

Predatory diversity of two demersal finfish species in the trawling grounds off Veraval

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ABSTRACT

Nemipterus japonicus is morphologically adapted to predate on small sized crustaceans like *Acetes* and penaeid prawns. *Saurida tumbil* is adapted to predate on larger and faster prey like finfishes and squids. *N. japonicus* predate on 35 prey groups compared to 22 by *S. tumbil*. Both the predators are asynchronous cyclic feeders. In a continuum between opportunistic and selective feeding, *N. japonicus* is towards opportunistic feeding and *S. tumbil* towards selective feeding. There are ontogenetic changes in the predatory pattern of both the species.

Introduction

Predation is an important part of interaction between species. It has profound influence on population dynamics, and is a key element on biological competition (Sainsbury, 1982). Different species of fishes have evolved individual predatory strategies so that they could avoid direct competition with each other (Cailliet and Ebeling, 1990). Off Veraval, the threadfin bream *Nemipterus japonicus* and the lizardfish *Saurida tumbil* inhabit the same fishing ground and have the opportunity of predated on the same prey species. These predators, because of their abundance, play a major role in the exchange of food between upper trophic levels. Earlier studies on these species were limited only to listing of food items found in the stomach (Kuthalingam, 1966; Rao, 1981; Rao and Rao, 1991) and there is no recorded observation on their predatory

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strategies. The present study is an attempt to understand the food items, the quantity consumed, the efficiency of predation and the degree of similarity/diversity exhibited in the predatory behaviour of these two species.

Materials and methods

Fresh specimens of *N. japonicus* (n=1318; length range = 50 to 310 mm) and *S. tumbil* (n=1245; length range = 70 to 555 mm) were collected during the years 1989-1991 from private trawlers operating off Veraval. Collections of both the species were made in the morning or in the evening from vessels engaged in daily cruises off Veraval to ensure that the material for the study is from the same ground. Data on total length (from tip of snout to tip of lower caudal lobe in the case of *N. japonicus*), weight, upper and lower jaw length, width of gape and number, size

and structure of gill rakers were taken. The length and diameter (at the midlength of the stomach) of stomach were measured using a vernier caliper. The stomach of all the fishes was cut longitudinally and categorized as empty, half full, full and gorged depending upon its fullness. The stomach contents were identified, wherever possible, to species level.

To understand the recency of feeding and stages of digestion, the ingested food items were categorised into the following 5 stages of digestion, Stage 1: freshly ingested and intact food; stage 2: recently ingested food but with onset of digestion; stage 3: moderately digested food with the possibility of identifying the prey; stage 4: well digested food with remote possibility of only guessing the prey; and stage 5 : fully digested food beyond recognition. As there was no appreciable difference in the food of males and females, the data collected separately on sexes were pooled (see also Rao, 1981). Total length, maximum body depth, volume and number of specimens of each prey species from the stomachs (in reasonably undigested condition) were taken. The maximum stomach capacity was estimated by measuring the volume (by displacement method) of all the food items in full and gorged stomachs. The maximum volume of food that could be ingested by predated 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 was estimated as a linear combination of its number (N), volume (V) and frequency of occurrence (F) (Pinkas *et al.*, 1971; Cailliet and Ebeling, 1990). The numerical importance of a particular prey was its average percentage volume and its percent frequency of occurrence was the percentage of its number and the total number of all items in the stomach, its

volumetric importance was the percentage of fish containing at least one individual. The combination resulted in $IRI=(N+V) \times F$, which is presented by the area of a rectangle resolved by plotting the three important measures of a three-way graph (Cailliet *et al.*, 1986). The value of IRI could range from zero, when all the three values are zero, to 20,000 when all the three indices are 100% (a monodiet). The IRI ranks the relative importance of the dietary items, and the three-way graph indicates the most meaningful measures of importance.

Results

Stomach emptiness

Samples of *N.japonicus* and *S. tumbil* collected from the wild had fairly large number of individuals with empty stomach. During the 3 year period, 49.6% *oiN.japon.icus* (n=1318) and 41.9% of *S. tumbil* (n=1245) had empty stomach. Earlier studies also revealed that 40 to 50% of individuals of these species collected from the wild had empty stomach (Kuthalingam, 1966; Rao, 1981; Vivekanandan, 1990). The empty stomachs of the individuals collected during the present study were in shrunken condition, suggesting that the fish did not ingest food for quite some time. Non-availability of preferred prey cannot be the cause for non-ingestion of food as the stomachs of fishes collected from the same haul were often in different states of fullness - from empty to gorged state. Moreover, about 40 to 50% of the fishes always had empty stomachs irrespective of the time of capture. This suggests that these fishes feed asynchronously, i.e. there is no particular time of day or night for feeding.

Recency of feeding and stages of digestion

The condition of the stomachs of *N.japonicus* (TL: 150-269 mm; n=103) and *S.tumbil* (TL: 270-519 mm; n=136)

collected in December, 1991 was examined. The samples offish caught at 1300 hrs in a single haul were collected at 1700 hrs on the same day. About 40 and 48% of *N.japonicus* and *S.tumbil* in the sample had empty stomach. In a sample, each stomach had food items in one particular

Feeding diversity

Three principal prey categories were observed in *N.japonicus* as well as *S. tumbil*. In *N.japonicus*, 26 fish, 3 cephalopod groups (squids, cuttlefishes and *Octopus*) and 4 crustacean (penaeid prawns, *Acetes*, crabs and *Squilla*) groups in addition to echinoderms and polychaetes were observed. Thus *N. japonicus* is more diverse (predating on 35 groups) in the feeding habit than *S. tumbil* (feeding on 22 groups).

The frequency of occurrence (FO) of crustaceans was 85.2%, followed by fishes (35.1%), cephalopods (33.4%) and others (6.8%) in the stomachs of *N. japonicus* (Fig. 2 a). The crustaceans gained numerical importance mainly due to ingestion of a very large number of *Acetes*.

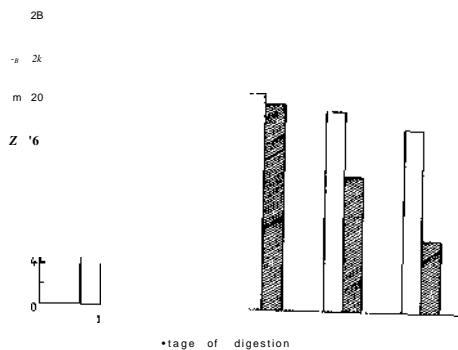


Fig. 1. Frequency occurrence of different stages of digestion in the stomachs of the predators *N.japonicus* and *S. tumbil*

stage of digestion; however, the same food item was in different stages of digestion in different stomachs. In *N.japonicus* (n=62), all the 5 stages of digestion were distributed almost equally in the sample (Fig.1). In *S.tumbil* (n=70), on the contrary, greater number (60%) of stomachs had food in very early stages of digestion (1 and 2).

The fish sample collected from any one haul had empty stomachs as well as stomachs with food. In each stomach where food items were available, the food were in any one stage of digestion. This suggests that these fishes feed asynchronously in a cyclic pattern. Had these fishes been feeding continuously without a cyclic pattern, food items in various stages of digestion would have been available in each stomach (assuming that there is no regurgitation while being caught and the prey are available to all the predators uniformly).

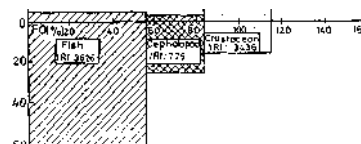
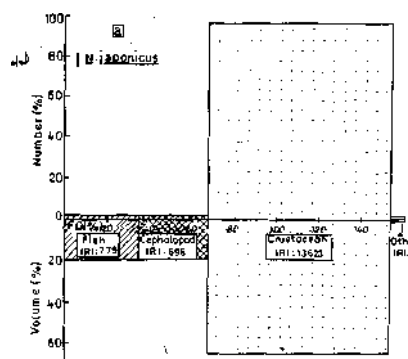


Fig. 2. Percent composition of prey items in number, volume and frequency of occurrence (% FO) and index of relative importance (IRI) of prey for (a) *N.japonicus* and (b) *S.tumbil*

In the entire sample analysed (n=664; TL : 55-310 mm), there were a total of 12,891 prey and the number of crustaceans was 12,300 (95.4%) with *Acetes* being dominant (9621 numbers and 74.6%). Fishes, cephalopod and others formed 2.1, 2.0 and 0.5% of the total number of prey, respectively. In terms of volume also, the crustaceans were dominant (64.5% of the total 1333 ml food; n=457) followed by fishes (20.1%), cephalopods (13.8%) and others (1.6%).

In *S.tumbil* (n=723; TL: 75-550 mm), the frequency of occurrence of the fish prey (55.7%) was the highest, followed by crustaceans (31.7%) and cephalopods (27.4%) (Fig.2b). The volume of fishes predated by *S.tumbil* (n=461) formed 58.0%

on the same group of prey, there was a clear difference in their predatory behaviour. *N.japonicus* predated mainly large numbers of small sized prey like *Acetes* and other crustaceans (IRI: 13,623). On the other hand, *S. tumbil* predated mainly on fishes (IRI:3,526) and crustaceans (IRI:3,436) in addition to cephalopods (IRI:775). On an average, individual *N.japonicus* ingests 19.4 prey (crustaceans forming 95.4%) accounting for 2.9 ml of the stomach volume (64.6% being occupied by crustaceans) (Table 1) but *S.tumbil* ingests only 12.6 prey (crustaceans forming 92%), filling 13.1 ml of stomach volume (84% being occupied by fishes and cephalopods). *N.japonicus* predated, on an average, 1.7 prey groups and *S.tumbil*

TABLE 1. Frequency of occurrence (FO), number, weight and volume of prey predated by *Nemipterus japonicus* and *Saurida tumbil*

Parameter	n	<i>N.japonicus</i>					n	<i>S.tumbil</i>				
		Fish (%)	Cephalo-pods (%)	Crusta-ceans (%)	Others (%)	Total (%)		Fish (%)	Cephalo-pods (%)	Crusta-ceans (%)	Others (%)	Total (%)
FO/predator	664	23.5	17.6	52.9	5.9	1.7	723	50.0	25.0	25.0	12	
Number of prey/predator	664	2.1	2.1	95.4	0.5	19.4	723	5.6	2.4	92.0	12.6	
Weight of prey(gVpredator)	457	19.7	13.2	65.8	1.3	3.1	461	56.8	27.3	15.8	13.9	
Volume of prey (ml) / predator	457	20.4	13.6	64.6	1.4	2.9	461	58.0	26.0	16.0	13.1	
ni	457-664	779	695	13623	14		461-723	3526	775	3436		

of the volume of all the prey items, followed by the cephalopods (25.6%) and crustaceans (16.3%). However, in terms of numbers, the crustaceans were dominant forming 92.1% of the total number of prey, followed by fishes (5.3%) and cephalopods (2.7%). *S.tumbil* also consumed a large (92% of the total) number of *Acetes*. Of the 8366 crustaceans in the stomachs (n=723) of *S.tumbil*, *Acetes* formed 66.3%.

Though *N.japonicus* and *S.tumbil* fed

predated prey belonging to 1.2 groups (calculated from the FO of the prey), indicating that *S.tumbil* concentrated on only a few prey items, and hence the narrow width of the IRI diagram.

Ontogenetic changes in feeding

The FO of the prey fishes increased from 35.7% (TL:<100 mm) to 57.1% (TL:>300 mm) whereas the FO of the crustaceans remained almost the same in all the length groups among *N.japonicus*

(Table 2). Following increase in the FO and volume of prey fishes, the IRI of crustaceans decreased and that of fishes increased as *N.japonicus* grew in length (Fig. 3a). Though the number of crustacean prey increased by nearly 7 times as the

fish grew from 55 mm (6.0 prey/predator) to 310 mm (41.4 prey/predator), the number of prey fishes increased only by about 2 times. With continued dependence on the crustacean prey, larger *N.japonicus* predate proportionately less number of large sized prey like fishes and cephalopods. This has resulted in increase in the food diversity of *N.japonicus* as it grew old; the youngest fish predated 1.6 prey groups and the oldest 2.1 prey groups (Table 2).

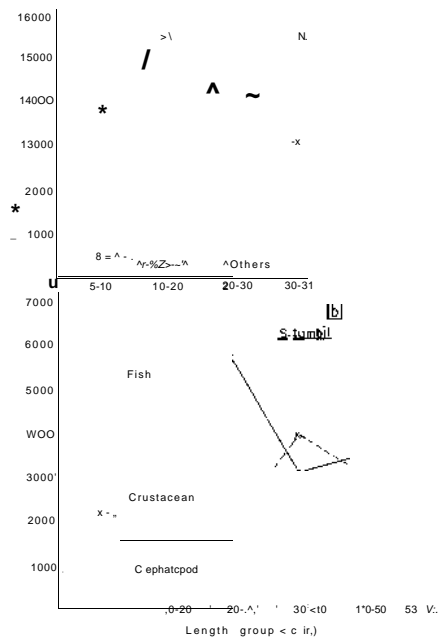


Fig. 3. Index of relative importance of prey for different length groups of (a) *N.japonicus* (n=664) and (b) *S.tumbil* (n=723); the values pertain to samples collected during 1989-'91.

Contrary to what is observed in *N.japonicus*, the IRI of prey fishes decreased and that of the crustaceans increased as the lizardfish grew in length (Fig.3b). The decrease in the FO (from 77.8% to 53.8%; Table 3) and the number/predator (from 1.2 to 0.8) of fish prey was however compensated by the increase in the FO and the number/predator of crustacean prey. The FO and number of the crustacean prey were very high in the largest group studied, resulting in very high IRI value for the crustaceans (Fig.3b).

It may be concluded that young *N.japonicus*, primarily a crustacean feeder, diversifies its feeding habit as it grows and depends on fishes and cephalopods as secondary prey items on attaining larger size. *S.tumbil*, primarily a piscivore when young, diversifies its feeding habit as it

TABLE 2. *Nemipterus japonicus*: Frequency of occurrence (%) of prey items and number of prey / individual predator

Length group (mm)	n	Frequency of occurrence (%)				FDF*	Number of prey / predator				Total
		Fish	Cephalopods	Crustaceans	Others		Fish	Cephalopods	Crustaceans	Others	
<100	241	35.7	34.4	80.9	5.4	1.5	0.4	0.4	6.0	0.1	6.9
101-200	220	30.0	30.9	85.9	5.9	1.5	0.4	0.4	18.7	0.1	19.6
201-300	196	39.3	34.2	89.8	9.2	1.7	0.4	0.4	32.9	0.1	33.8
301-310	7	57.1	57.1	85.7	14.3	2.1	0.7	0.7	41.4	0.4	43.2
Total	664	35.1	33.4	85.2	6.8	1.6	0.4	0.4	18.5	0.1	19.4

* Food Diversity Factor = Total FO (%) of all prey items / 100

TABLE 3. *Saurida tumbil* : Frequency of occurrence of prey items and number of prey / individual predator

Length group (mm)	n	Frequency of occurrence (%)				Number of prey/predator			
		Fish	Cephalopods	Crustaceans	FDF*	Fish	Cephalopods	Crustaceans	Total
70-100	18	77.8	33.3	27.8	1.39	1.2	0.4	3.8	5.4
101-200	125	64.8	30.4	24.0	1.19	0.8	0.5	1.9	3.2
201-300	173	53.8	27.2	30.1	1.11	0.8	0.3	1.2	2.3
301-400	188	50.5	26.6	33.5	1.11	0.5	0.3	18.7	19.5
401-500	167	55.1	25.7	31.1	1.12	0.6	0.3	4.7	5.6
501-550	52	53.8	26.9	48.1	1.29	0.8	0.2	68.1	69.1
Total	723	55.7	27.4	31.7	1.15	0.7	0.3	11.6	12.6

* Food Diversity Factor = Total FO(%) of all prey items / 100

grows and depends on crustaceans as secondary prey on attaining larger size. Ontogenetic changes in the diet of *N.japonicus* (Vivekanandan, 1990, Rao and Rao, 1991) and *S.tumbil* (Rao, 1981) have been reported by earlier authors also.

Predator-prey relationship

(i) *Mouth opening and prey size:*

N.japonicus has smaller mouth than *S.tumbil*. The mean ratio of upper jaw length to standard length was 8.5 for *N.japonicus* (n=153; length range : 105-275 mm) but 5.5 for *S.tumbil* (n=140; length range : 125-370 mm). The gape width (GW) of *N.japonicus* (TL: 250 mm; n=3) is only 15 mm (TL:GW ratio = 16.7:1) whereas that of *S.tumbil* (n=4) is 25 mm

TABLE 4. Comparative morphology of *Nemipterus japonicus* (n=3) and *Saurida tumbil* (n=4), each measuring 250 mm total length; the values represent mean and SD

Parameter	<i>N.japonicus</i>	<i>S.tumbil</i>
Weight (g)	175 ± 12.3	140 ± 1.6
Standard length (mm)	205 ± 12.3	220 ± 13.1
Maximum body depth (mm)	65 ± 3.5	35 ± 1.7
Pre-anal distance (mm)	110 ± 6.6	140 ± 7.3
Upper jaw length (mm)	24 ± 0.9	40 ± 1.1
Lower jaw length (mm)	20 ± 1.2	38 ± 1.7
Maximum mouth opening (mm)	15 ± 0.4	25 ± 0.4
Area of mouth opening (mm ²)	135 ± 9.9	350 ± 16.5
Number of gill rakers/arch	15 ± 1.5	33 ± 3.9
Number of gill filaments / arch	150 ± 13.5	230 ± 11.1
Area of each gill arch (mm ²)	320 ± 23.7	900 ± 101.0
Stomach length (mm)	37 ± 2.2	54 ± 3.9
Intestinal length (mm)	120 ± 8.5	85 ± 7.0
Diameter of empty stomach (mm)	8 ± 0.6	7 ± 0.3
Volume of empty stomach (ml)	1.8 ± 0.38	1.8 ± 0.30

However, for an equal mouth opening (15 to 19 mm in Fig.5) of the predators, the body depth of the prey was almost equal.

(ii) Stomach volume and prey size

The stomach of *N.japonicus* is thin-walled and short and the intestine is long and coiled. On the contrary, the stomach of *S.tumbil* is thick-walled and long with 6 to 8 longitudinally running ridges, which aid in expansion of stomach whenever

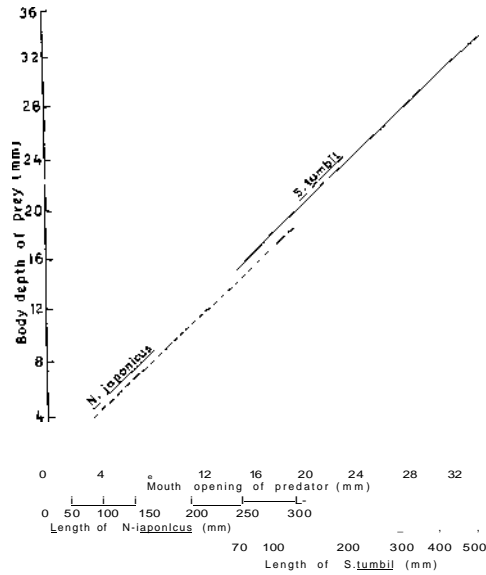


Fig. 5. Relationship between mouth opening (gape width) of the predators and maximum body depth of prey caught; values of linear regression on analysis are given in Table 5 (SI.No.3); the total length of the predators to the corresponding mouth opening are provided.

required; the intestine is straight. The stomach length of *N.japonicus* (n=153) and *S.tumbil* (n=140) averaged 17.5 and 24.8% of the respective standard lengths; the corresponding intestine lengths were 58.9 and 38.0% of the respective standard lengths.

Though the stomach of *N.japonicus* was shorter, the stomach capacity was equal to that of *S. tumbil* due to the slightly

larger opening of the stomach after oesophagus. For instance, the (empty) stomach lengths of a 250 mm TL *N.japonicus* (n=15) and *S.tumbil* (n=22) were 37 and 54 mm, respectively; the stomach volume for both the fishes was 1.8 ml.

The length of the stomach increased linearly with increasing length (Fig. 6) of the predators (SI.No.4; Table 5). Consequently, the length of the prey increased linearly with the increasing length of the predators (SI.No.5; Table 5). At any given length of the predators, the length of the prey was longer than the length of the empty stomach. For instance, the lengths of the empty stomachs of 100 mm and 300 mm TL *N.japonicus* were 15.0 and 43.1 mm, respectively; the corresponding average lengths of the prey in full/gorged stomachs of the predator were 18.8 and 45.7 mm (Fig. 6). It is possible for the predators to accommodate prey longer

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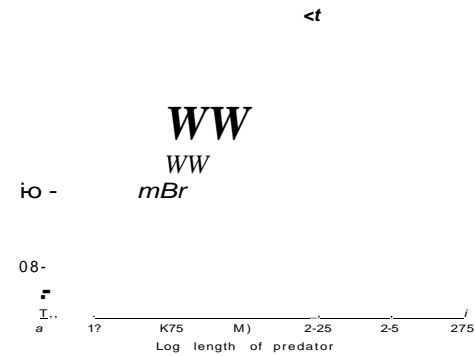


Fig. 6. Linear increase in predator's stomach length (for regression values, refer SI.No. 4 of Table 5) with increasing total length of the predators

than the length of the stomach due to distensibility of the stomach. It could be further deduced from fig. 6 that *S.tumbil* has the capacity to distend the stomach more than *N.japonicus*. For instance, a 100 mm TL *S. tumbil* expanded its stomach by about 44% compared to 25% by *N.japonicus*. The proportion of (empty) stomach length in the total length of *N.japonicus* (14.7%) and *S.tumbil* (21.7%) is constant in all the length groups. However, there was an inverse relationship between the length of the predators and the proportion of prey length in the predator's length (Sl.No. 6; Table 5). For instance, a 50 mm TL *N.japonicus* has the capacity to predate prey which is 21.4% of its own length but could predate prey which is only 15.2% of its length when it grows to 300 mm TL. A 100 mm TL *S.tumbil* predated prey equal to 38.5% of its length but a 500 mm TL fish could predate prey which is only 27.4% of its length.

The total prey volume also increased with increasing length of the predators (Sl.No. 7,8,9; Table 5). For instance, the volumes of food in the full/gorged stomachs of 50 and 300 mm TL *N.japonicus* were 0.07 and 14.45 ml, respectively (Fig.7a). Due to the distensibility, the stomach capacity increased by 2.5 to 7.0 times depending upon the size of the predator. Of the total stomach capacity, *N.japonicus* could fill up 0.03 (50 mm TL) to 7.87 (300 mm TL) ml of the stomach as single prey; i.e. about 50% of the stomach is filled as a single large prey and the rest as many smaller prey. Comparatively, the prey volumes in the full/gorged stomachs of 100 mm and 500 mm TL *S.tumbil* were 1.10 and 101.10 ml, respectively (Fig. 7b). Due to higher distensibility, *S.tumbil* could increase the stomach capacity by about 10 times. The lizardfish fills up 0.84 (100 mm TL) to 53.90 (500 mm TL) ml of the stomach as single large prey, i.e. 50 to 76% of the stomach is filled as a single large

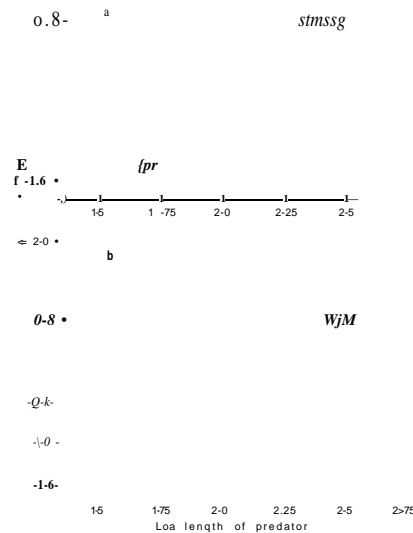


Fig. 7. Linear increase in volume of empty stomach, total stomach capacity and capacity to handle single large prey (for regression values, refer Sl.No. 7,8,9 of Table 5) with increasing total length of the predators (a) *N.japonicus* and (b) *S.tumbil*.

prey and the rest as many smaller prey.

From Fig. 7 a & b, it is also clear that the stomach distensibility and the consequent increase in the stomach volume is more pronounced in *S.tumbil* than in *N.japonicus*. Whereas the stomach distensibility is only marginal in large sized *N.japonicus*, it is uniformly high in all the length groups of *S.tumbil*. Whereas the percentage volume of single large prey increased in the stomach of *N.japonicus* as it grows, a reverse trend was observed in *S. tumbil*.

Discussion

Though *N.japonicus* and *S.tumbil* inhabit the same area and largely depend on the same prey groups, the differences in the morphology of jaws and teeth between them resulted in their adapting to diverse predatory strategies. The small gape width and mouth area enable

N.japonicus predate on smaller prey. With more teeth and larger oral area, *S. tumbil* can grasp and hold large and active prey. Alexander (1967) stated that fishes with small mouth are better adapted for sucking their prey, whereas those with large mouth can grasp large and more elusive prey. The diversity of feeding and resorting to the secondary prey items may be considered as an adaptation toward increasing the range of food supply of a population, by enabling the species as a whole to assimilate a variety of diets (Nikolskii, 1969).

The size and structure of gill rakers also differ markedly between the two species (Fig.8). Each gill arch of *N.japonicus* has 14 to 17 gill rakers and 140 to 160 gill filaments. The gill rakers which are soft structures with bristle-like edges, may tend to sieve and prevent the escape of small prey. In contrast, the gill arch of *S.tumbil* is large, flattened and has 30 to 35 short and spiny gill rakers. Each gill arch of *S.tumbil* covers a large rectangular area (900 mm²) compared to the gill arch (320 mm²) of *N.japonicus*. Gut length also influences the size and quantity

of food eaten. Groot (1969) and Darnell (1970) found that fishes with relatively longer guts tended to eat smaller prey. *N.japonicus* has long intestine whereas *S.tumbil*, with short intestine but long stomach, is capable of accommodating single large prey. The longitudinally running ridges provide elasticity to the stomach of *S.tumbil* in holding large prey.

Fishes feeding randomly on small prey are generally believed to be better adapted for continuously gorging themselves and those fishes which take larger prey are known to feed sporadically (Cailliet and Ebeling, 1990). The present study shows that both *N.japonicus* and *S.tumbil* do not continuously gorge themselves but feed asynchronously. Cessation of feeding is probably obligatory for these fishes for proper digestion. As large-sized prey are digested at slower rates (Tyler, 1970), the process of digestion in *S. tumbil* may extend for longer period than that of *N.japonicus*.

Based on the feeding behaviour, fishes are classified into two categories: opportunistic and selective feeders (Wetherbee *et al.*, 1990). Opportunistic feeder consumes whatever prey is encountered and the selective feeder ignores available prey for a preferred prey. The stomach of the opportunistic feeder contains a variety of prey, similar to the composition and abundance of the prey fauna in the predator's habitat. The stomach of selective predator would be expected to contain a predominant prey type, which in some cases, may not be abundant in the habitat. Compared to *S.tumbil*, *N.japonicus* predate a wide variety of prey and abundance of *Acetes* in the stomach is similar to its abundance in the habitat. However, considering the negligible occurrence of the prey groups other than the 3 dominant groups (fishes, crustaceans and cephalopods), and the change in the feeding habit of the adult, it is not proper to classify *N.japonicus*, as an

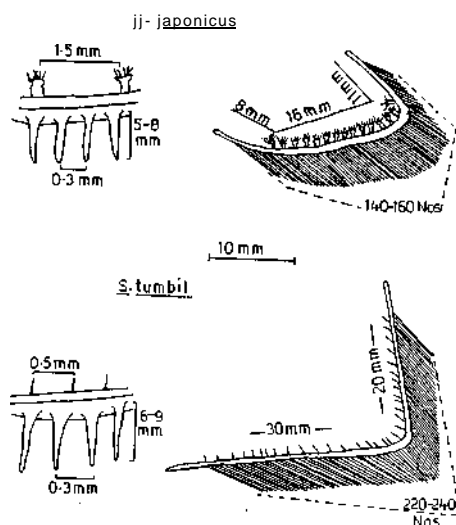


Fig. 8. Lateral view of gill arch and rakers of *N.japonicus* and *S.tumbil*

opportunistic feeder. The smaller variety of prey (in contrast to the greater variety available in the vicinity) in the stomachs of *S.tumbil* indicates that this is a selective predator. It has also been seen that all the prey groups are abundant in the habitat off Veraval but the predator species under study predate selectively on the abundant prey. In such situations, it is difficult to recognise the difference between opportunistic and selective feeders. It may be concluded that in a continuum between opportunistic and selective feeding *N. japonicus* is on the side of opportunistic feeding and *S.tumbil* on the selective feeding. The fishers are known to select their place in the continuum, from where they achieve predatory profitability, which is the objective of predation (Townsend and Winfield, 1985).

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