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GILL RAKERS MORPHOMETRY AND FILTERING MECHNISM IN SOME MARINE TELEOSTS FROM RED SEA COASTS OF YEMEN

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ABSTRACT

Functional morphology of gill rakers in eight marine fish spaecies collected from Yemeni Red Sea coasts near Hodeida was investigated, aiming to study the possible role of gill raker in feeding stratigy. Considerable variation in the structure, number , length and width of gill rakers among the studied species were noticed. Shape of gill rakers in *Epinephalus areolatus*, *Euthynnus affinis*, *Carangoides malabaricus, Prestipomides filamentous* and *Lethrinus mahsena* showed typical characters of carnivorous fish of cylindrical rakers with hook-like ends and hard structure. Blade-like structure and narrowly triangular shapes represent omnivorous feeding habits of *Pomadasys maculatus* and *Aprion virescens*. Plankton filter feeder *Rastelliger kanagurta* possesses komb-like dense rakers.The total number of gill rakers varied significantly among the eight teleost species. *Rastelliger kanagurta* showed dense long and thin (0.05 – 0.18 mm) rakers, *Euthynnus affinis* and *Carangoides malabaricus* possess longer rakers reaching 4.5 and 7.5 mm.. On contrary carnivores such as *Lethrinus mahsena* and other predators possess thin (0.2-0.4), short (0.1 – 0.5 mm) and wide seperated rakers to enable predation of large prey. Efficiency of filteration area increased with decreasing the space between rakers in planktivores *Rastelliger kanagurta,* omnivores *Euthynnus affinis* and large sizes (> 55cm) carnivores *Carangoides malabaricus.* Both raker gap and filtering area increased linearily with increasing body length.

INTRODUCTION

Gill rakers in fish are known to have a leading role in determining the size of food particles eaten by fish. Their structure and numbers are closely related to feeding behaviour (Bentz, 1976; King & Macleod, 1976), and might change with the growth of fish (Mummert & Drenner, 1986). Fish with numerous, elongate rakers tend to be efficient filter feeders, whereas species with few short, undeveloped rakers are mainly omnivores and carnivores (Moodie, 1985). Among the pioneer studies relating gill rakers morphometry to feeding mechanisms, was the work of Gibson, (1988) which calculate the filteration area and the gap between rakers in a rational and scientific way.

Eight commercially important species from the Red Sea coasts of Yemen have been selected for the present investigation. They include:

Areolate grouper (Khulkhul) *Epinephalus areolatus* Fam. Serranidae)

Green jobfish (Antak) *Aprion virescens* (Fam. Lutianidae)

Mahsena emperor (Gahash) *Lethrinus mahsena* (Fam. Lethrinidae)

Indian Mackerel (Bagha) *Rastelliger kanagurta* (Fam. Scombridae)

(Sharwa) *Euthynnus affinis* (Fam. Scombridae)

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(Naqim) *Pomadasys maculatus* (Fam. Haemulidae)

(Bayadh) *Carangoides malabaricus* (Fam. Carangidae)

(Murjan or Asmosy) *Prestipomides filamentosus* (Fam. Lutjanidae)

Few reports have been published on food and feeding habits of the studied species in the Red Sea fisheries of Yemen (Morcos, and Varely, 1990; Heba, 1999; Salman *et al.,* 2003). In other part of the Red Sea, however, plenty of studies have been published on the food and feeding habits of similar fish species (Fauda & El-sayed, 1996; Bakhsh, 1996; Rizkalla, and Faltas, 1997). Apart from using gill rakers as a meristic classification characters, only few works have focused upon the relationship between gill rakers morphometry and feeding habits of local fish species in the Red Sea area (Abuzinadah, 1995).

The aim of the present work is to study the functional morphology of gill rakers in these species and to determine the efficiency of filtering mechanism in their feeding strategy.

MATERIALS & METHODS

Fish Samples:

A total of 160 fish specimens at the rate of 20 fish per species were collected from the commercial catch of Hodeidah fishing port during the period between March 2002 to June 2003. Consideration was taken to select various available sizes for each fish species at the time of sampling. Accordingly, fish captured by nets of different mesh sizes were used. Fish were transported to the laboratory in styropore boxes filled with ice. They were, then measured for standard length(SL) to the nearest mm, and weighed (W) to the nearest 0.1 g.

Sampling and Measuring Gill Rakers:

All gill rakers were dissected carefully from fresh fish, preserved in 5% neutral formalin and kept at 4 ˚C in a refrigerator for further examination . For each gill arch taken from the left side of the fish, the following measurements were made under a binocular microscope supplied with an occular micrometer:

1. Gill arch length (L) representing distance between first and last gill raker on each arch.
2. Number of gill rakers on each arch (N).
3. Average length of five gill rakers representing all parts on the arch.
4. An estimate of the average thickness at the base of three rakers (T) on different portions of each arch.

Calculations:

The average spacing (gap) between gill rakers (G) was calculated as :

G (in mm)= L-(N-1 x T)/(N-1) (Gibson, 1988)

The filtering area (F) which represents the area of open space between gill rakers through which water can flow was calculated as:

F (in mm^2)= ($\sum L - L_{max}$) x G (Gibson, 1988)

Where ∑L is the total length of all rakers on the arch or on all arches, and L_{max} is the length of the longest raker on the arch. Values of all arches were calculated to estimate total filteration area or average gap, taking into account the other side of the fish.

Statistical Analysis:

Regression equations were calculated for the relationships between body size and both filteration area and average gap as:

G or F = a x TL^b

Where TL is the total length of fish in mm, a and b are constants representing intercept and regression coefficient respectively. One-way analysis of variance was performed for statistical comparisions between species.

RESULTS & DISCUSSION

The Gill Arch Morphmetry

Morphological features of the gill arches of fish, especially their lengths and foldings are of great importance for the feeding studies. The studied species can be devided in two groups regarding their gill arch lengths (Table 1). Those possessing short gill arches include, *Lethrinus mahsena & Pomadasys argenteus.* Other fish species possess longer gill arches.

In all species, the first (outer) arch was longer than other inner arches (Fig.1). Simillar observations were recorded by Berry & Low (1970) and Lammens *et al*. (1986) in other species, and were related to respiratory (gasseous exchange) and osmoregulatory (ion exchange) functions (Hughes, 1984), as well as filter feeding mechanism (Wright *et al.,* 1983; Gibson, 1988). As seen from table (1) gill arches in all species are higher in length in big fish than small ones. There was almost a linear relationship between fish length and gill arch length in all species.

Gill Rakers Morphometry:

1. Rakers Structure :

Wide differences have been noted in the shape of gill rakers among the studied fish species. In khulkhul *Epinephalus areolatus,* The longer rakers are conical in shape with thick base, the smaller one tend to be flattened and triangular in shape. Margins were serrated by acute and triangle shape spinules. In the first arch, two rows of rakers were noticed (Fig 2-a). In Antak *Aprion virescens* they were fattened with narrow base. Each raker carry fine spinules covering all the internal surface. Anterior and posterior rows of rakers were detected in all arches. They varied in length in the first arch carrying long and short rakers respectively but became identical in the other arches (Fig 2-b).

Rakers in Gahash *Lethrinus mahsena* are short and pointed ones with fine needle spinules covering the raker tips. They were located in two rows at relatively wide seperating distance (Fig. 2-c). In *Lethrinus nebulosus* from Saudi coasts, a comparable shape was recorded by Abuzinadah (1995). Bagha *Rastelliger kanagurta* was characterized by its long dense rakers arranged in two rows in all arches and covered internally by fine spinules. Rakers of the first arch are longer reaching almost the length of the opposite filaments and project into oral cavity. They appeared in a feather-like shape due to comb like structure (Fig. 2-d).

Rakers of Sharwa *Euthynnus affinis* are found in two rows, with rakers of the anterior first arch are different in shape and longer than the rest flattened, wide based rakers in other arches. They are serrated internally with knife like protrusions or small spinules. In Naqim *Pomadasys maculatus* rakers looked like projecting pads or knobs. They were small, flattened rakers with wide base and small spinules turning into undeveloped ones in the inner arches.The rakers of Bayadh *Carangoides malabaricus* in the anterior row of the first arch are cylindrical pointed inward and covered internally by blade like triangular spinules. The rakers of the posterior row as well as the rakers of other arches were small, oval shape covered with fine needle like spinules. Rakers of Murjan *Prestipomides filamentosus* are small flattened with narrow base and numerous fine spinules. They were perpendicular on the mid line of the arch. Rakers of the first arch, however, are longer triangular in shape seperated by wide distance.

Table (1): Length of gill arches (mm) in two fish sizes

Fish species	SL (mm)	1st arch	4th arch
Epinephalus areolatus	180	53	40
Epinephalus areolatus	254	80	52
Aprion virescens	220	60	46
Aprion virescens	360	102	70
Lethrinus mahsena	135	18	13
Lethrinus mahsena	165	28	20
Rastelliger kanagurta	145	51	20
Rastelliger kanagurta	192	65	35
Euthynnus affinis	370	65	35
Euthynnus affinis	555	99	39
Pomadasys maculatus	*152*	*29*	*13*
Pomadasys maculatus	290	55	25
Carangoides malabaricus	182	42	22
Carangoides malabaricus	648	166	82
Prestipomides filamentous	207	51	25
Prestipomides filamentous	237	56	27

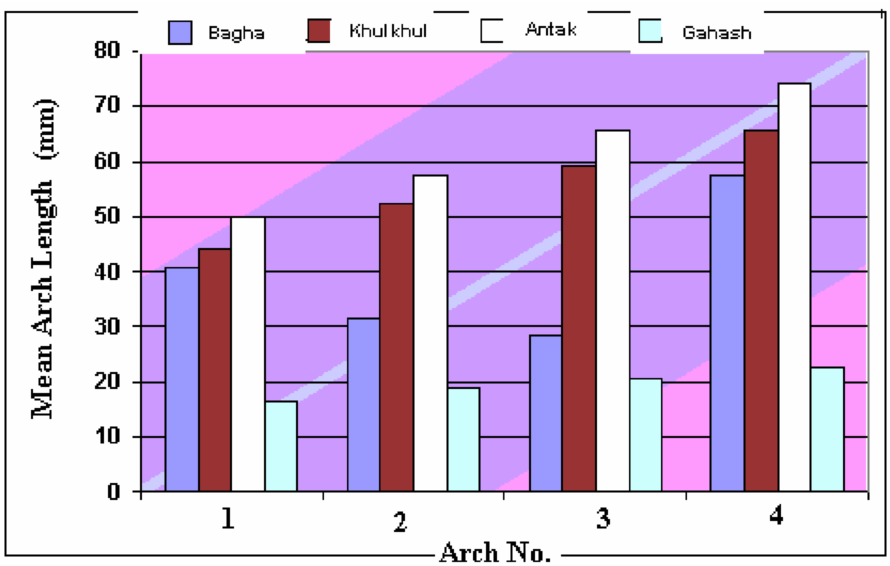


Figure (1). Gill arch length (mm) of four studied species.

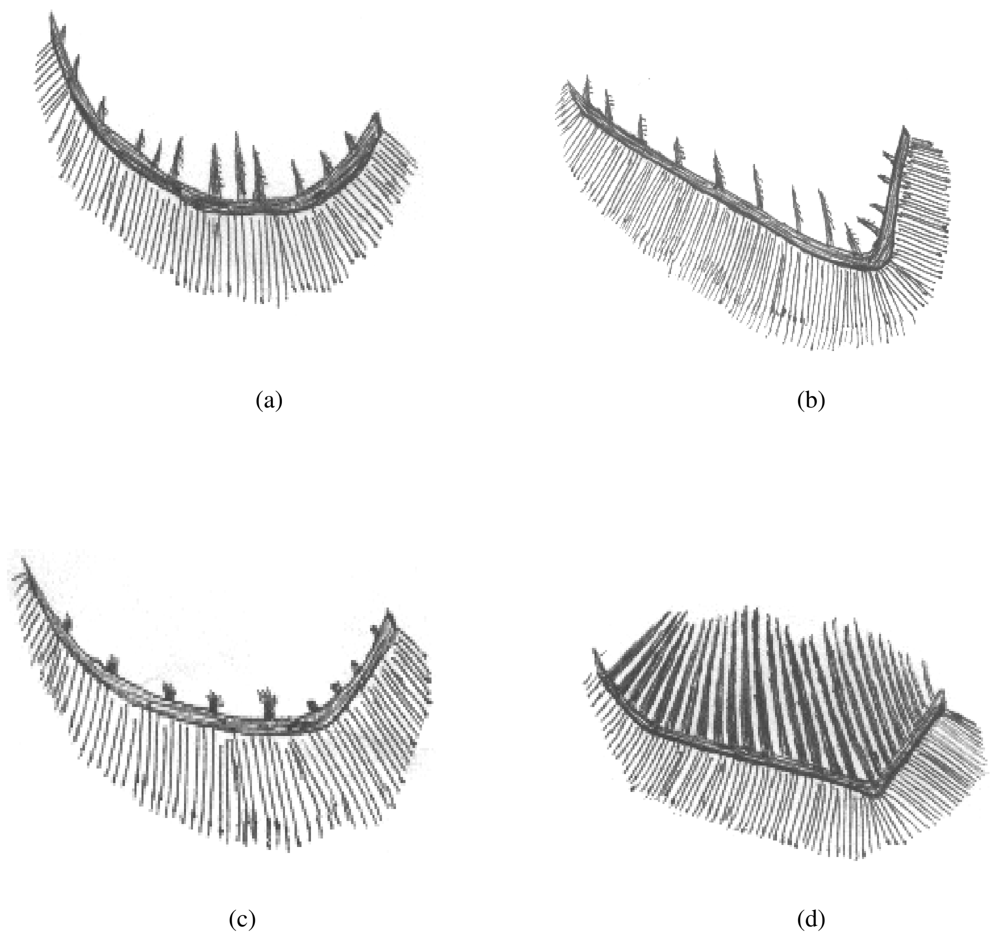


Figure (2): Morphology of gill arches and rakers in
a: *Epinephalus areolatus* b: *Aprion virescens*
c: *Lethrinus mahsena* d: *Rastelliger kanagurta*

Abuzinadah (1995) described the structures of rakers in some marine species of Saudi Arabia coast of Red Sea. Observations recorded in the present study are comparable to those given by Abuzinadah (1995) for *Epinephalus areolatus, Rastelliger kanagurta and Euthynnus affinis.* Typical characters of carnivorous fish of cylindrical rakers with hook-like ends and hard structure (Agrawal & Sharma, 1966) have been found in most of the studied species. They include *Epinephalus areolatus, Euthynnus affinis, Carangoides malabaricus, Prestipomides filamentous* and *Lethrinus mahsena.* Blade-like structure and narrow triangular shapes which represent omnivorous feeding habits were shown by some other species such as *Pomadasys maculatus* and *Aprion virescens*. .Plankton feeders species such as *Rastelliger kanagurta* possesses komb-like dense rakers, representing the typical filter feeding mechanism. Such characters have previously been reported in Herring species belonging to family Clupiedae (Gibson, 1988).

The functioning of the rakers, as described by Gibson (1988) depends mainly on the selectivity of the filtered particles present in the incoming water current. This can be affected by the extent to which the mouth was opened, folding of the gill arches and the orientation of the gill rakers. The effective mesh size of the filter might also be affected by the number and orientation of the teeth-like processes on the rakers which determine the size of prey (King & Macleod, 1976).

2. Raker Numbers :

The total number of gill rakers varied significantly ($P < 0.05$) among the eight teleost species. *Rastelliger kanagurta* stands first in having the largest number of rakers per row, while *Lethrinus mahsena* showed the lowest value (Table, 2). This may exhibits the presence or absence of efficient raker filter beside reflecting obvious differences in feeding habits. Number of gill rakers recorded for five species from Yemeni coasts of Red Sea were slightly higher than those recorded for the same species in Saudi Arabia (*Epinephalus areolatus*, 20-22; *Rastelliger kanagurta*, 30-32*; Euthynnus affinis,* 23-25) and two different species of similar genus *(Lethrinus mahsena*, 15 –17 *; Carangoides malabaricus,* 30-32).

In all species, distribution of rakers on the four arches were not equal, as the number was superior on the first arch. Furthermore, differences between number of posterior (external) and anterior (internal) rakers on the two rows of the same arch were not significant, being one or two rakers. Apart from *Rastelliger kanagurta*, no obvious relationship was found between number of raker and body length, despite the linear relationship with the length of gill arches. This mean that no increase in raker number as the fish grew up. On the contrary, distance between rakers might increase in bigger non plankton feeder fish. The total number and distribution of rakers could determine the filteration efficiency of the species (King & Macleod, 1976; Bentz, 1976; Gibson, 1988). This might explain the efficient filter noticed in *Rastelliger kanagurta* compared with other species.

3. Rakers Length:

Length of the raker is an important character in determining filtering area (Gibson, 1988: Salman *et al.,* 1993). Wide variation in the raker length was noticed among the studied species ($P < 0.01$) due to differences in feeding habits and sizes. Large sized fish such as *Euthynnus affinis* and *Carangoides malabaricus* possess longer rakers reaching 4.5 and 7.5 mm (Table 2). In those species, linear relationship between fish length and raker length was noted. On the other hand, fish like *Rastelliger kanagurta* showed long dense rakers especially on the first arch to increase the efficiency of particle retention in this plankton feeder species. Long but seperated rakers of *Prestipomides filamentous* may be modified to determine the size of prey eaten by this species which feed in the coral reef area. Similar conclusions have been reported by Wright *et al.* (1983). Small rakers (0.1 – 0.5 mm) recorded by the rest of species confirms the absence of a role for the rakers in retaining food items, which may be considered as a character of carnivores.

Longer rakers are usually located on the first outer arch which faces the respiratory water current, giving this arch major role in particles retention. Length of rakers decreased considerably in the inner arches. The positioning of the longest raker on the first arch has also been investigated. In most species, they occupied the middle region of the arch (ceratobranchial) approaching the oral chamber (Berry & Low, 1970). It has also been noted that rakers on the opposite arches are alternatively arranged to increase filtering efficiency (Shamsul-Hoda & Tsukahara, 1971).

4. Raker Width

Width of the raker is an important character which determines the average spacing and mesh size of the filter (Gibson, 1988: Salman *et al.,* 1993). Significant differences in rakers width ($P < 0.01$) was noted between studied species. Thin rakers (0.05-0.18 mm) are shown in the plankton feeder *Rastelliger kanagurta* (Table 2) to reduce spacing and increase filtering efficiency. On the contrary, carnivores such as *Lethrinus mahsena* possess thin (0.16 – 0.38) but seperated rakers to enable predation of large prey. Other predators exhibited similar characters with raker widths ranging between 0.2 – 0.4 mm (Table2). Thick rakers showed by *Carangoides malabaricus* and *Euthynnus affinis* (1.2 – 1.7 mm) could be attributed to the large size of fish samples.

5. Gill Raker Gap and Filteration Area

Variations among species :

Calculated values of average spacing (gill raker gap G) and total filteration area (F) for the examined species are shown in table (3). Wide variation was noticed between the eight species, but can be categorised statistically in groups where non-significant differences ($P > 0.05$) occurred. As far as raker gap is concerned, two groups can be recognized. Those with raker gap less than 1 mm include *Rastelliger kanagurta, Euthynnus affinis* and *Carangoides malabaricus*. This was associated either with plankton feeders Bagha (Abuzinadah (1995), or omnivores Naqim (Salman *et al,* 2003). These results are comparable to those of Salman *et al.* (1993) in herbivores and omnivores species. They were significantly different ($P < 0.05$) from the values of the second group, which include the rest of species in which raker gap exceeded the value of 1 mm (Table 3). The relatively large raker gap is associated with carnivorous feeding habits, since these values are comparable to the piscivorous Hake (Bentz, 1976).

Values of filteration area followed, for some extent, those of the gap in contrary terms, i.e they increased with decreasing the space between rakers. Such trend was obvious in the plankton filter feeder *Rastelliger kanagurta* and the omnivore *Euthynnus affinis* (Table 3). This could be attributed to the close accumulation of numerous number of thick rakers leading to an efficient filter with narrow mesh size (Gibson, 1988; Salman *et al,* 1993). Such character is typical in planktivorous species like Pilchard and Anchovy (King & Macleod, 1976). The second group with significantly ($P > 0.01$) large filtering area include fish with large sizes (> 55cm) such as *Carangoides malabaricus* and *Euthynnus affinis.* The third group which include the rest of species possess small filtering area indicating carnivorous feeding habits suitable for macro-organisms.

Variations with Body Size :

As seen from the data of table (3) and regression equations illustrated in figure (3), both raker gap and filtering area increased linearly with increasing body length. Such relationships have been previously noted in several studies (Gross & Anderson, 1984; Croeder, 1986; Lammens *et al.,* 1986). The increase in gill raker gap could be attributed to the increase of gill arch length while the number of rakers remain nearly unchanged , as seen in most of the examined fishes. Similar observations have been recorded in the Herring *Clupea harengus* (Gibson, 1988). Changes in raker numbers and width as the fish grew up may lead to a change in the feeding behaviour (June & Carlson, 1971).

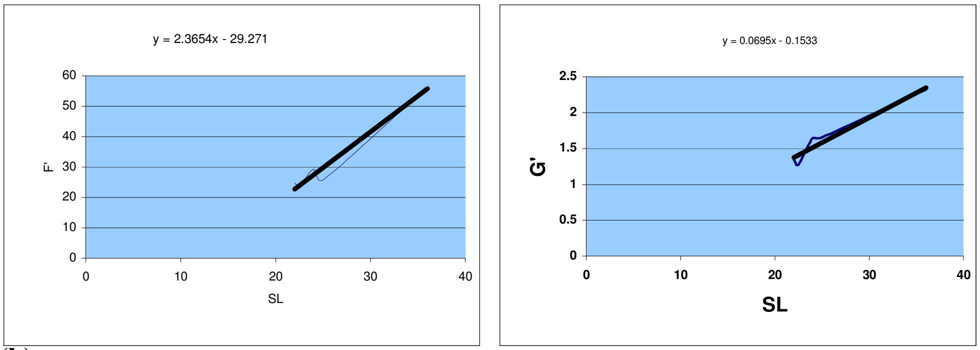
The rate of increase as seen by the slopes of the equations was different between the studied species (Fig. 3). This could be attributed to differences in feeding behaviour throughout the life span of each species. Some carnivores need to increase the gap as the fish grew bigger to be able to eat larger preys. On the other hand, fish depend on filtering to feed need to increase the efficiency of that filter to face their nutritional requirements by increasing the filtering area Lammens *et al.* (1986).

Table (2): Number of gill rakers per row in the studied species

Fish species	Standard Length (mm)	No. of Rakers per Row	Raker length (mm)	Raker width (mm)
Epinephalus areolatus	180-254	30 – 31	0.56-0.67	0.25-0.29
Aprion virescens	220-360	32 – 35	0.53-0.76	0.25-0.28
Lethrinus mahsena	135-165	18 – 19	0.18-0.27	0.16-0.34
Rastelliger kanagurta	145 -192	85 – 94	0.75-1.17	0.05-0.18
Euthynnus affinis	370 -555	27 – 30	4.30-7.36	1.42-1.78
Pomadasys maculatus	152- 290	52 - 58	0.53-1.14	0.24-0.43
Carangoides malabaricus	182-648	22 – 25	2.50-4.50	1.30-2.50
Prestipomides filamentous	207-237	18 – 19	1.43-2.41	1.22-1.37

Table (3): Observed and calculated (in brackets) gap (G) and filteration (F)

Fish species	SLmm	G (mm)	F (mm^2)
Epinephalus areolatus	180	1.387 (1.241)	25.56 (28.652)
Epinephalus areolatus	254	2.073 (1.851)	34.702 (43.342)
Aprion virescens	220	1.344 (1.376)	24.703 (22.768)
Aprion virescens	360	2.322 (2.349)	56.522 (55.883)
Lethrinus mahsena	135	0.507 (0.568)	2.118 (2.563)
Lethrinus mahsena	165	1.169 (1.135)	3.552 (4.350)
Rastelliger kanagurta	145	0.339 (0.255)	24.939 (22.749)
Rastelliger kanagurta	192	0.369 (0.342)	44.725 (42.152)
Euthynnus affinis	365	0.692 (0.711)	49.441 (41.92)
Euthynnus affinis	555	0801 (0.875)	95.252 (89.42)
Pomadasys maculatus	152	0.135 (0.146)	3.471 (4.423)
Pomadasys maculatus	290	0.352 (0.399)	18.852 (20.014)
Carangoides malabaricus	182	0.452 (0.828)	6.253 (9.763)
Carangoides malabaricus	648	3.210 (3.195)	80.152 (79.194)
Prestipomides filamentous	207	1.145 (1.525)	39.761 (37.605)
Prestipomides filamentous	237	0.993 (1.189)	18.473 (16.215)



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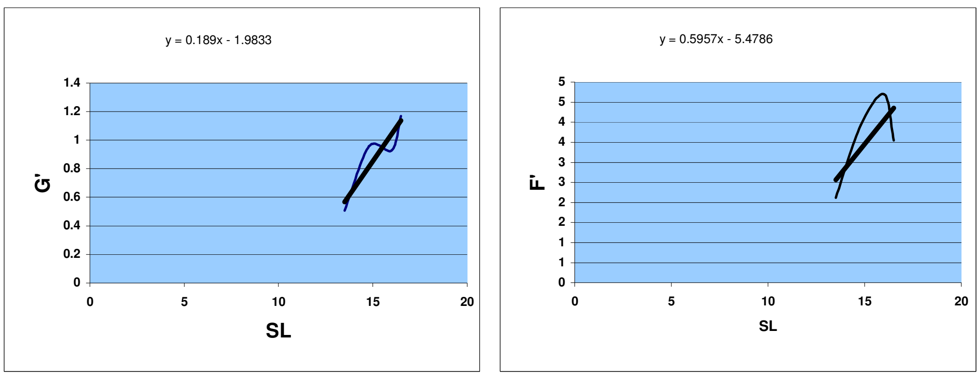

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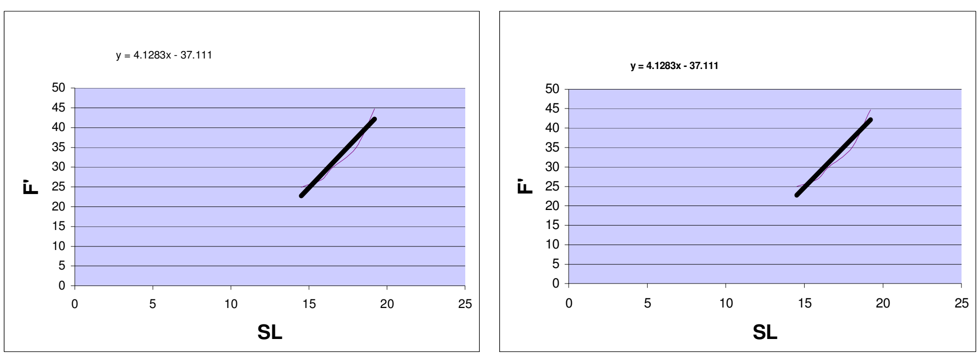

(d)

Figure (3): Linear relationship between raker gap (G in mm) and filteration area (F in mm^2) with standard length (SL in cm.) in:
a: *Epinephalus areolatus* b: *Aprion virescens*
c: *Lethrinus mahsena* d: *Rastelliger kanagurta*

RRFERENCES

Abuzinadah, O.A. (1995). Gill raker morphology in some Red Sea fish of different feeding preferences. J. KAU: Mar. Sci. 6 : 193-122.

Agrawal, V. P. and Sharma, U. (1986) Morpho-histological studies of the digestive tract of *Mystis vitatus* (Bloch). Proc. Nat. Acad. Sci., B36: 441-456.

Bakhsh, A.A. (1996). The biology of Thread Bream, *Nemipterus japonicu* (Bloch) from the Jizan Region of the Red Sea. J. KAU: Mar. Sci. 7: 179 – 190.

Bentz, K.L.M. (1976). Gill arch morphology of the Cape Hakes *Merluccius capensis* Cast and *M. Paradoxus* Franca. Fish Bull. S. Afr. 8:17-22.

Berry, F.Y. and Low, M.P. (1970) Comparative studies on some aspects of the morphology and history of *Ctenopharyangedon idellus*, *Aristachyths noblis* and their hyprid (Cyprinidae).Copeia,4: 708-726.

Crowder, L.B. (1986) Ecological and morphological shift in Lake Michigan fishes. Env. Biol. Fish, 16 (1): 147 – 157.

Fauda, M.M. & El-sayed, A.M. (1996) Distribution and feeding habits of two Sergeon fish *Zebrasoma xanthurum* and *Ctenochaetus striatusin* the Gulf of Aqaba, Red Sea. J. KAU: Mar. Sci. 7: 233 - 244.

Gibson, R.N. (1988) Development, morphometry and particle retention capability of the gill rakers in the herring *Clupea harengus* L. J. Fish Biol., 32:949-962.

Gross, H.P. and Anderson, J.M. (1984) Geographic variation in the gill rakerand diet of the Eurepeon three spine stickle backs.*Gasterosteus aculeatus* . Copeia , 1 : 87 – 97.

Heba, H.M. (1999) Identification of fish nursery grounds near Al-Luhaia coats (Red Sea coast of Yemen). UNDP & EPC Report, 53 pp

June, F.C. and Carlson, F.T. (1971) Food of Atlantic menhaden *Brevoortia tyrannus* in relationto metamorphosis. Fishery Bull. Fish Wild Serv. U.S. 68 493 – 512.

Hughes, G. M. (1984) General anatomy of the gills. In: Fish Physiology, Vol. 10, Hoar, M. & Randall, D. J. (eds.), Academic Press, London, pp. 1 - 72.

King, D.P.F. and Macleod, P.R. 9 1976) Comparision of the food and filtering mechanism of Pilchard *Sadinops ocellata* and Anchovy *Engraulis capersis* of South-West Africa. Sea Fish Branch Invest. Rep. No. 111, 29 pp.

Lammens, E.R., Geurse, and McGilaury, P.T. (1986) Shift feeding effeciency and coexistance of Bream *Abramis brama*, Roch *Rutilus rutilus* and White Bream *Blicca bioerkna* in hypertrophic lakes. In: Interaction between fishes and the structure of fish communities in dutch shallow eutrophic lakes.pp. 50 – 64.

Moodie, G.E.E. (1985) Gill raker variation and the feeding niche of some temprate and tropical freshwater fishes. Env. Biol. Fish, 13(1):71–76.

Morcos, S.M. and Varely, Y. A. (1990) . Red Sea, Gulf of Eden and Suez Canal : A bibliography of oceanographic and marine environmental research . UNESCO, Paris. 198 pp.

Mummert, J.R. and Drenner, R. W. (1986) Effect of size on filtering efficiency and selective particle ingestion of filter feeding clupeid. Trans. Am. Fish. Soc. 115: 522 – 528.

Rizkalla, S. and Faltas, S.N. (1997) Feeding habit of chub mackerel *(Scomber japonicus)* in Egyptian Mediterranean waters. J.K.A.U. Mar. Sci. 8:127-136.

Shamsul-Hoda, S.M. and Tsukuhara, H. (1971) Studies on the development and relative growth in the carp *Cyprinus carpio* L. J. Fac. Agr. Kyusha Univ., 16 (4): 387 – 511.

Salman, N.A., Ahmed, A.A. and Al-Rudainy A.J. (1993) Gill rakers morphometry and filtering mechanism in four cyprinid species. Marina Mesopotamica, 8 (1): 25 – 34.

Salman, N.A., Heba, H.M.A. and Al-Mahdawi, G.J. (2003) Feeding ecolgy of Naqim *Pomadasys maculatus* from Red Sea Coasts of Yemen. J. KAU Mar. Sci. Vol. 13 (in press).

Wright, D.I. Obrine, W. J. and Luecke, C. (1983) A new estimate of zooplankton retention by gill rakers and ts ecological significance. Trans. Am. Fish. Soc., 112 : 638 – 646.

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