and prey cross-sectional area (P_A) were estimated as:

$$M_A = \pi \times 0.25 \times (M_V \text{ x } M_H) \qquad (1)$$

where, M_A is the mouth area, P_A is the prey cross-sectional area, M_V is the vertical opening and M_H is the horizontal mouth opening or the prey width (Erzini *et al*., 1997; Karpouzi and Stergiou, 2003; Cruz-Escalona *et al*., 2005).

Depending upon the fullness, the fish stomachs were categorized as "gorged", "full", "3/4 full", "1/2 full", "1/4 full", "trace" and "empty". Length, weight, volume and diameter (at the mid length of the stomach) were also measured. Various food items were separated, identified and volume and weight of each food item were measured. To understand the recency of feeding and stages of digestion, the ingested food items were categorized into the following 5 stages of digestion: (1) freshly ingested and intact food; (2) recently ingested food but with onset of digestion; (3) moderately digested food with the possibility of identifying the prey; (4) well-digested food with remote possibility of only guessing the prey; (5) fully digested food beyond recognition (Vivekanandan, 2001). The alimentary canal was carefully separated from other visceral organs, straightened out to its full length and the length was measured from the pyloric outlet to the anus.

Number of food items, total length, maximum body depth and volume of each prey item from the stomachs (in reasonably undigested condition) were recorded. The maximum volume of food that could be ingested by predating single largest prey was also estimated by measuring the volume of the single prey (usually fish, cephalopod or prawn) in full or gorged stomachs.

The index of relative importance (IRI) of each prey item was estimated for food-containing fish as a linear combination of its numerical importance (N), volumetric importance (V), and frequency of occurrence (F) (Pinkas *et al*., 1971; Cailliet and Ebeling, 1990; Vivekanandan, 2001). The numerical importance of a particular food item is the percentage ratio of its abundance to the total abundance of all items in the contents. Its volumetric importance is its average percent volume. Its percentage frequency of occurrence is the percentage of fish containing at least one individual. The combination resulted in:

$$IRI = (\%N + \%V) \times \%FO \qquad (2)$$

The value of IRI ranges from zero (when all three values are zero) to 20,000 (when all three indices are 100%, a mono diet).

Results and discussion

Morphology of the predators

During the present study, the occurrence of mud and detritus in the mouth and stomach in significant quantity along with benthic organisms confirmed that *N. japonicus* and *S. tumbil* inhabit the same muddy bottom of demersal zone. Similar findings have been reported by Vinci (1982). Even though they occupy the same ecological niche and get equal opportunity to utilize similar variety of food items, they show dietary differences which may be attributed to the variations in the morphology of food capturing devices. This observation is also supported by Barel (1983). The two predators, considered for the present study differ greatly in their morphology. The bream shaped body of *N. japonicus* with forked caudal fin is designed for moderately fast swimming (Rao and Rao, 1991). Piscivorous fishes usually possess large body and mouth size (Hugueny and Pouilly, 1999), as in *S. tumbil*, which helps it to predate upon large preys like fishes. Large eyes of both the predators and the presence of active and motile prey organisms in their diet indicate that they feed by sight. Keast and Webb (1966) also suggested that mouth and body structures combine with food specializations and habitat preferences to greatly restrict interspecific competition within the fauna, and therefore, a great deal could be predicted about ecology of fish species from a study of body morphology.

Descriptive statistics of the various morphometric characters of the two species revealed a marked difference in the shape and size of gill rakers, mouth and alimentary canal (Table 1). Gatz (1970) also emphasized on a direct relationship between the cranial morphology and feeding habits in fishes.

N. japonicus has small jaw length and consequently its vertical and horizontal mouth openings are small. Therefore, the mouth area is also small, which has a curvilinear relationship with its standard length (Fig. 1). The vertical mouth opening (GV) and horizontal mouth opening (GH) are linearly related to standard length [$GV=0.1255(SL)+2.3031$; $r^2=0.7966$; $F_{1,204}=798.72$; $p<0.0001$; and $GH=0.1437(SL)-3.8218$; $r^2=0.8021$; $F_{1,204}=826.86$; $p<0.0001$]. Moreover, the disposition of its mouth is more suited for browsing and pecking off small food from the ground (Krishnamoorthi, 1971). The gill

Table 1. Descriptive statistics of *N. japonicus* and *S. tumbil*

Measurements (mm)	*N. japonicus*					*S. tumbil*				
	N	Minimum	Maximum	Mean ± SE	CV (%)	N	Minimum	Maximum	Mean ± SE	CV (%)
Total length	211	84	282	147 ± 2.5	24.8	169	162	389	253.4 ± 3.6	18.3
Standard length	211	66.9	220	116.5 ± 1.9	24.1	169	133	326	209.1±2.9	18
Head length	211	21.1	75	39.2 ± 0.7	26.8	163	35	83.1	55.3 ± 0.8	19.3
Body depth	199	21.2	72	40.2 ± 0.7	25.6	153	18.1	59.7	32.3 ± 0.7	25.9
Upper jaw length	211	7.4	27	13.8 ± 0.3	26.8	169	23.2	53.9	36.6 ± 0.5	18.5
Lower jaw length	211	6.7	26	12.9 ± 0.2	27.9	169	22	50.4	33.8 ± 0.5	18.4
Vertical gape size	211	10	28	16.9 ± 0.3	21.8	169	35	72.5	46.6 ± 0.6	16.5
Horizontal gape size	211	6.1	29	12.9 ± 0.3	33.6	164	16	54	30.8 ± 0.7	27.6
Upper gill arch	198	4	14	8.1 ± 0.1	25.7	169	13.3	36.8	22.3 ± 0.3	18.5
Lower gill arch	198	9	32	17 ± 0.4	30.1	169	14.4	43.7	27.7 ± 0.5	23.1
Intestine length	71	78.5	228	140.8 ± 4.1	24.4	57	69.1	283	141.5 ± 6.2	33
Stomach length	183	14.7	54	29.8 ± 0.6	27.8	169	10	183	116.4 ± 2	21.9
Stomach diameter	183	3.2	28.5	10.3 ± 0.3	44.4	169	5	42	11.5 ± 0.4	48.3
Weight[a]	211	8.5	300	55.3 ± 2.9	75.9	169	29.6	510	130.8 ± 6.2	61.6

([a] the parameter is in grams)

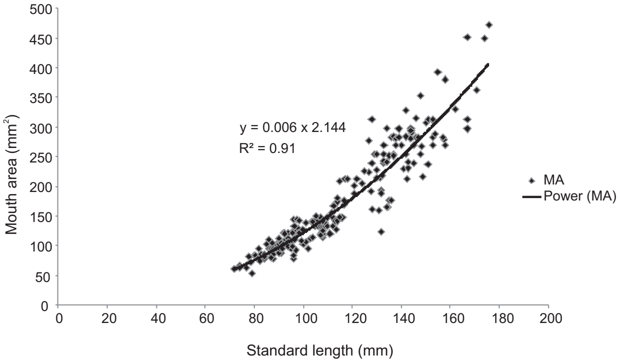

Fig. 1. Curvilinear relationship of mouth area (MA) with standard length (SL) in *Nemipterus japonicus*.

arches are soft having short and stout bristle-like gill rakers, which are less in number and widely spaced. This may prevent the escape of small prey (Krishnamoorthi, 1971; Rao and Rao, 1991). However, the teeth are small, villiform and are present only on the jaws.

In order to get hold of a large live prey, a predator fish requires some extra adaptations such as protrusibility of jaw, large mouth gape, well developed dentition and ability to jump over the prey suddenly (Yasuda, 1960a, b; Keast and Webb, 1966; Ray and Datta, 2003). These characters are well developed in *S. tumbil*. In comparison, the upper and lower jaws are longer. Accordingly, the vertical and horizontal mouth openings are large. The linear relationship of vertical mouth opening (GV) with standard length is established as: GV=0.1432(SL)+16.611; r^2=0.5034; $F_{1,152}$=154.08; $p<0.0001$; and horizontal mouth opening as, GH=0.202(SL)-11.168; r^2=0.6331; $F_{1,152}$=262.62; $p<0.0001$. The wide mouth area has a curvilinear relationship with standard length (Fig. 2). The gill arches are hard and strong with small spine-like depressible gill rakers closely arranged in 3-4 series.

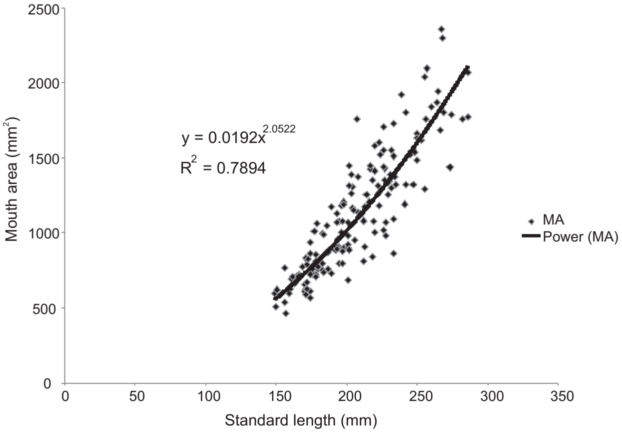

Fig. 2. Curvilinear relationship of mouth area (MA) with standard length (SL) in *Saurida tumbil*.

Larger gill rakers are seen towards the centre of the rows and the smaller on either side. Such type of gill rakers may aid in holding the prey (Vivekanandan, 2001). The species has several rows of teeth on upper and lower jaws; the innermost are the largest and depressible. Teeth are also present in two rows on either side of the palate of mouth, vomer and also on tongue.

The intestinal morphology is also consistently related to the diet of the fish (Al-Hussaini, 1947). Gut length and pyloric caecae may influence size and quantity of food eaten (Cailliet and Ebeling, 1990). Fishes with relatively longer guts eat smaller prey items (Groot, 1969; Darnell, 1970). In general, carnivorous fishes tend to have the shortest intestine followed by omnivores. Herbivores and detritivorous fishes have longer intestine (Ward-Campbell and Beamish, 2005). In *N. japonicus*, the stomach is small and thin-walled and the intestine is long possessing 6-7 pyloric caecae, which is meant for ingesting small prey. Adaptations in *S. tumbil* include elongated and thick-walled stomach, having several inner longitudinal folding, making it highly distensible bearing 16-22 pyloric caecae, in order to digest and absorb larger preys.

Feeding behaviour

Most of the specimens examined showed low to moderate feeding. However, empty stomachs occurred in fairly high percentages. It has been reported that the predators feed asynchronously, *i.e.*, there is no particular time of day or night for feeding (Vivekanandan, 2001); which may be the reason for getting fishes with different degree of stomach fullness in the same sample during the present study. Most of the prey items obtained from the stomachs of the two species were in the later stages of digestion. About 28% of stomachs of *N. japonicus* contained prey items in 4th and 26% in 5th stages of digestion, while 21% stomachs of *S. tumbil* contained prey items in 4th and 17% in 5th stages of digestion. The later stages of digestion recorded in both species indicate that till the food is properly digested, it does not ingest fresh prey. Thus, cessation of feeding is probably obligatory for these fishes for the digestion to take place properly (Vivekanandan, 2001). Also, as large-sized preys are digested at slower rates (Tyler, 1970), the process of digestion in *S. tumbil* may extend to longer periods than that of *N. japonicus.*

Both the species were found to prey upon three major prey categories, namely, fishes, crustaceans and cephalopods. In addition, *N. japonicus* preyed upon gastropods, polychaetes, bivalves and worms also. The frequency of occurrence of crustaceans was 50% in *N. japonicus*, with its numerical percentage at 84.7%. This was due to the high occurrence (28.9%) of *Acetes* spp. in great numbers (73%). Volume-wise too, crustaceans ranked first with 47.8% of total volume of prey items. Apart from *Acetes* spp., the fish also fed on shrimps, *Squilla* spp. and crabs in the crustacean group. Fish (4 to 5 species) was the next important prey with frequency of occurrence 21.9%, numerical percentage 9.7% and volumetric percentage 31.1%, followed by cephalopods, gastropods and polychaetes (Table 2). Index of relative importance (IRI) was calculated for both species to know the relative importance of the prey items. Based on IRI also, crustaceans ranked first (IRI=6625; IRI%=84.4%), followed by fishes (IRI=893.5; IRI%=11.4%), molluscs (IRI=184.1; IRI%=2.3%) and polychaetes (IRI=14.8; IRI%=0.2). This is an indicator of predaceous, carnivorous and bottom feeding habit (Acharya *et al*., 1994; Raje, 2002). Its carnivorous feeding habit has also been reported (Kuthalingam, 1965; George *et al*., 1968; Krishnamoorthi, 1971; Selvakumar, 1971; Qasim and Jacob, 1972; Vinci, 1982; Rao and Rao, 1991). Along with cannibalism (Kuthalingam, 1965), a difference in the feeding habits in different depths (Vivekanandan, 1990) have also been recorded in the species.

On the contrary, fishes (14 species) formed the most important part of diet of *S. tumbil*, with 63.29% frequency of occurrence, numerical percentage 70.5% and volumetric percentage 88.9%. This was followed by crustaceans (FO%=24.05; N%=26.7%; V%=3.5%) which included *Acetes* spp. and shrimps, and cephalopods (FO%=3.8%; N%=2.9%; V%=7.7%). Index of relative importance value also indicated first rank for fishes (IRI=10088.4; IRI%=92.9%), followed by crustaceans (IRI=726.3; IRI%=6.7) and cephalopods (IRI=40.3; IRI%=0.4) (Table 3). The species also shows cannibalism. Similar results were also reported by Rao (1981), Singh *et al*. (1995), Vivekanandan (2001) and Metar (2005).

Two types of feeding behaviour, namely, opportunistic and selective feeding, can be explained based on the variety of prey consumed by the fish (Wetherbee *et al.*, 1990). The stomach of opportunistic feeder contains a variety of prey, similar to the composition and abundance of the prey fauna in the predator’s habitat, whereas, the stomach of selective feeder would be expected to contain a predominant prey type (Vivekanandan, 2001). The results of the present study clearly showed that *N. japonicus* predated upon a large variety of prey items, whereas, *S. tumbil* more selectively predated on fish as about 90% of food was composed of fish alone.

Table 2. Number (%N), volume (%V), frequency of occurrence (%FO), index of relative importance (%IRI) for prey items observed in stomachs (n=114) of *N. japonicus*

Prey items	FO%[b]	N%	V%	IRI	IRI%
Unidentified fish	14.9	7.1	14.7	324.8	8.3
Semi digested fish	5.3	1.8	5.0	36.0	0.9
Nemipterus mesoprion	0.9	0.2	2.9	2.8	0.1
Eel	1.8	0.4	5.8	11.2	0.3
Saurida spp.	0.9	0.2	2.3	2.3	0.1
Myctophids	0.9	0.4	0.5	0.8	0.02
Total Pisces	21.9	9.7	31.1	893.5	11.4
Acetes spp.	28.9	73.0	23.4	2787.4	71.0
Shrimps	21.9	7.1	19.5	582.5	14.8
Squilla spp.	3.5	1.8	3.0	16.8	0.4
Crab	7.9	2.9	2.0	38.7	1.0
Total Crustaceans	50	84.7	47.8	6625	84.4
Loligo spp.	5.3	1.8	17.3	101.2	2.6
Sepia spp.	0.9	0.7	2.0	2.4	0.1
Total Cephalopods	6.1	2.4	19.4	133.0	1.7
Gastropods	1.8	0.1	0.7	1.4	0.02
Total Molluscs	7.9	3.3	20.0	184.1	2.3
Polychaetes	5.3	1.8	1.0	14.8	0.4
Total Annelids	5.3	1.8	1.0	14.8	0.2

[b] Because %FO is a nonadditive index (Cortes, 1997) for grouping prey items into higher taxonomic groups (*i.e*. Pisces, crustaceans, *etc*.), the %FO value was recalculated by considering the number of stomachs with the respective higher taxonomic category. This recalculation affects both the IRI and %IRI values.

Table 3. Number (%N), volume (%V), frequency of occurrence (%FO), index of relative importance (%IRI) for prey items observed in stomachs (n=79) of *S. tumbil*

Prey Items	FO%[c]	N%	V%	IRI	IRI%
Unidentified fish	13.90	12.4	8.5	290.5	13.3
Semi digested fish	26.60	24.8	19.4	1175.7	54.0
Goatfish (*Upeneus vittatus*)	1.30	1.0	1.8	3.6	0.2
Nemipterus japonicus	2.50	2.9	15.2	45.3	2.1
Nemipterus mesoprion	3.80	3.8	7.0	41.0	1.9
Silverbellies	3.80	11.4	1.6	49.4	2.3
Sardine	1.30	1.0	10.4	14.8	0.7
Myctophid	1.30	1.0	0.2	1.6	0.1
Sciaenid	1.30	1.0	1.0	2.6	0.1
Flatfish	2.50	1.9	1.3	8.0	0.4
Decapterus russelli	6.30	4.8	15.8	129.8	6.0
Eel	1.30	1.0	1.8	3.6	0.2
Carangid	1.30	1.0	1.8	3.6	0.2
Saurida tumbil	1.30	1.0	1.3	3.0	0.1
Thryssa spp.	1.30	1.0	0.8	2.3	0.1
Clupeid	1.30	1.0	0.9	2.5	0.1
Total Pisces	63.29	70.5	88.9	10088.4	92.9
Acetes spp.	10.13	15.2	0.4	158.0	7.3
Shrimp	13.92	11.4	3.1	201.8	9.3
Total Crustaceans	24.05	26.7	3.5	726.3	6.7
Cephalopods	3.80	2.9	7.7	40.3	1.8
Total Cephalopods	3.80	2.9	7.7	40.3	0.4

[c] Because %FO is a nonadditive index (Cortes, 1997) for grouping prey items into higher taxonomic groups (*i.e.*, pisces, crustaceans, *etc*.), the %FO value was recalculated by considering the number of stomachs with the respective higher taxonomic category. This recalculation affects both the IRI and %IRI values.

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