



Research Article

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## Ecomorphology of the Feeding Characteristics in Selected Reef Fishes from South Andaman Islands: A Preliminary Study

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### Abstract

The feeding apparatus of 11 species of reef fishes from four families, Chaetodontidae, Pomacentridae, Acanthuridae and Scaridae were studied in an ecomorphological perspective. The behavioural ecology was studied through observations during snorkeling. The morphology of the feeding apparatus was analysed through dissections and morphometric studies. The morphology and the ecology of feeding were correlated in the light of previous ecomorphological studies. It was concluded that the species with higher gape angle and higher protrusion used the scraping mode of feeding. TuL/HL ratio seems to be the key factor which allows *Chaetodon falcula* to feed in a unique pattern. Obligate corallivores exploit all the angles of feeding and their feeding frequency is high. The study has indicated a lack of previous literature regarding specific aspects of feeding ecomorphology. It was observed that both the food items and the method of feeding had a connection with the morphological characters. So ecomorphological traits seem to have more interlinks than previously thought. Cluster analysis provided an alternative way of grouping the species according to the ecomorphological traits.

### Keywords

Ecomorphology; Reef; Fishes; Feeding; Andaman; *Chaetodon*

### Introduction

The study of how body parts operate and how environmental selection pressures have influenced their construction and operation is called ecomorphology [1]. Adaptations in fishes concerned with feeding certainly involve structures used in food acquisition and processing, such as jaw bones and muscles, teeth, gill rakers and the digestive system. There are 30 moving bony elements and more than 50 muscles that make up the head region of most fishes. All these are involved in the functional morphology of the feeding.

Relatively small differences in morphology can have a highly profound influence on the feeding behavior [2]. Amongst fishes inhabiting the coral reef ecosystem, more morphological specializations can be expected since the diversity of coral reefs is higher and hence the food availability is also diverse. It has been proposed that the trophic biology of reef fishes is intimately intertwined with their feeding mechanics and that morphological

diversity has profound implications for their ecological diversification [3]. Also, the exceptional species richness of reef fish communities alone makes them prime candidates for studying trophic radiation.

Ecomorphological studies in general, consider both the food item and the feeding behaviour as part of the ecological analysis to link them with the observed morphology. Though the importance of the varied properties (shape, size, elusive nature, texture, etc.) of a food item cannot be underestimated, there are no direct links of morphology to any one preferred resource or food item, since many species, albeit having a preference for a single resource, can still feed on a score of other food items mediated through slight modifications in feeding mechanisms. It was indicated that in Chaetodontidae, morphology influences how the fish feed, rather than what they feed on [4]. The present study was mainly undertaken to test the validity of this hypothesis in South Andaman islands. The study focuses on the ecomorphology of the feeding apparatus of 11 species of reef fishes belonging to four families, Chaetodontidae, Pomacentridae, Scaridae and Acanthuridae.

### Materials and Methods

#### Choice of species

Though fishes have their own taxonomic tree based on the phylogeny, there is yet another classification based on their ecology. The coral reef fishes are believed to have undergone an adaptive radiation in conjunction with the radiation of modern scleratinian corals which took place at the start of the Tertiary Period. The most characteristic groups, in the sense of being most completely associated with coral reef environments are [5]:

1. Three labroid families: the Labridae or the wrasses, the Scaridae or parrotfishes, and the Pomacentridae or damselfishes.
2. Three acanthuroid families: the Acanthuridae or surgeonfishes, the Siganidae or rabbitfishes and the Zanclidae or Moorish idols containing a single species, the archetypal coral reef fish.
3. Two chaetodontid families, the Chaetodontidae or the butterflyfishes and the Pomacanthidae or angelfishes.

The choice of families was governed by the above classification. At least one representative family from each group was chosen. The choice of individual species was governed by relative abundance in all the three study areas. The species chosen for study were: (1) *Chaetodon auriga* Forsskal, 1775 (2) *Chaetodon decussatus* Cuvier, 1829 (3) *Chaetodon falcula* Bloch, 1793 (4) *Chaetodon lunula* (Lacepede, 1802) (5) *Chaetodon rafflesii* Bennett, 1830 (6) *Chaetodon trifasciatus* Park, 1797 (7) *Chaetodon vagabundus* Linnaeus, 1758 (8) *Abudefduf vaigiensis* (Quoy & Gaimard, 1825) (9) *Stegastes lividus* (Bloch & Schneider, 1801) (10) *Scarus ghobban* Forsskal, 1775 (11) *Ctenochaetu sstriatus* (Quoy & Gaimard, 1825).

#### Study area

North Bay (11°42'N latitude, 92°45'E longitude), Chidiyatapu (11°29' N latitude, 92°42' E longitude) and Marina Park (11°40'N latitude, 92°45'E longitude) were chosen as study areas based on their diverse nature and different ecological aspects.

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## Behavioural observations

The behaviour of all the species, which were chosen for study, were observed by snorkeling during low tide (Maximum water depth 10 meters). Various data related to feeding, feeding frequencies per minute, number of bites per feeding, approximate angle of feeding, method of feeding and the type of food were noted and recorded [4]. Triplicate values were taken and mean values were calculated in order to eliminate error in data collection. Any unusual behavioural patterns were simultaneously noted.

## Sampling and identification

10 individuals were collected from each species under the study. Care was taken to see that the sampling was random, i.e. it included both the specimens observed underwater and unobserved specimens, to avoid intra-specific variation and sampling bias. The specimens were collected by using cast nets (mesh size 1 inch) and scoop nets (mesh size 2 mm) during low tide, since at that time the sampling was found to be easier. All the morphometric details and meristic counts were done for the specimens and the species were identified using standard keys [6-9].

## Morphometrics

Standard measurements viz., total length, standard length, Head length, head depth and Tube length were made according to the definitions [10]. Certain unique measurements like mandibular length [11], Maxillary length [11] and Angle of mandibular depression [4] were also noted.

To measure the angle of maximal jaw opening the specimen was placed on plain paper. The maximal jaw opening was then affected manually. Then a line was traced out from each jaw till the angular. These two lines were then extrapolated (if needed) and the angle was measured with a protractor.

## X-ray studies

An X-ray study was performed to compare the head profiles of the various species. The weight of every specimen was taken prior to the dissection. To prepare the skull for X-ray studies, the scales and the major muscle bundles were surgically removed. To facilitate the easy removal of the muscles, freshly frozen samples were immersed in boiling water, the muscles were surgically removed and the frozen skulls were washed and prepared by removing muscle scraps. Any unusual osteological or myological pattern in the head region was simultaneously noted. The prepared skulls were arranged in an order on a black sheet of paper and the x-ray was taken [2]. The gill rakers were surgically removed and counted. The gill rakers were analysed under a microscope and photographs were taken. The teeth bearing jaws were surgically removed and the muscles were cleaned to provide a good view of the teeth. The teeth were analysed under a microscope and pictures were drawn [4].

## Statistical analysis

Data was analysed with the statistical package PAST and Cluster analysis was performed to group the species into individual clusters. Bray Curtis distancing was used in Cluster analysis as it was found to be the most appropriate for ecological data. Both behavioral and morphometric traits were included for the analysis. In case of a non-numerical result, ranking/values were given. For example, the presence of protrusion was indicated by '1' and its absence was indicated by '0'.

## Results

Eleven species, viz., *Chaetodon auriga*, *Chaetodon decussatus*, *Chaetodon falcula*, *Chaetodon lunula*, *Chaetodon rafflesii*, *Chaetodon trifasciatus*, *Chaetodon vagabundus*, *Abudefduf vaigiensis*, *Stegastes lividus*, *Scarus ghobban* and *Ctenochaetus striatus* were studied. In each species, a minimum of three specimens were analysed for ensuring accuracy.

All the observed behavioural parameters are given in Table 1 and the morphometric data is given in Table 2. The percentage of head length in standard length is referred as head protruberosity as per [12]. Though the details of the food consumed by the individual fish species were taken during snorkeling and in the laboratory through dissection, it was felt that the data was insufficient to make an ecomorphological study. Further, all the food items, including occasional and rare ones, had to be included in the analysis for an effective testing of the hypothesis. So, the trophic levels and dietary items were found for each fish from the previous literature [9]. This trophic level data is presented along with some observed morphometric data in Table 3.

The behavioral details are presented in Table 1. *Chaetodon trifasciatus* feeds almost perpendicularly (90°) and flat on the substratum (180°). Two different feeding behaviours were observed in *Ctenochaetus striatus*. The feeding frequency range was very wide, from 0.6 in *Stegastes lividus* to 14 in *Chaetodon trifasciatus*. Most of the species in the study showed a nipping mode of feeding. The resource utilization was highly negligible in *Chaetodon vagabundus*. *Ctenochaetus striatus* and *Scarus ghobban* were found in heterospecific shoals, which consisted of *Acanthurus nigricauda*, *Zebbrasoma scopas*, *Cetoscarus bicolor*, *Scarus niger*, *Scarus globiceps*, *Scarus rivulatus*, *Scarus rubroviolaceus*, *Chlorurus sordidus*, *Calotomus sp.*, *Acanthurus triostegus* and *Siganus virgatus*. Individual members of the heterospecific shoal had no influence on the actual feeding location of the other, though the overall site selection is influenced (Supplementary file).

It is inferable from Table 2 that morphometric data is a very distinguishing feature even among members of the same genus. The size range is very wide, with the smallest specimen, *Chaetodon lunula*, measuring only 92 mm as opposed to the 241.5 mm of the longest *Scarus ghobban*. Even though it is called as a "long jawed fish" [8], the head profile ratio i.e. head length to head depth ratio is 1.00 in *Chaetodon falcula*. This is due to its deep and compressed body. The tube length to head length ratio had a range of 0.17 to 0.48. TuL/HL ratio is not given for *Ctenochaetus striatus* and *Scarus ghobban* as the mouth is non-protractile.

Table 3 gives the key morphological characters of the feeding apparatus of the species in the study. The gape angle or the maximally open mouth was the highest for *Ctenochaetus striatus* and the lowest angle was found in *Chaetodon rafflesii*. Most of the species had terminal mouths. All chaetodontids had bristle teeth and *Scarus ghobban* had a dental plate. The mouths of *Ctenochaetus striatus* and *Scarus ghobban* were non-protractile. *Ctenochaetus striatus* and *Scarus ghobban* had the maximum number of gill rakers.

The head protruberosity is expressed as the percentage of head length in the standard length of the species and the values are presented in Figure 1. The values of the percentage of tube length in

**Table 1:** Behavioural parameters observed through snorkeling.

Species	Foray per min	Bites per feed	Feeding mode	Type of feed	Angle of feeding (to the substratum)	Solitary/ shoal feeder	Foraging
<i>Chaetodon auriga</i>	6	1.5	Nipping combined with a scraping action	Algal cover	45° and 80°	Feeds in pairs, occasionally solitary	Random selection
<i>Chaetodon decussatus</i>	2	1	Scraping with a whole body jerk (1 second duration)	Algal cover & Corals	Acute angle	Solitary	Random selection
<i>Chaetodon falcula</i>	8.5	1	Nipping	Algae & sessile invertebrates	Acute angle	Feeds in pairs	Random
<i>Chaetodon lunula</i>	3	1	Nipping	Algae	Acute angle	Solitary feeder	Semi-territorial
<i>Chaetodon rafflesii</i>	9	3	Nipping	Algae	Acute angle	Solitary	Semi-territorial
<i>Chaetodon trifasciatus</i>	14	3.5	Nipping	Scleratinian corals including <i>Acropora</i> and <i>Pavona cactus</i>	45° frequently 90° and 180°	Always feeds in pairs	Random selection of substratum within a fixed broad area
<i>Chaetodon vagabundus</i>	12.5	2.5	Scraping with a whole body jerk (3 second duration)	Algae and Corals	Acute angle	Feeds both as solitary and in pairs	Highly random
<i>Abudefduf vaigiensis</i>	2	Data unavailable	Feeds just above the bottom in the water column (5 cm away from the bottom)	Planktons	Data unavailable	Always feeds as a shoal	Random
<i>Stegastes lividus</i>	0.6	2	Nipping	Algal cover which the fish itself "guards"	Variable	Feeds as a group in a "feeding frenzy"	Not available as the fish feeds only in its "farm"
<i>Scarus ghobban</i>	4	6	Scraping - Upper jaw is placed first, and then lower jaw pressure is applied.	Coral and Algal cover ( <i>Porites sp</i> )	All angles	Feeds in a heterospecific shoal	Random
<i>Ctenochaetus striatus</i>	4	A long single bite	1. When the gape angle is minimum - brushing the surface with bristle tooth. 2. When the gape angle is maximum – energetic grasping bites with full pressure	1. Detritus and fine algae. 2. Reef substrate	Mostly 80°	Feeds in a heterospecific shoal	Random selection of substratum within a fixed larger area

**Table 2:** Morphometric data obtained from Dissection.

Species	TL (mm)	SL (mm)	UJTL (mm)	LJTL (mm)	HL (mm)	HD (mm)	HD (mm)	H/H/D	TuL/HL	HL/SL
<i>Chaetodon auriga</i>	142	126	2	2.5	40	39.75	39.75	1.01	0.31	0.32
<i>Chaetodon decussatus</i>	108.5	91.5	1.5	1.5	28	31	31	0.90	0.27	0.31
<i>Chaetodon falcula</i>	145	125	3	3	40	40	40	1.00	0.48	0.32
<i>Chaetodon lunula</i>	92	76	3	2	30	26	26	1.15	0.27	0.39
<i>Chaetodon rafflesii</i>	116	100	2	2	35	36	36	0.97	0.20	0.35
<i>Chaetodon trifasciatus</i>	112.66	95.33	3	3	26.5	39.5	39.5	0.67	0.21	0.28
<i>Chaetodon vagabundus</i>	116	95.5	2	2	30	35	35	0.86	0.17	0.31
<i>Abudefduf vaigiensis</i>	144.66	198.66	2.466	2.46	32	39.6	39.6	0.81	0.30	0.16
<i>Stegastes lividus</i>	94	81.6	1.166	1.166	21.3	24	24	0.89	0.25	0.26
<i>Scarus ghobban</i>	241.5	204.5	7.5	7.5	64.5	70.5	70.5	0.91	0	0.32
<i>Ctenochaetus striatus</i>	195.5	148.25	2	2.5	40.75	28.25	28.25	1.44	0	0.27

head length for each species are presented in Figure 2. Head profile i.e., the ratio of head length to head depth is given in Figure 3. The values for the percentage increase in head length after protrusion is presented in Figure 4, which is a measure of the relative magnitude of protrusion.

### X-ray analysis

The x-ray image taken with the surgically removed head regions is shown in Figure 5. It can be seen that the x-ray supports the relative difference in various ratios among the species, especially TuL/HL and Head profile.

### Cluster analysis

The results of the cluster analysis are given in Figure 6. The

cluster analysis presents an alternative relatedness based on their ecomorphological characteristics.

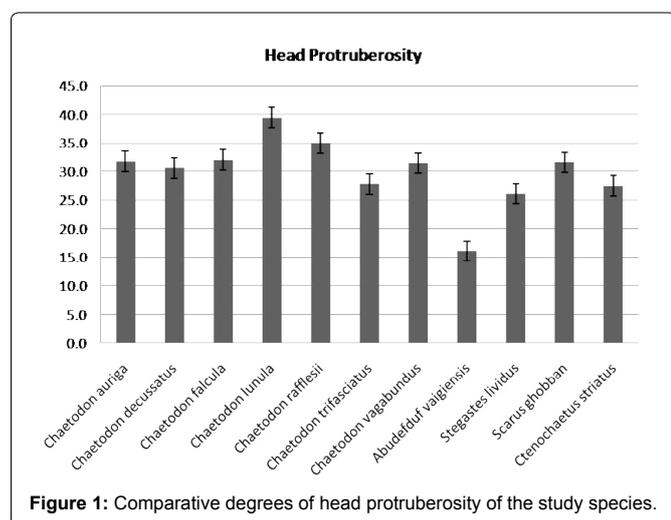
### Discussion

The study mainly focuses on the family Chaetodontidae and the other co-occurring species belonging to different were included for comparison.

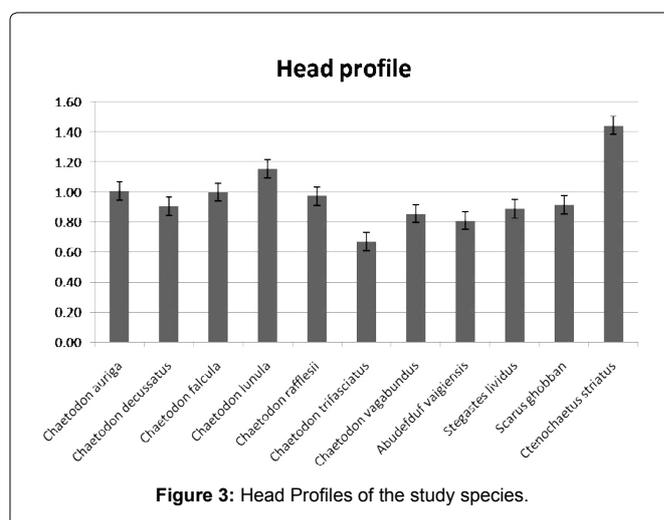
In *Chaetodon auriga* there is almost a 12.5% increase in head length during protrusion. Also, the tube length to head length percentage is the second highest of all the chaetodontid species studied. This helps the fish to combine the scraping action during nipping and this is advantageous, especially when feeding on hard corals. This however, is not advantageous during algal feeding as the fishes do not use protrusion when feeding on algae [4]. The fish was never found to

**Table 3:** Additional morphometric data appropriate for analysis.

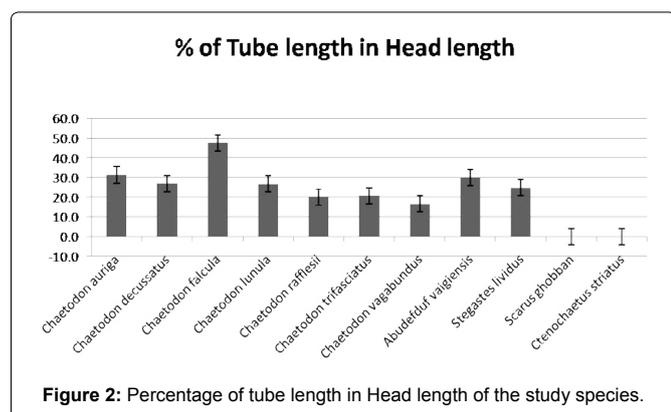
Species	Maximum Gape Angle	Angle of the maximum mandibular depression	Mouth Position	Teeth	Mouth Protrusible or not	Number of Gill Rakers	Trophic level
<i>Chaetodon auriga</i>	18.5°	10.6°	Terminal	Bristle – individual teeth almost invisible	Protrusible	15	3.22
<i>Chaetodon decussatus</i>	28.5°	11°	Terminal	Bristle – individual teeth almost invisible	Protrusible	16	2.64
<i>Chaetodon falcula</i>	20°	24.5°	Terminal	Bristle – individual teeth almost invisible	Protrusible	14	3.50
<i>Chaetodon lunula</i>	11.5°	41°	Superior	Bristle – individual teeth almost invisible	Protrusible	12	3.35
<i>Chaetodon rafflesii</i>	6°	11.6°	Superior	Bristle – individual teeth almost invisible	Protrusible	11	3.33
<i>Chaetodon trifasciatus</i>	14°	23°	Terminal	Bristle – individual teeth almost invisible	Protrusible	10	3.34
<i>Chaetodon vagabundus</i>	22.5°	12°	Terminal	Bristle – individual teeth almost invisible	Protrusible	11	3.33
<i>Abudefduf vaigiensis</i>	94.5°	71°	Terminal	Bristle – individual teeth visible but not countable	Protrusible	14	2.59
<i>Stegastes lividus</i>	128°	24.5°	Terminal	Bristle – individual teeth visible but not countable	Protrusible	13.3	2.0
<i>Scarus ghobban</i>	43°	Not applicable as mouth non protractile	Inferior	Distinct dental plate where the individual teeth are visible only in the edges	Not	22.5	2.0
<i>Ctenochaetus striatus</i>	170°	Not applicable as mouth non protractile	Inferior	Long bristle like teeth with significant spacing	Not	22.5	2.0



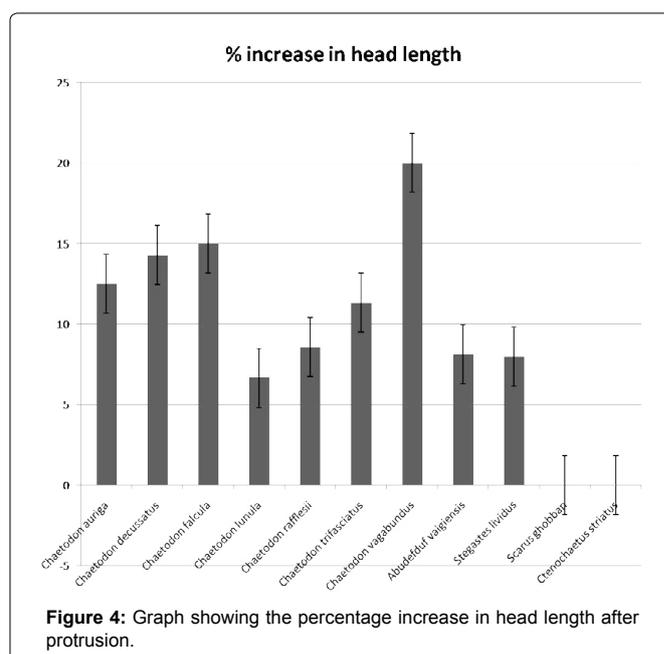
**Figure 1:** Comparative degrees of head protruberosity of the study species.



**Figure 3:** Head Profiles of the study species.

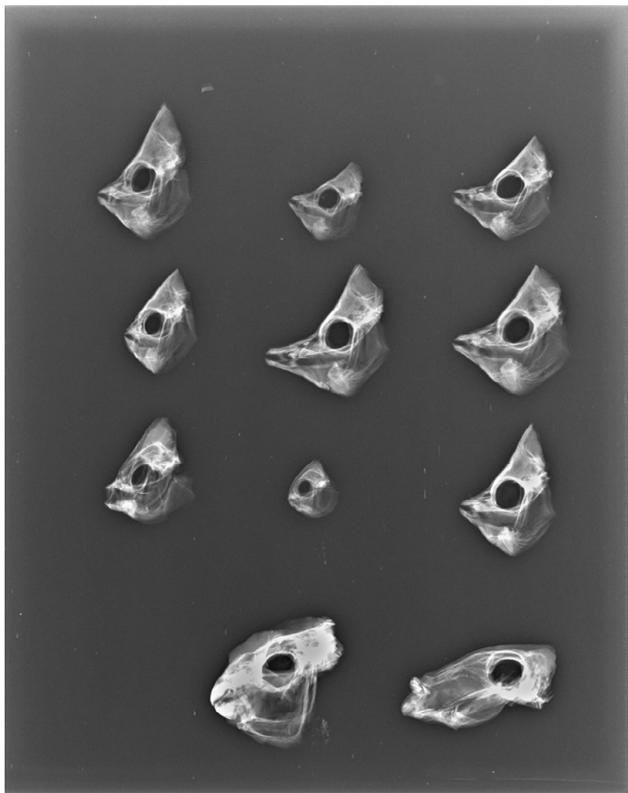


**Figure 2:** Percentage of tube length in Head length of the study species.



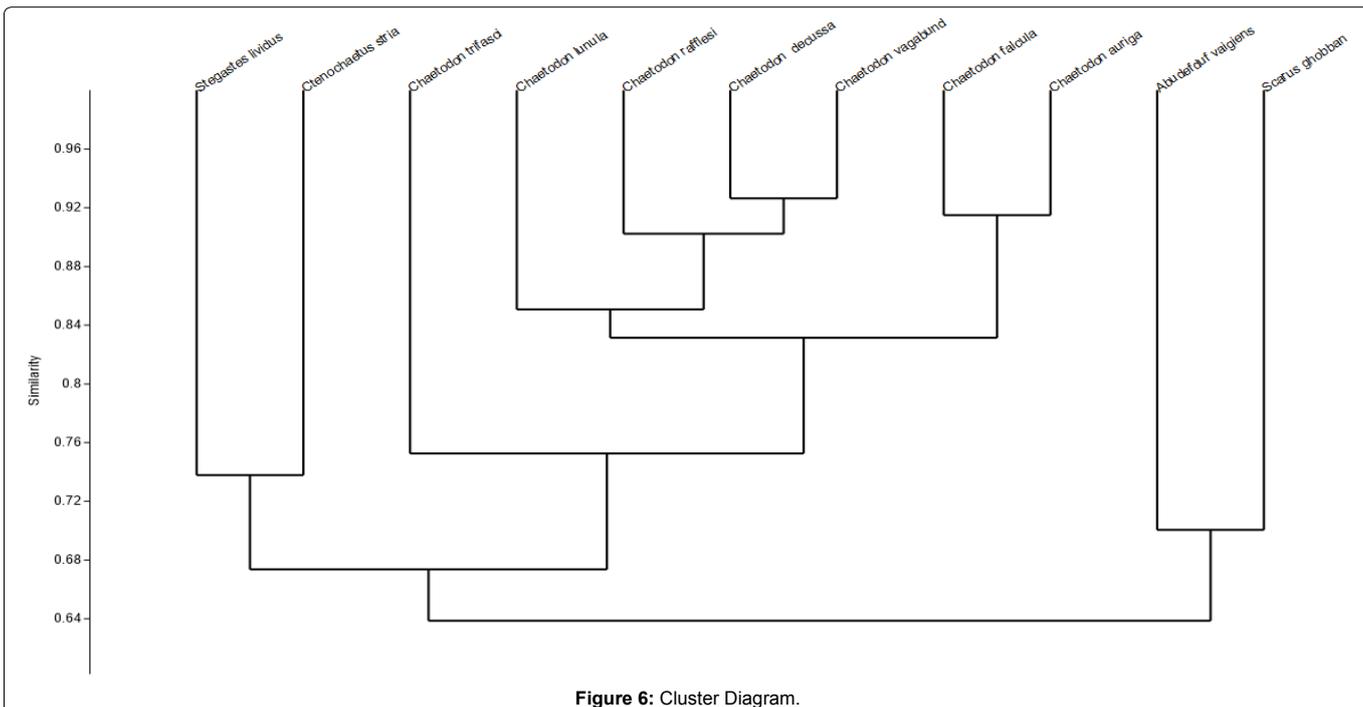
**Figure 4:** Graph showing the percentage increase in head length after protrusion.

feed perpendicular to the substratum. The maximum achieved angle of feeding was 80°. This was found to be a common feature of the fishes where the TuL/HL ratio is considerably high. The long jaw could be manipulated and bent to feed from the substratum. Even then, it was found out that this species occasionally feeds almost at an angle of 90°. This may be probably when it had to feed on cryptic fauna hidden inside the substratum. It has a considerable gape angle. It was found



**Figure 5:** X-ray image. Species from left to right  
 First row: *Chaetodon rafflesii*, *Chaetodon lunula*, *Chaetodon decussatus*  
 Second row: *Chaetodon auriga*, *Chaetodon falcula*, *Chaetodon trifasciatus*  
 Third row: *Chaetodon vagabundus*, *Stegastes lividus*, *Abudefduf vaigiensis*  
 Fourth row: *Ctenochaetus striatus*, *Scarus ghobban*

out that higher gape angles almost always correspond to scraping action, which is probably due to the fact that the increased gape angle provides increased contact with the surface [13]. This increases the holding capacity and strength increases. Higher holding capacity directly translates to successful scraping. Though by its trophic level it is a species which feeds mainly on animals, previous studies indicate that it is a “feeding generalist”. So the particular features of its morphology cannot be correlated with the diet. Only the method of feeding could be correlated with the morphology. Though *Chaetodon decussatus* is an omnivorous fish, the morphology was specialized. There is a whole body jerk associated with the scraping action, the duration of which is lesser than that of *Chaetodon vagabundus*. This can be understood by the comparison of the morphological features of both the fishes. The percentage increase of head length is longer in *C.vagabundus* so it has to jerk its whole body with more vigour and for a longer time than *C. decussatus* because there is an increased distance of the held prey from the head. However, the TuL/HL ratio is much higher than that of *C. vagabundus*. This means that for a given head length, the tube or pipette mouth contributes more in *C. decussatus* than the *C. vagabundus*. The ecological implications for this are unclear. *Chaetodon decussatus* has the highest gape angle among the chaetodontids in the study. This, as discussed for *C. auriga*, helps in the scraping action as increased gape angle provides increased contact with the surface [13]. *Chaetodon falcula* shows the maximum percentage of tube length in head length. This data is found to directly correlate with the fact that of all the chaetodontid species studied, this is the only fish which laid almost flat on the substratum, bent its tube mouth formed due to protrusion and grabbed the feed with a nipping action. It was found to be feeding polyps at that particular feeding mode. The angle of jaw depression was found to be high. This enhances protrusion [11] and this could help the fish feed in the unique pattern as described above. Also, this species and *Chaetodon lunula* are called predators which hunt macrofauna. For such actions, maximum protrusion is preferred as the protrusion increases the force exerted on the prey [14]. In *Chaetodon lunula* the



**Figure 6:** Cluster Diagram.

degree of head protruberosity (HL/SL) was found to be the highest yet no ecological or dietary significance could be inferred. The mouth was found to be supra-terminal or superior, characteristic of surface feeders or fishes that live in bottom and feed the prey swimming overhead, like the Uranoscopid fishes [16]. Dietary or ecological significance could not be correlated. This species has the highest angle of jaw depression of all the chaetodontid species studied. Increase in angle of mandibular depression enhances protrusion [11]. This fish is the only chaetodontid whose diet detritus is a component, among the species studied. This might probably explain the need for protrusion. Detritus feeders need suction force to take up the detritus. Protrusion increases the suction force [15]. However, with a supraterrminal mouth, the choice of detritus as a feeding item is associated with trade-offs as detritivores with supraterrminal mouths have lesser defence when they are feeding [16]. *Chaetodon rafflesii* has a very small gape of 6° with no observed ecological significance. The mouth was found to be supra-terminal or superior, characteristic of surface feeders or fishes that live in bottom and feed the prey swimming overhead, like the Uranoscopid fishes [16]. Dietary or ecological significance could not be correlated. *Chaetodon trifasciatus* is the only “feeding specialist” in the study. Even then, most of the characteristics were found to be suitable for the category of “morphological generalist”. The difference was there only in the number of gill rakers (highest among the chaetodontids studied) and the morphology of the gill rakers (considerably short). This species is an obligate corallivore. Corallivory is a feeding specialization which is associated with maximum constraints and trade-offs [13], which means obligate corallivory is actually disadvantageous. However, there was a unique feeding method in this species where the individual fishes form an angle of 90° as well as 180° with the substratum. This was not observed in any other species in the study. This might be probably an effort to increase the amount of feeding, though this perpendicular and horizontal feeding makes it difficult for the fish to escape when surprised by a predator [16]. The feeding frequency was the highest in this species. This can also be associated with corallivory. The species feeds more frequently and at all angles when compared to disadvantage, as maximum energy has to be obtained from a single source which is associated with trade-offs. It is a coral scraper according to a previous study [4]. In this study, however, it was found to be a coral nipper. *Chaetodon vagabundus* species showed the highest increase in head length during protrusion. As mentioned earlier, this percentage always correlates with the scraping action during feeding. The gape angle also was found to be higher. It is also correlated with the scraping as increased gape angle provides increased contact with the surface [13].

*Abudefduf vaigiensis* and *Stegastes lividus* belong to the family Pomacentridae. An omnivorous species, most of the characters of *Abudefduf vaigiensis* fit into the category of “morphological generalist”, except for the gill rakers. Very numerous gill rakers are tightly packed, which correlates with the fact that planktons are included in the diet of the fish. [17]. The angle of maximum jaw protrusion was found to be high which correlates with the omnivorous nature and hence the need for enhanced protrusion to enhance feeding success [15]. Herbivore/Detritivore in trophic analysis, *Stegastes lividus* has the least increase in head length during protrusion. This is understandable as there is no planktonic component in the diet. Also, the mouth is inferior. It helps the fishes to feed on the algae and detritus. The gape angle was found to be obtuse. This facilitates easy suction of a large amount of algae/detritus. A high number of gill rakers packed tightly, filter the organic particles from the sediments [16].

Though this is placed in the same trophic level as *Stegastes lividus* and *Ctenochaetus striatus*, the major difference for *Scarus ghobban* is the presence of dental plates with which it scrapes the algae off the coral substrates. The presence of dental plates is a common feature in all the species of this family. These dental plates provide the required efficiency even though the angle is only 43° as opposed to the obtuse gape angles of other herbivores/detritivores. A robust pharyngeal mill was observed in this species. This mill helps take prey into the oesophagus and crush and disarticulate it. The main action is the synchronous occlusion (coming together) of the upper and lower jaw, which crushes hard bodied prey [16]. This is very advantageous as the parrotfish lacks a stomach and hence there is no HCl in the digestive system to dissolve the bones [16]. This leads to a condition that maximum food processing must be carried out before the hindgut, without the help of acids. This is achieved by the pharyngeal mill. A high number of gill rakers packed tightly, filter the organic particles from the sediments [16]. *Scarus ghobban* completely exploits the resources of a selected area. Usually it starts with the most accessible region (side) of the substratum, and has the nearest bite just above it until it covers the flat top area, feeding almost perpendicularly to the substratum. This behavior could not be correlated with any morphological features.

The gape angle was found to be obtuse in *Ctenochaetus striatus*. This facilitates easy suction of a large amount of algae/detritus. There are numerous gill rakers packed tightly, filtering the organic particles from the sediments. Two feeding modes were observed. Individuals did not open mouth in the maximum gape angle at all the times. The common mode of feeding was a minimal mouth opening, almost brushing the substratum with the mouth. A less frequent mode was when the individuals opened their mouth in maximum gape angle and fed from the surface with significant “jerks” in the body. During the second type of feeding mode, however, the knobby dentiform structure which is right behind the bristle tooth seems to contact the surface, hence giving the chance for bioerosion [18]. The teeth pattern in this species is highly unique. The teeth are elongate with expanded incurved tips which bear only lateral denticulations. Review of previous studies revealed that this type of teeth is found only in the genus *Ctenochaetus* [19]. This peculiar dentition would permit a large degree of contact with the substratum when scraping, even over uneven surfaces, but would permit only a weak scraping action [2]. Also, the lower jaw of this species was found to be V shaped. This actually was found to be a hindrance for effectively cropping turf algae [2] and no advantages for this peculiar lower jaw has been proposed so far. The unique gizzard like gut morphology found in this species can be directly related to the detritus ingesting habit of the species. This stomach serves to break down the cell walls of cyanobacteria, bacteria, diatoms and filamentous red and green macroalgae that are ingested along with the sand [20].

The cluster analysis (Figure 6) clearly shows all the species belonging to the family Chaetodontidae in a single group. *Stegastes lividus* and *Ctenochaetus striatus* belong to a group. This could be due to their algal and detrital feeding. There are many dissimilarities in general between *Scarus ghobban* and *Abudefduf vaigiensis*. *A. vaigiensis* is a plankton feeder. It belongs to the family Pomacentridae. *S. ghobban* is a coral feeder. It belongs to the family Scaridae. However, *S. ghobban* is not grouped with coral feeders and *A. vaigiensis* is not grouped with *S. lividus*. This might be due to their unique characteristics.

There were many morphological patterns with no ecological

connections and vice versa. These may better be explained with more studies on the biomechanics of feeding, which were not conducted since it was beyond the scope of the study. Though it is acknowledged that the narrow study period and the limited number of individuals studied can highly limit the accuracy of these findings and their application in waters other than these islands, the current study has provided many new insights for which no correlations could be ascertained. Further investigations involving multidisciplinary approaches are needed to clarify these. The results of this study provide limited support for Motta's hypothesis [4]. It was found that both the food items (what the fishes feed on) and the feeding mechanism (how they feed) have a link to the morphology. It can be concluded, hence, that ecomorphological correlates are more interlinked than previously thought. It is acknowledged that the present work is limited in area and time and this may not be conclusive enough to prove or disprove a hypothesis. However, it also indicates that there is a chance for a deeper interlinkage since contradictory patterns have emerged even in a limited-period study. Though the exact interlinking mechanisms could not be elucidated, ecomorphological parameters seem to be influenced by hitherto unknown factors in the environment. The actual mechanism, feeding preference and the choice of food item are all governed by a multitude of factors which operate on a scale extremely diverse. Also, as indicated by [13], feeding specializations do not seem to always relate to morphological specialization. Specialization in feeding, especially in the case of corallivorous fishes seem to make the fish morphologically more generalized so as to reduce the trade-offs. Cluster analysis has indicated an alternative way of classifying these species based on trophic ecomorphological correlates. Further detailed studies, including experiments on captive species in aquariums, can throw more light on the feeding behaviour, morphological specializations and feeding mechanisms of these species.

## Conclusion

The ecomorphology of the feeding apparatus of 11 species of co-occurring reef fishes were studied. Many significant observations were obtained. Species with higher gape angle and increased protrusion use a scraping mode of feeding. Obligate corallivores exploit all the angles of feeding and their feeding frequency is high. The dental plates of the parrotfishes allow it to exploit maximum resources even though the gape angle is relatively low when compared to other scrapers. The gizzard of *Ctenochaetus striatus* characterises its detritivory. The maximum TuL/HL ratio of the *Chaetodon falcula* allows it to feed in the unique pattern.

There is a higher interlink between ecomorphological correlates than previously thought. The main thing which was observed in the study was that very little previous work was done in this field when compared to other subdivisions of Ichthyology. For example, no previous study has been made on the ecomorphological correlations of feeding angle (angle of mouth to the substratum when feeding). Some features could not be ecologically correlated at all due to this lacuna. Also, some correlations could only be hypothesized due to lack of previous research. There exists a wide lacuna in the previous research in the field of ecomorphology which limits the complete ecomorphological studies. More research is suggested.

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