

## Ontogenetic dietary shifts and morphological correlates in striped mullet, *Mugil cephalus*

Bradley T. Eggold\* & Philip J. Motta

*Department of Biology, University of South Florida, Tampa, FL 33620, U.S.A.*

\* *Present address: Wisconsin Department of Natural Resources, P.O. Box 408, Plymouth, Wisconsin 53073, U.S.A.*

Received 3. 10. 1990

Accepted 5. 4. 1991

**Key words:** Fish, Feeding, Cluster analysis, Gill rakers

### Synopsis

Ontogenetic dietary shifts are well studied in fishes. However, these shifts are rarely correlated with habitat and morphology. This study investigates: (1) ontogenetic dietary changes in mullet; and if dietary shifts do occur (2) whether they are correlated with feeding location, feeding behavior and/or feeding morphology. Stomach contents from eight size classes, each with 25 individuals, were analyzed using a gravimetric sieve fractionation procedure, Czechanowski's Quantitative Index and cluster analysis. Core samples (5 mm deep) were also analyzed in the same manner. Morphological characters were measured to detect differences among the size classes. Cluster analysis showed three distinct trophic units for *Mugil cephalus* in Cross Bayou: (1) 20.0 mm standard length – 30.0 mm SL; (2) 30.0 mm SL – 40.0 mm SL; and (3) 40.0 mm SL – > 100 mm SL. Comparison of the gut contents to the sediment contents for each size class showed an increase in similarity as the fish grew. Mullet gut contents from fish 20–25 mm SL were only 45% similar based on the weights of the prey items to the sediment subsample prey items, while stomach contents from fish > 100 mm SL were 84% similar to the sediment subsample contents. Gill raker length and interraker spacing of four gill arches were allometric with respect to standard length. Prey particle size within size classes appeared to be more correlated with feeding behavior than gill interraker spacing because smaller particles than predicted by the interraker spacing were ingested. It is suggested that smaller fish may be browsing more selectively than larger fish which graze.

### Introduction

Ecomorphological studies of fishes are important for our understanding of fish feeding. Several contrasting hypotheses concerning the role of morphology in regulating fish diets have emerged. Chao & Musick (1977) found that dietary differences among sciaenid species are probably due to differences in feeding behavior imposed upon them by adaptive morphological limitations such as the position, size and protrusibility of the mouth, the

type of teeth and gill raker structure. Moyle & Senanayake (1984) found that morphological differences in the mouth position and size, barbels and gill raker structures in Sri Lankan fishes were associated with dietary and/or microhabitat specializations. In contrast, Liem (1980) analyzed cichlid feeding repertoires and found that a highly specialized rock scraper *Petrotilapia tridentiger* possessed eight distinct feeding methods. Its feeding behavior was not limited by morphological limitations but rather expanded by alternative feeding

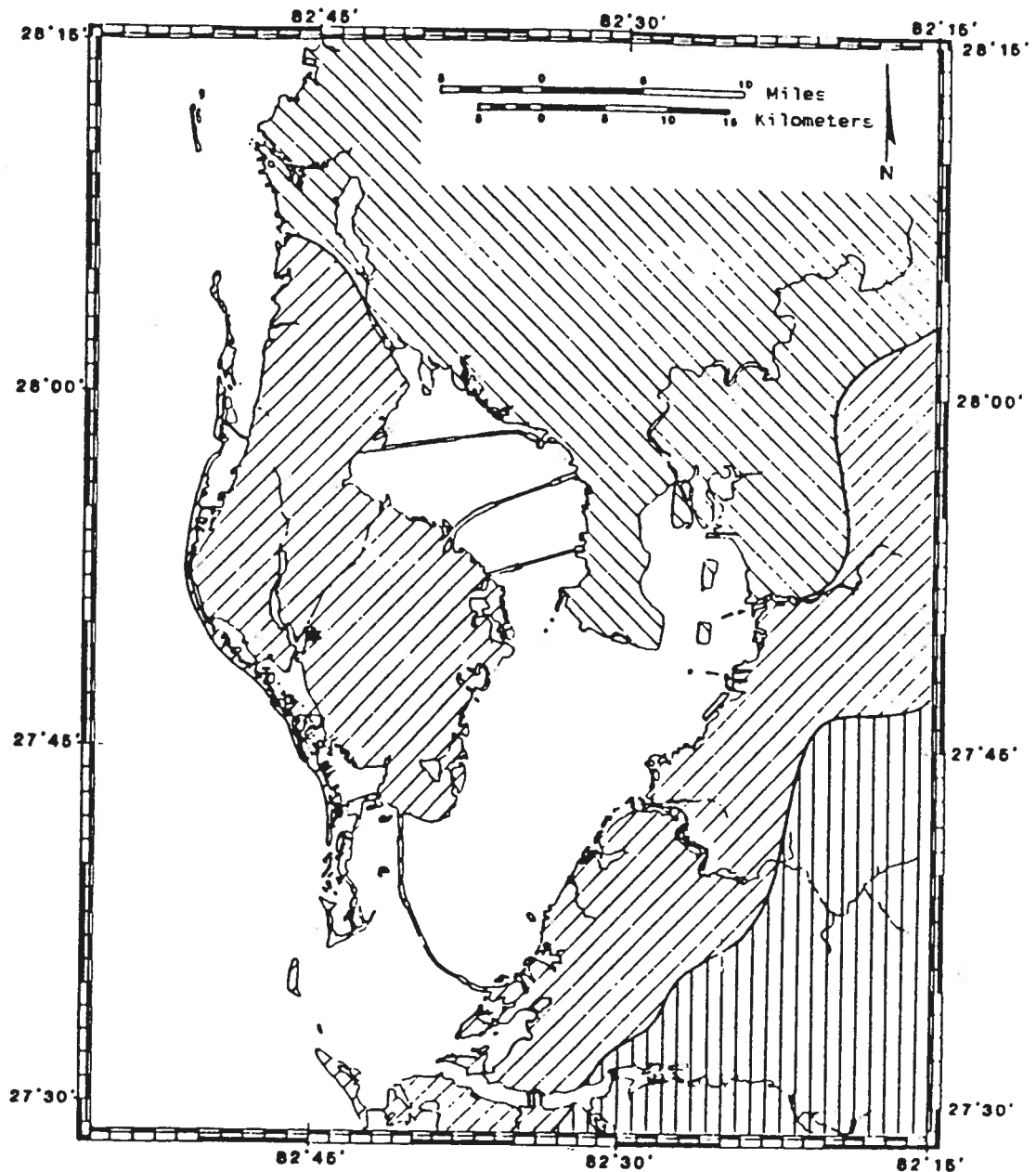


Fig. 1. Study site near St. Petersburg, Florida. Asterisk denotes study site location.

pathways. Also, Gatz (1979) suggested that for 44 species of stream fishes, size of prey was the most important component in separating the diets, and vertical position of the prey was the second most important component. Methodological differences among the studies may be one reason the role of

morphology in regulating fish diets has been both supported and rejected.

Dietary choice in fishes has not only been correlated with morphological features but also with ontogeny and availability of suitable food types. Both ontogeny (Huh & Kitting 1985, Keast 1985) and availability of suitable food types, which are

influenced by environmental factors, such as seasonality effects (Keast & Welsh 1968, Bell et al. 1978a, b, Harmelin-Vivien et al. 1989), time of day (Hobson 1974, Marais & Erasmus 1977, Bison 1978, Robertson & Howard 1978), locality (Feller & Kaczynski 1975, Love & Ebeling 1978) and tidal fluctuations (Odum 1970, Marais & Erasmus 1977), if confounded, can influence the conclusions of the studies. To eliminate these potential problems, studies should encompass as many of these factors as possible in their experimental design or eliminate them by holding them constant throughout the study.

Many studies quantify diet according to feeding guilds (Smith 1978), which are often based on taxonomic criteria (Chao & Musick 1977), location of feeding (Harmelin-Vivien & Bouchon-Navaro 1983), or type of feeding (Hiatt & Strasburg 1960, Hobson 1968). Examples of these guilds include molluscivores, benthic feeders, or suction feeders respectively. However, these categories may be useful in ontogenetic studies but must be applied to a specific size class. Livingston & Stoner (1984) suggested the use of 'ontogenetic trophic units'. These units are ontogenetic intervals in diet as revealed by studies of diet and cluster analysis for individual species. Those groups of individuals from one or many species found to consume the same prey items (80% similar) are clustered into an ontogenetic trophic unit. In this manner, groups of fish analyzed by size class can be clustered into an ontogenetic trophic unit. The same species may occupy several trophic units depending on its ontogenetic progression in diet.

The majority of studies (Hiatt 1944, Pillay 1953, Ebeling 1957, Odum 1968, Hickling 1970, Blaber 1976, Marais 1980, Minckley 1982, Das & Chowdhury 1983, Romer & McLachlan 1986) on different species of mullet (i.e. *Mugil cephalus*, *M. curema*, *Liza tricuspidens*, *L. ramada*, *L. aurata*, *L. richardsoni*, *L. subviridis*, *Valumugil speigleri* and *Xenomugil* sp.) have shown that the adult diet (fish > 30 mm SL) consists of detritus, diatoms, sand grains, crustaceans, algae and decomposed organic matter. The studies on juvenile mullet (fish < 30 mm SL) are less extensive (Ebeling 1957, Blaber & Whitfield 1977, De Silva 1980, Loftus et al. 1983).

Juveniles are mainly carnivorous, eating plankton, microcrustaceans, shrimp larvae and zooplankton.

The above studies suggest that *Mugil cephalus* undergoes an ontogenetic shift in its diet. However, this shift has rarely been correlated to the feeding location (i.e. seagrass beds, sandy substrate) in which each size class is found or to ontogenetic changes in feeding morphology or behavior. Wood (1953) & Odum (1968) both measured and compared the particle size in the digestive tract of mullet with that of the habitat sediment. *Mugil cephalus* selected smaller particles over larger particles in the sediment. Therefore, this preference could be correlated with (a) the availability of suitable food types found in the sediments or (b) selectivity for the prey items due to morphological parameters such as the size of the mouth, length of the gill rakers, interraker distances and the length of the intestines. Several investigators (Odum 1968, Grant & Spain 1975, Wijeyaratne & Costa 1986, 1987) have related morphology to diet but rarely has feeding morphology been correlated with ontogenetic dietary changes in mullet. The purpose of this study is to investigate ontogenetic dietary shifts in a population of striped mullet, *Mugil cephalus*, in Cross Bayou, Florida and determine if dietary differences are correlated with changes in feeding location, feeding behavior or feeding morphology.

## Materials and methods

### Sampling

The striped mullet *Mugil cephalus* was studied in Pinellas County east of Cross Bayou (82°45'W, 27°50'N; T 30S; R 15E; Township 36, Pinellas County, St. Petersburg, Florida, U.S.A.) (Fig. 1). The tidal area was approximately 60 × 300 m with a mean water depth at low tide of 0.5 m. The sediment consists of very fine sand and mud approximately 15 cm in depth. The tidal area had an average salinity of 30 ppt.

### Ontogenetic dietary shift

To detect ontogenetic dietary shifts, juveniles of *M. cephalus* were sampled repetitively until 25 individuals were obtained for a given size class. Stomach contents were analyzed as to percent composition using a modified gravimetric sieve fractionation procedure of Carr & Adams (1972). Czechanowski's Quantitative Index was calculated based on the weights of the prey items and used in cluster analysis for detection of trophic units.

Individuals of *Mugil cephalus* were collected from March 1989 to May 1990 in the morning hours between sunrise and noon and during times of low tide to eliminate variation in feeding and to aid in the capture of the fish. Sampling continued on a bimonthly schedule during low tide (see below) until each size class was represented by 25 individuals.

Large *Mugil cephalus* (> 40 mm SL) were collected with a bag nylon seine (15 mm × 25 m). Smaller mullet (< 40 mm SL) were collected with a mullet cast net (2 m diameter × 15 mm) and a large bagless seine (5 mm × 30 m).

The fish were grouped into eight size classes: 20–25 mm SL (size class 1), 25–30 mm SL (2), 30–35 mm SL (3), 35–40 mm SL (4), 40–50 mm SL (5), 50–70 mm SL (6), 70–100 mm SL (7) and > 100 mm SL (8). To achieve 90% food item representation, twenty-five individuals from each size class were used in the analysis. Dates of collection, from April 1989 to May 1990, are indicated in Figure 8. All fish in a size class were collected from the same location about 20 m from each other. Fish were placed in 10% buffered formalin/rose bengal solution after capture and later stored in 70% buffered ethyl alcohol for further examination.

All stomach contents from the same size class were pooled together and analyzed as to percent composition using the modified gravimetric sieve fractionation procedure of Carr & Adams (1972). This procedure was followed except: (1) The petri dish was gridded at 10 lines per 10 mm; and (2) Organic matter from each sieve fraction was teased apart and analyzed on a gridded slide (10 lines per 10 mm). Frequency of occurrence was taken according to the procedure of Carr & Adams (1972).

Similarity of the feeding habits among size classes was measured using Czechanowski's Quantitative Index (C.Q.I.):

$$\frac{2 \sum \min(x_{ij}, x_{kj})}{\sum (x_{ij} + x_{kj})}$$

where  $x_{ij}$  was the food item percentage for the  $i$ th size class and  $j$ th food item and  $x_{kj}$  was the food item percentage for the  $k$ th size class and  $j$ th food item. This method has been used extensively in describing ontogenetic variation in diets of fishes and invertebrates (Field & McFarlane 1968, Dauer & Simon 1975, Livingston 1980, Stoner 1980, Livingston & Stoner 1984). This method determines whether the diets of all size classes were similar (i.e. a priori judged as 80% similar, sensu Livingston 1982).

Cluster analysis using Czechanowski's Quantitative Index was used to measure the similarity of feeding habits between size classes, revealing ontogenetic feeding relationships among the size classes. In this study, a cluster was interpreted as a distinct ontogenetic dietary progression or trophic unit (Livingston & Stoner 1984).

### Feeding location

To determine if ontogenetic dietary shifts are correlated with feeding location, sediment cores were taken on the days of fish capture. Prey items in the sediment cores were analyzed as to percent composition using the modified gravimetric sieve fractionation procedure outlined above. Czechanowski's Quantitative Index was calculated based on the weights of the prey items found in the sediment and used in cluster analysis. Similarly, the stomach contents and sediment contents were analyzed together using C.Q.I. and cluster analysis.

Sediment sampling was conducted at the same time of fish capture and included two replicates for each date of fish capture. The sediment was sampled with a core sampler (5 cm<sup>2</sup>) to a depth of 5 cm and preserved in 10% buffered formalin/rose bengal solution. It was found using C.Q.I. and cluster

analysis that two replicates were sufficient to accurately describe the prey items at major taxon levels in the sediment. These replicates were haphazardly taken near the site of fish capture with at least one meter between replicates. These replicates are designated 'a' and 'b' (i.e. April 7a, April 7b).

A pre-analysis experiment on *Mugil cephalus* was done to determine the depth of feeding. Sediment from the sampling site was placed in a 25 l aquarium and allowed to settle. Three mullet of 40 mm, 105 mm and 110 mm SL were placed separately into the aquarium and allowed to feed on the benthos for two days. Based on this experiment (see Results), the sediment samples taken at the study site were allowed to settle for one day and a subsample was taken from the upper 5.0 mm. Each of the subsamples (replicates) were then analyzed separately using the gravimetric sieve fractionation procedure.

Cluster analysis using Czechanowski's Quantitative Index was first used to compare all replicates (2 replicates per sampling day) to each other. Secondly, it was used to compare the similarity between the prey items found in the stomach contents and in the sediment subsamples. For example, fish 20–25 mm SL and 25–30 mm SL were captured on April 7, 1989. The prey items in the stomach contents were compared to the prey items in the two subsamples of two replicate sediment cores taken on April 7, 1989.

#### *Morphological measurements*

To determine if ontogenetic dietary shifts are correlated with feeding morphology each individual of each size class was measured for standard length, total length, mouth size (gape height and gape width), intestinal length, wet weight of intestine and wet weight of the fish. In addition, each of the four gill arches was measured for interraker spacing and gill raker length on each specimen. Interspine spacing was measured on the first arch of five fish from each size class. Regression analysis was used to test the null hypothesis that these parameters do not differ among size classes.

The relationship between gape height and gape width to standard length for all 25 individuals of each size class was examined. Gape width was taken at the widest point on the inside of the open mouth and gape height was taken at the highest point after opening. Measurements were taken to the nearest tenth of a millimeter with Vernier calipers.

To test for differences in potential prey retention capabilities, measurements were taken on the largest distance between five gill rakers and length of the five longest gill rakers on each of the four gill arches from the left side of the fish. Typically these measurements were taken at the border between the ceratobranchial and epibranchial (Fig. 2, 3). Interspine distances between five spines on the first arch from five individuals per size class were taken at the same location as the previous measurements. The distance measured was the largest distance between adjacent spines (Fig. 3). Measurements for each fish of each size class were taken with a JENA GF-P dissecting microscope fitted with an ocular micrometer.

The intestines less the stomach were dissected and uncoiled from the mullets from each size class and measured to the nearest millimeter. Measurements including total length and standard length followed Hubbs & Lagler (1958).

Regression analysis was used to test the null hypothesis that the gape height, gape width, intestinal length, gill raker length and interraker spacing do not differ among size classes. The data were multiplied by a constant to eliminate decimals, log transformed and plotted against the log of standard length.

Specimens as well as their alimentary canal from stomach to rectum (including gut contents) were weighed in order to obtain for each size class, mean weight of fish ( $W$ ) and mean weight of guts ( $I$ ). The global repletion index  $R = I/W \cdot 100$  was then calculated (Harmelin-Vivien & Bouchon-Navaro 1983).

Absolute interraker distance, interspine distance, mouth width, mouth height and intestinal length for each size class were obtained from existing data. These measurements were compared to

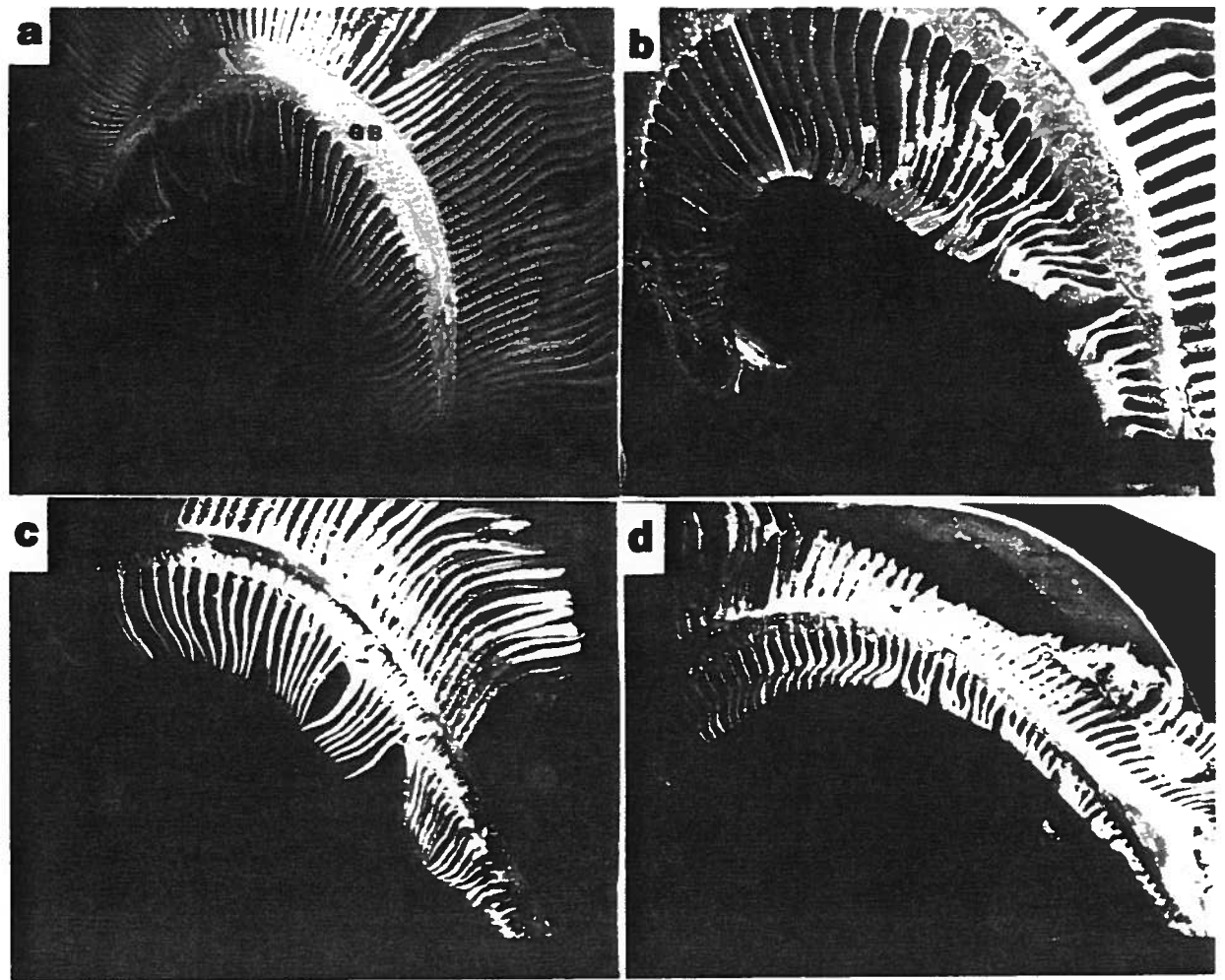


Fig. 2. Scanning electron micrographs of the four gill arches from a 100 mm SL *Mugil cephalus*: a-first gill arch; b-second gill arch showing measurement of the length of the gill rakers; c-third gill arch; d-fourth gill arch. GD = gill bar; GF = gill filament; GR = gill raker; l = length of gill raker; SUP = superior area of the gill arch.

the cumulative percent by sieve size of prey item weights in the stomach contents. Correlations between the size of the particles found in the stomach contents and these morphological parameters were analyzed.

Storage, retrieval and analysis of data were performed using SAS and SYSTAT Inc. All cluster analyses were run using Czechanowski's Quantitative Index. BMDP1M, using average linkage, provided the similarity coefficients to construct the cluster diagrams.

#### *SEM preparation*

The four gill arches from the left side of freshly killed mullet were fixed for 24 hours in 2.5% glutaraldehyde/2.0% formaldehyde buffered in seawater, critical point dried and coated with gold/palladium. A Zeiss Novascan 30 scanning electron microscope was used to examine the gill arches.

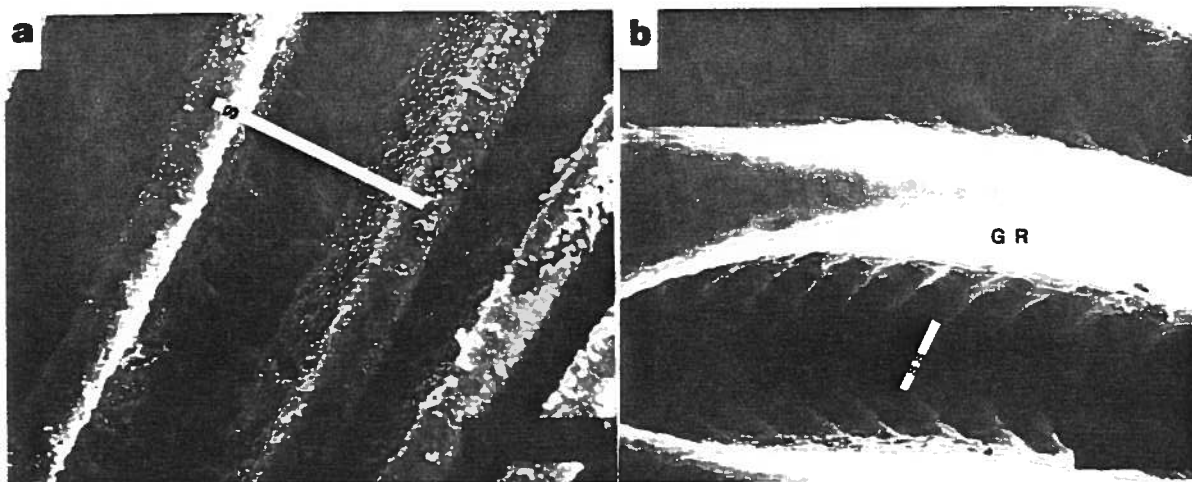


Fig. 3. Scanning electron micrographs of gill rakers: a-first gill arch showing measurement of the interraker distance between adjacent gill rakers; b-third gill arch showing measurement of the interspine distance between adjacent spines. GR = gill rakers; s = interraker spacing; SP = spines; ss = interspine spacing.

## Results

### Stomach contents

In the stomach of *Mugil cephalus*, diatoms, desmids, green algae, crustaceans, nematodes, invertebrate eggs, polychaetes, foraminiferans, siliceous spines, detritus and sand are present (Table 1). At the level of identification used here, the number of different food items is greater (13) for the largest size class (> 100 mm SL) than for the smaller fish (< 40 mm SL, mean prey categories for the four size classes = 10.5). This is due to the increase in the number of diatom species and invertebrate eggs found in fish > 100 mm SL.

*Mugil cephalus* undergoes an ontogenetic shift in diet (Fig. 4, 5). Early growth stages (20–25 mm and 25–30 mm SL) are characterized by small amounts of sand, large amounts of organic matter, algae and the diatom, *Diploneis* sp.. Sand accounts for 13.0% and 17.6% of the stomach contents for fish 20–25 mm SL and 25–30 mm SL, respectively. Organic matter, defined as spheroid particles that cannot be identified, contributes 27.0% and 26.1% and *Diploneis* sp. accounts for 24.6% and 23.7% of the diet of fish 20–25 mm SL and 25–30 mm SL, respectively. Algae contributes 18.11% and 12.5% of the diet of fish 20–25 mm SL and 25–30 mm SL, respec-

tively. Overall, these size classes have a less variable diet than the larger size classes (Fig. 4). With growth (30–35 mm and 35–40 mm SL), the striped mullet includes more sand and less organic matter and *Diploneis* sp. in its diet. Sand accounts for 25% of the stomach contents of fish 30–35 mm SL and 27% of the contents of fish 35–40 mm SL. The diatom, *Diploneis* sp. contributes 16.5% and 16.6% of the stomach contents for fish 30–35 mm SL and 35–40 mm SL, respectively. Organic matter decreases to 19% for both size classes. Further growth (40–50 mm, 50–70 mm, 70–100 mm and > 100 mm SL), is accompanied by the addition of more sand particles and a wider variety of diatom genera as well as other food particles. Sand accounts for approximately 57% of the stomach contents in each of the remaining size classes. The amount of organic matter decreases to 20%, 13.8%, 10.8% and 13.8%. *Diploneis* sp. becomes less important but the other diatom genera increase in the percent weight of the stomach contents. The combined addition of sand and organic matter contributes greatly to the ontogenetic progression of the diet.

Three ontogenetic trophic units are revealed through clustering (Fig. 5). The first unit consists of fish 20–25 mm SL and 25–30 mm SL which are 88% similar in diet. Mullet 30–35 mm SL and 35–40 mm



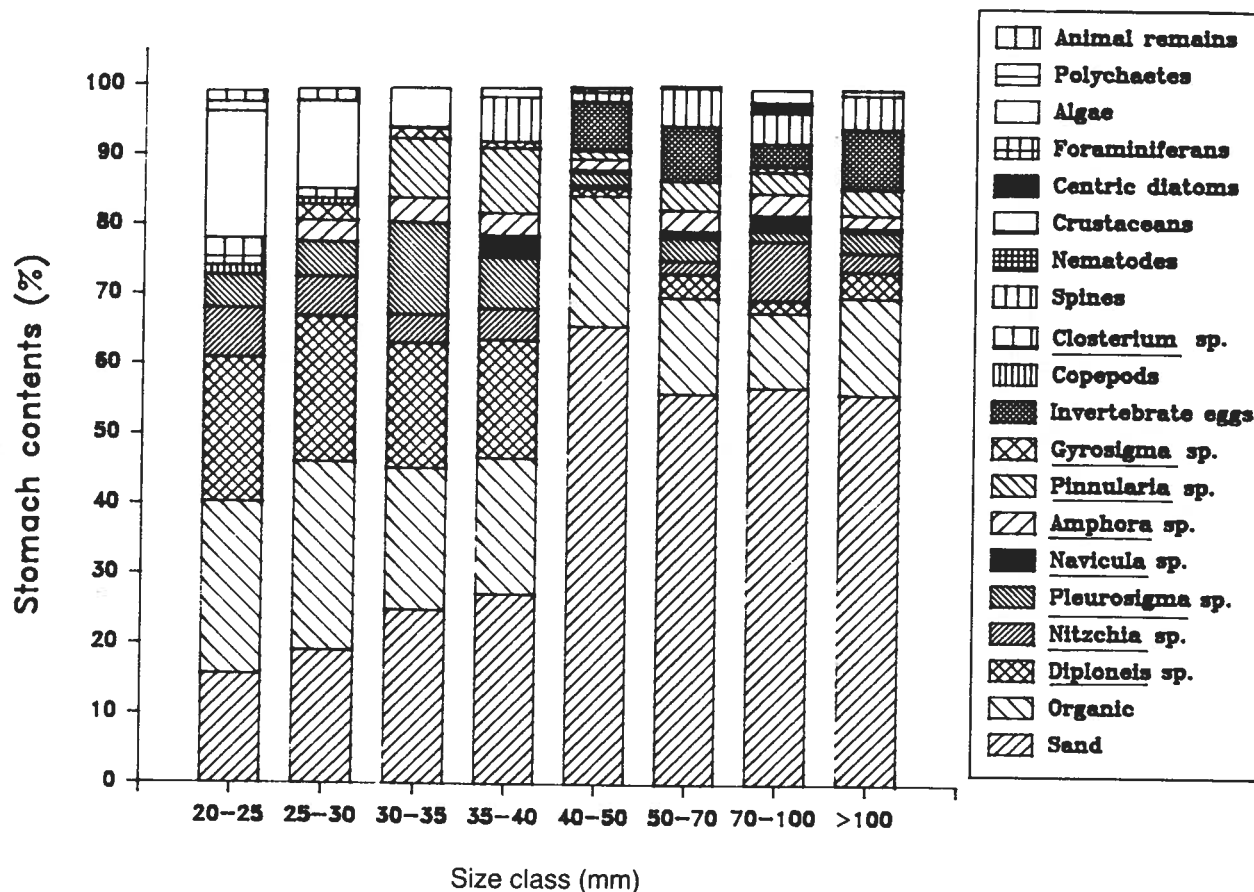


Fig. 4. Stomach contents of mullet. Bar graph for each size class shows percentage of total stomach contents attributed to individual food items.

included in the analysis to remain consistent with the stomach content analysis. Cluster analysis performed on subsamples without sand had high similarity among them (not illustrated; similarity > 74% for all dates). Organic matter ranges from 16.0% (July 14) to 29.5% (June 27). These two items contribute over two-thirds of the weight of each sediment subsample and the homogeneity found in these parameters greatly contributes to the similarity found among the subsamples. Diatoms represent 11.2% – 26.4% by weight. The most common diatom genera are *Diploneis* and *Amphora* which account for an average weight of 2.5%. Meiofauna, including polychaetes, copepods, amphipods, ostracods and bivalves are rarely present in high numbers and usually contribute less than

2.0% of the weight. Plant matter, including decaying mangrove leaves and other leaf litter, account for 1.8% of the subsamples.

In the sediment subsamples, diatoms, algae, copepods, amphipods, ostracods, cumaceans, nematodes, invertebrate eggs, polychaetes, fish embryos and larvae, bivalves, foraminiferans, siliceous spines, organic matter and sand are present. Table 2 indicates presence/absence of each prey item for each sampling date. In addition to sand, each subsample contained at least 6 species of diatoms and always contained algae, siliceous spines, and organic matter. Many of the food items present in samples are rarely found in the stomach contents. Meiofauna is under-represented in the diet as is

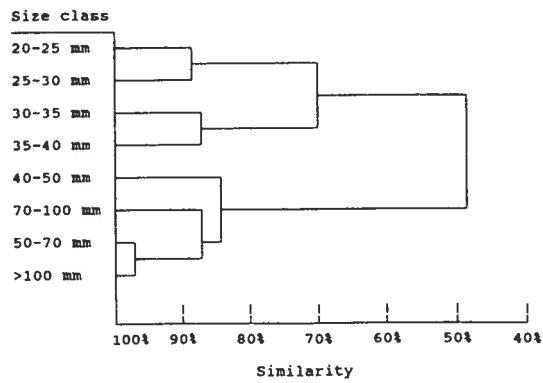


Fig. 5. Cluster analysis of prey similarity among size classes of mullet. Ordering of trophic units from individual size classes ( $n = 25$  size per class) were based on similarity coefficients greater than 0.80.

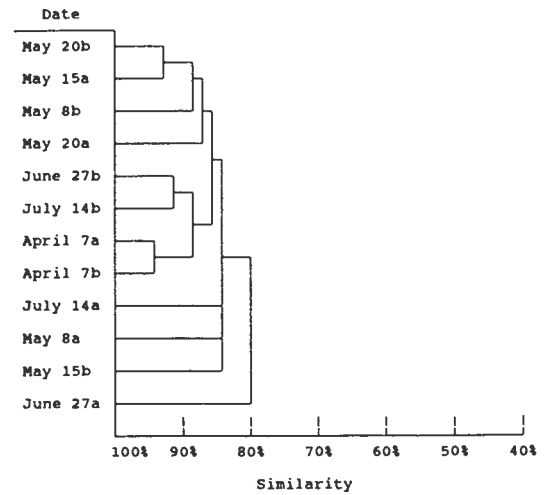


Fig. 6. Cluster analysis of similarity among sediment subsamples taken in Cross Bayou. a = replicate 1, b = replicate 2.

Table 2. Contents found in the sediment subsamples. Each date represents two replicates. (+) = present, (-) = absent.

	Date of sediment sample					
	7 Apr	8 May	15 May	20 May	27 Jun	14 Jul
Macroalgae	+	+	+	+	+	+
Desmid:						
<i>Closterium</i>	-	-	-	-	-	-
Diatoms:						
<i>Diploneis</i>	+	+	+	+	+	+
<i>Nitzschia</i>	+	+	+	+	+	+
<i>Pleurosigma</i>	+	+	+	+	+	+
<i>Navicula</i>	+	+	+	+	+	+
<i>Amphora</i>	+	+	+	+	+	+
<i>Pinnularia</i>	+	+	+	+	+	+
<i>Gyrosigma</i>	+	-	+	+	-	+
Centric diatoms	+	+	+	+	+	+
Crustacea:						
Copepods	+	+	+	+	+	+
Amphipods	+	+	+	-	+	+
Ostracods	+	+	+	-	+	+
Cumaceans	-	-	+	-	-	+
Nematoda	+	+	+	+	+	+
Invertebrate eggs	+	+	+	+	+	+
Polychaeta	+	+	+	+	+	+
Fish larvae	-	-	+	-	-	-
Bivalve	-	-	-	-	+	+
Foraminifera	-	-	-	+	+	-
Siliceous spines	+	+	+	+	+	+
Organic matter	+	+	+	+	+	+
Sand	+	+	+	+	+	+

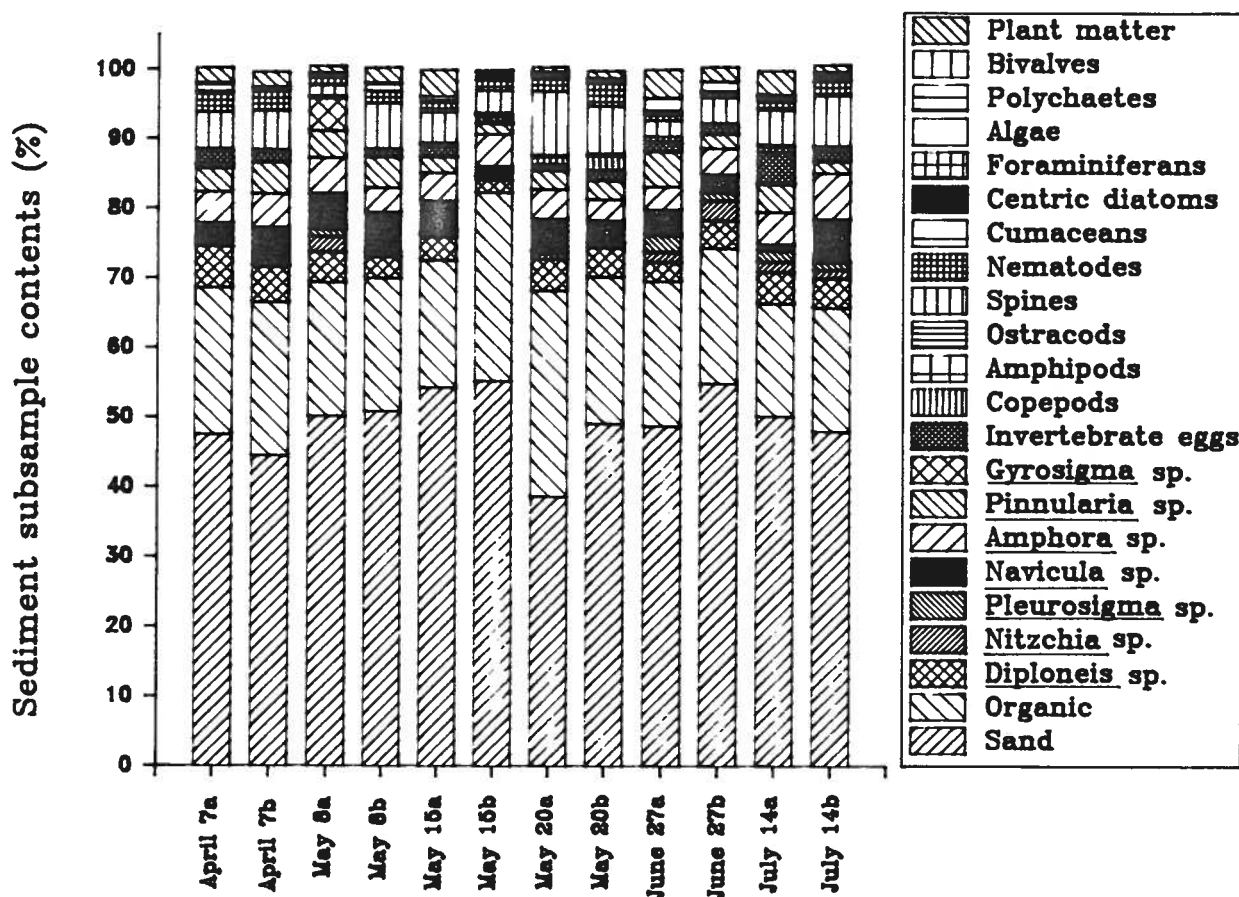


Fig. 7. Sediment contents in sediment subsamples. Bar graph for each sampling date shows percentage of total sediment contents attributed to individual items. a = replicate 1; b = replicate 2.

plant matter. Most of the other items are present in similar but varying amounts (Fig. 4, 7).

Comparison of the gut contents (including sand) with the subsample contents (including sand) for each size class using C.Q.I. and cluster analysis based on prey item weight (Fig. 8) shows a gradual increase in similarity as the fish increases in size. The prey items found in the gut contents were compared to the prey items from the subsample contents taken on the day that particular size class was captured (see Materials and methods). Stomach contents from 20–25 mm SL fish are 45% similar to the sediment subsamples, 25–30 mm SL are 54% similar to the sediment subsamples, 30–35 mm SL fish are 58% similar to the subsamples, 35–40 mm SL fish are 67% similar to the subsamples, 40–50 mm SL fish are 70% similar to the subsam-

ples, 50–70 mm SL fish are 82% similar to the subsamples, 70–100 mm SL fish are 83% similar to the subsamples and > 100 mm SL fish are 84% similar to the subsample contents.

#### Morphometrics

Mean gill raker length, mean interraker spacing, mouth height, mouth width and intestinal length are each positively correlated with mullet standard length (Fig. 9–12). Each regression line consists of data from all eight size classes ( $n = 200$ ).

Mean gill raker lengths for all four gill arches show allometric growth with each gill raker slope being significantly different from a predicted slope of 1.0 ( $p < 0.001$ , Fig. 9). The first and fourth gill



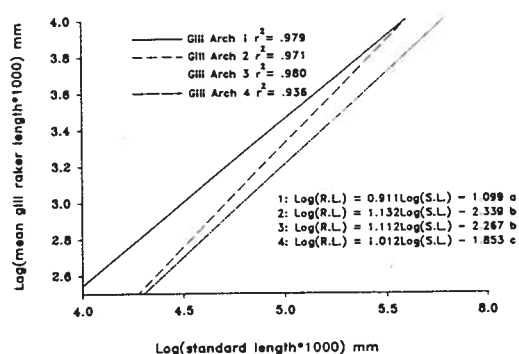


Fig. 9. Plot of Log(standard length) vs. Log(mean gill raker length) for the left gill arches one to four in *Mugil cephalus*. Similar letters beside regression equations denote that those equations are not significantly different.

same size as the interspine distances and the majority of the particles are larger than the interspine distances. The cumulative percent of prey item weights in the sediment subsamples is approximately the same as the stomach contents (Fig. 13b, c). Over 75% of the prey items by weight are retained in the three smallest sieve sizes. These small particles are smaller in diameter than the interraker distance but larger than the interspine distances.

## Discussion

The main tenet of the ecomorphological hypothesis is that morphological specializations limit prey utilization and thus species with similar morphologies should possess similar diets (Wiens & Rotenberry 1980, Findley & Black 1983). There has been no clear consensus from this apparently simplistic working hypothesis. Studies by Karr & James (1975), Chao & Musick (1977), Gatz (1979), Findley & Black (1983) and Moyle & Senanayake (1984) have shown that the diet is correlated to morphology. Wiens & Rotenberry (1980) found that the few correlations between prey size and suites of covarying morphological traits were quite weak. Grossman (1986) found little support for the ecomorphological hypothesis when he failed to find correlations between feeding morphology, particularly size of the head and jaws, protrusibility and orientation of the jaws, number of gill rakers,

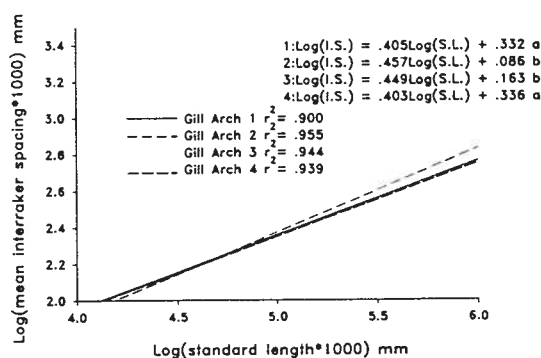


Fig. 10. Plot of Log(standard length) vs. Log(mean interraker spacing) for the left gill arches one to four in *Mugil cephalus*. Similar letters beside regression equations denote that those equations are not significantly different.

and dietary analysis. His results suggest that behavior is more important than morphology in determining prey utilization. Liem (1980) also has shown that morphologically specialized African cichlids can behaviorally alter their feeding modes. Further complicating the ecomorphological hypothesis is ontogenetic dietary change that occurs in most animals. Therefore, one approach to aid in the understanding of ecomorphological relationships is to study dietary determinants during ontogeny.

## Diet

*Mugil cephalus* undergoes an ontogenetic shift in diet. Fish of 20–30 mm SL ingest small amounts of sand and large amounts of organic matter and diatoms. Copepods, amphipods, ostracods, polychaetes, and bivalves contribute minimally to the diet. These results conflict with previous studies which report *M. cephalus* to be primarily carnivorous at these sizes (Ebeling 1957, Odum 1970, Blaber & Whitfield 1977, De Silva 1980, Loftus et al. 1983). However, De Silva & Wijeyaratne (1977) obtained similar results for mullet 20–55 mm TL. The first ontogenetic trophic unit includes mullet 20–25 mm SL which are 88% similar in diet to fish 25–30 mm SL (Fig. 5).

The second ontogenetic trophic unit reported here occurs at 30–40 mm SL. These mullet ingest more sand, less organic matter, no zooplankton

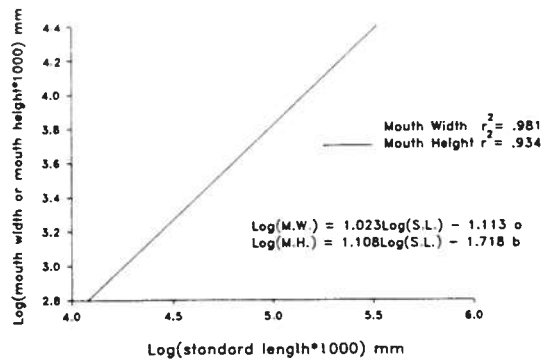


Fig. 11. Plot of Log(standard length) vs. Log(mouth width) and Log(mouth height) for the left gill arches one to four in *Mugil cephalus*. Similar letters beside regression equations denote that those equations are not significantly different.

and more species of diatoms than the previous size classes (Fig. 4, Table 1). The higher amounts of sand present in the diet suggest that these fish may be transitional from a browsing feeding habit to a grazing one. Mullet of 110 mm SL were found to dig an average of 6.75 mm, 6.16 mm and 4.9 mm into the sediment during three separate feeding experiments. Mullet < 40 mm do not dig into the sediment during feeding but browse on the surface film. The relatively and absolutely greater mouth height and mouth width may permit these larger mullet to scrape deeper into the sediment. The second ontogenetic trophic unit (30–40 mm SL; Fig. 5) includes mullet 30–35 mm SL which are 87% similar in diet to 35–40 mm SL fish.

The third ontogenetic trophic unit occurs at > 40 mm SL, including fish 40–50 mm, 50–70 mm, 70–100 mm, and > 100 mm SL. This interval is characterized by greater ingestion of sand and diatom species and less ingestion of organic matter (Fig. 4). Benthic grazing is typical of mullet in this size range and larger (Odum 1968, 1970, Hickling 1970, Blaber 1976, Blaber & Whitfield 1977, De Silva & Wijeyaratne 1977, Marais 1980, Das & Chowdhury 1983, Romer & McLachlan 1986). Fish 50–70 mm SL and > 100 mm SL are 97% similar in diet composition. This cluster is 87% similar to fish 70–100 mm SL and 83% similar to fish 40–50 mm SL.

Odum (1970) found that adult *M. cephalus* select fine sand particles that are rich in adsorbed organic

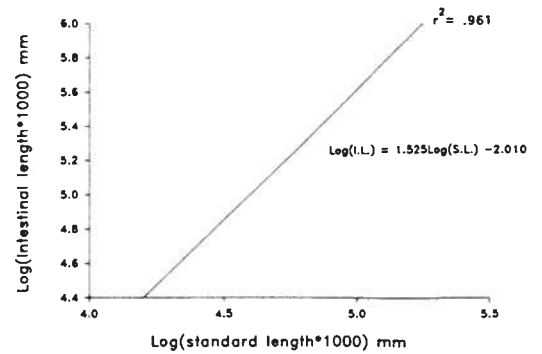


Fig. 12. Plot of Log(standard length) vs. Log(intestinal length) for *Mugil cephalus*.

matter, Protozoa and bacteria. In this study, sand particles contained high amounts of organic matter but bacteria and Protozoa were not observed. Lewis & Peters (1984) have shown that certain types of detritus are 60–75% digestible by menhaden and are nutritionally adequate to support growth of detritivores. Darnell (1961) found that organic detritus, including phytoplankton, vegetation and other material in stages of bacterial decomposition, have a major contribution to the total food volume of fishes of the Lake Pontchartrain community. Vallet et al. (1970) consider detritus to be a good source of vitamin B<sub>12</sub> for mullet. The fact that mullet of all size classes feed on the benthos and ingest large amounts of detritus supports the concept that detritus may be an important food source for mullet.

Comparison of prey items from stomach contents and sediment cores using C.Q.I. and cluster analysis reveals increasing similarity with increasing size class. The diets of fish 20–35 mm SL are only 54% similar to the sediment, while those of fish 40–50 mm SL and > 100 mm SL are 76% similar to the sediment (Fig. 8). The high percentage of sand in the diet of mullet could account for the high similarity among the size classes. However, analysis of the diet with sand excluded also has the same trophic units and high similarities between and among clusters.

Therefore, evidence that a change in feeding behavior from browsing to grazing determines ontogenetic dietary change are three fold. Experiments on the depth of feeding by mullet indicate

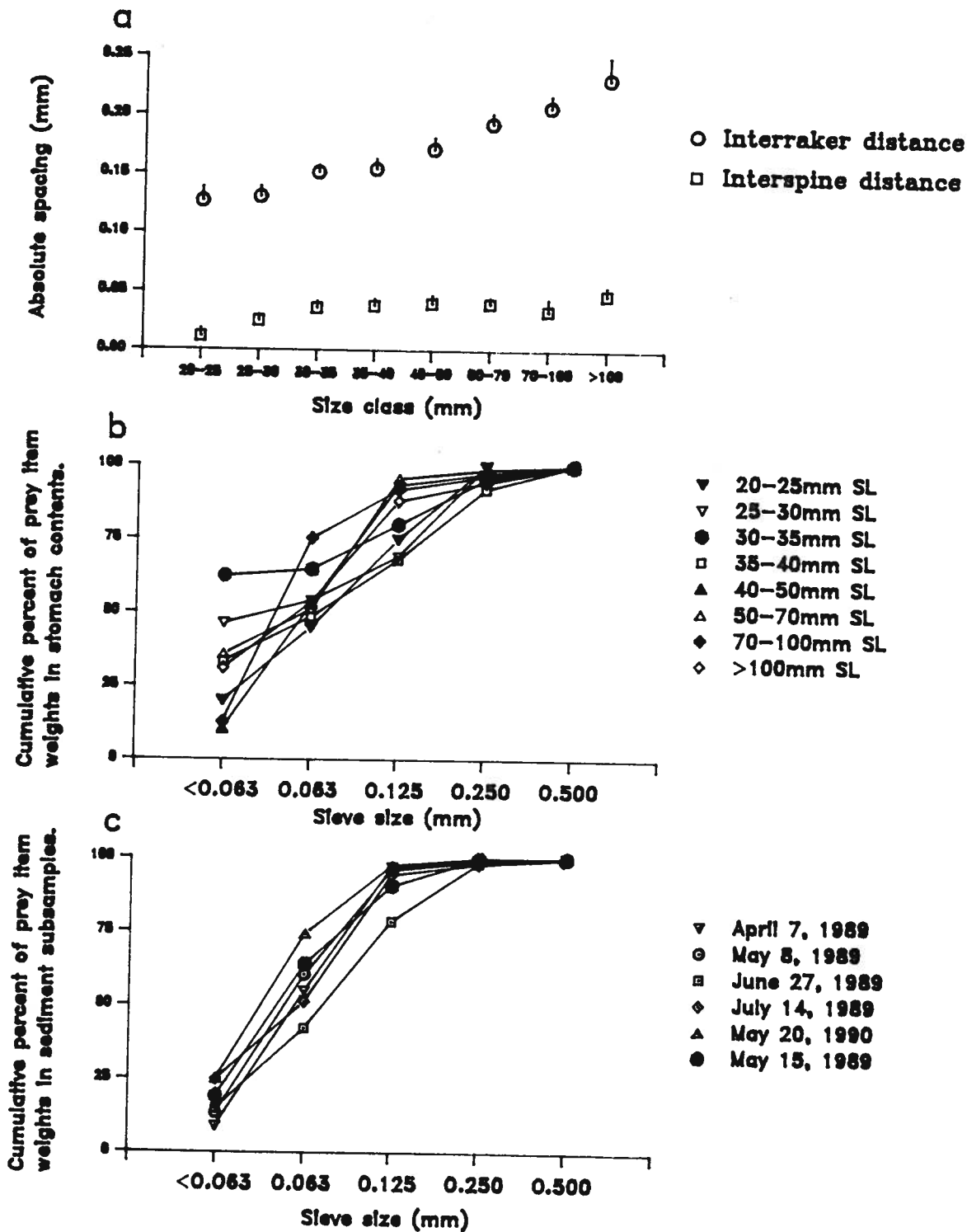


Fig. 13. a-gill interraker and interspine spacing from gill arch 1; b-cumulative percent of prey item weights of each sieve fraction in the stomach contents; c-cumulative percent of prey item weights of each sieve fraction in the sediment subsamples.

that mullet 105 mm SL and 110 mm SL graze to a depth of approximately 5.0 mm into the sediment while mullet < 40 mm SL select prey items from the surface by browsing, leaving no marks in the sediment during feeding. Secondly, the diet contains more sand as size increases. Thirdly, cluster analysis reveals that the diet of *Mugil cephalus* becomes more similar to the sediment during ontogeny.

#### Feeding location

Ontogenetic dietary shifts in mullet do not occur due to changes in feeding location. Mullet from all size classes were captured at the same location and under similar conditions (i.e. tide, time of day). Intra-habitat differences in prey items as measured by sediment subsample content similarity are very low. Similarity of the prey items found in the sediment subsample contents among sites and locations within the sites is > 80% (Fig. 6). Therefore, neither feeding location nor intra-habitat differences account for the ontogenetic dietary shift of mullet. However, the location of this study differs greatly from the habitat of other studies (i.e. oceanic and bay waters). Tampa Bay is an estuarine habitat with inflow from five major rivers (Comp & Seaman 1988). The bay is characterized by nitrogen and phosphorus enrichment (Johansson et al. 1982), high productivity of seagrass epiphytes, benthic microalgae and phytoplankton, with a 81% reduction in seagrass meadows in some areas (Lewis et al. 1982, Heffernan & Gibson 1982). This detrital-rich ecosystem contrasts to that of other studies on mullet feeding. Hiatt (1944) studied *Mugil cephalus* in Hawaiian fish ponds, Blaber (1976) and Blaber & Whitfield (1977) collected *M. cephalus* and other species from the St. Lucia lake system and various estuaries in south-east Africa, Marais (1980) examined feeding of *Liza dumerili* and *L. richardsoni* from Swartkops Estuary in South Africa, and Das & Chowdhury (1983) studied grey mullet in the Matamhury River estuary, Bangladesh. Consequently, this may account for the relatively larger proportion of organic matter and diatoms in the guts of juvenile *M. cephalus* (< 40 mm SL) in the Tampa Bay estuary.

#### Feeding morphology

Gill raker length on each of the four gill arches is allometric with respect to standard length (Fig. 9). The rakers on gill arch one are negatively allometric while the others are positively allometric. Therefore, smaller fish have relatively longer rakers on the first arch and larger fish have relatively longer rakers on the remaining arches. The first branchial arch has the most developed and elongated gill rakers and is responsible for the majority of the prey retention found in filter-feeding fish (Drenner et al. 1978, Wright & O'Brien 1984).

Mean interraker spacing on each of the four gill arches is negatively allometric with respect to standard length (Fig. 10). Therefore, larger fish have relatively closer spaced gill rakers. Perhaps a better measure of gill filtering size is interspine distance (Fig. 3) which is less than interraker distance and does not change appreciably in fish greater than 30 mm SL (Fig. 13a). These long, relatively closely spaced gill rakers may be suited for planktonic feeding in small mullet (< 40 mm SL) which has been observed in other studies (Ebeling 1957, Blaber & Whitfield 1977, De Silva 1980, Loftus et al. 1983). Among all fish sizes, over 68% of the prey items by weight in the stomach contents are less than or equal to 0.125 mm in diameter (Fig. 13b). This size (0.125 mm) is greater than the interspine distance but less than the interraker distance indicating that the spines could act as an effective filter in retaining prey.

Three processes by which fishes might use their gill rakers to retain prey are: (1) mechanical capture, (2) dynamic capture, and (3) active selection. Mechanical capture (Rosen & Hales 1981, Drenner et al. 1984.) occurs when fish swim through the water column with their mouths open and strain all particles from the water. Dynamic capture (MacNeill & Brandt 1990) occurs when fish actively adjust their interraker spacing to match the size of the particles they are ingesting. Whether or not any filter-feeding species actually does vary the interraker spacing in relation to prey size is unknown. Active selection (Brooks & Dodson 1965, Galbraith 1967) is a process by which fishes actively pursue and ingest certain sizes of plankton. Those

particles smaller than the interraker spacing are passed through the gill rakers and out the gill opening. In addition, gill rakers are thought to act as either a non-sticky or sticky filtering mechanism. The sticky filter hypothesis suggests that smaller particles than expected are retained due to mucus present in the gills. Weisel (1973) states that numerous mucus secreting cells in the gill epithelium of paddlefish may provide a means by which food in the gill rakers that would ordinarily be too small is retained. Robotham (1982) describes mucus producing goblet cells in the buccal cavity of the spine loach, *Cobitis taenia*, and proposes a mechanism for food separation utilizing mucus. *Mugil cephalus* retains prey of approximately the same size and larger than the interspine distance (Fig. 13) perhaps indicating that the gill rakers are used solely as a mechanical filter. Particles smaller than the interspine distances, diatoms and algae, may be trapped in organic matter and ingested. On the other hand, the gill rakers may play a limited role in benthic feeding as evidence by the high similarity among the stomach contents of fish > 50 mm SL and the sediment subsamples (Fig. 8). Also, the cumulative percentages of prey item weights in the sieve fractions (Fig. 13b, c) from the stomach contents and sediment subsamples are very similar. The mullet may not be filtering the particles but rather ingesting all available particles found in the sediment. Each of these concepts must be tested to determine which if any are occurring in mullet.

Intestinal length (Fig. 12) is strongly positively allometric with respect to standard length. The length is relatively greater in large mullet (> 100 mm SL) than in small mullet (< 40 mm SL). Increase in relative intestinal length with growth is characteristic of herbivorous fishes (Harmelin-Vivien & Bouchon-Navaro 1983, Wijeyaratne & Costa 1987). Symbiotic algae in coral and in sediment result in essentially a herbivorous diet. Supporting this concept are studies (Ebeling 1957, Blaber & Whitfield 1977, De Silva 1980) that have shown small mullet to be carnivorous and large mullet to be herbivorous (Hickling 1970, Blaber 1976, Marais 1980, Minckley 1982). However, in this study, all size classes were found to be herbivorous and

indicates that this parameter should not be used by itself to predict a fish's diet.

The global repletion index (Table 3) varies with size class and does not clearly show an increase in importance of the intestine with growth. However, this index is based on the weight of the intestine and can vary depending upon the amount of food present in each intestine. A better predictor of the importance of the intestines would be to measure empty intestines. This may provide a stronger correlation between the weight of intestines and the importance of herbivory in the diet.

The explanation that a change in feeding morphology results in the ontogenetic dietary change in mullet is not supported. Despite increasing gill raker length, interraker spacing, mouth width and height during ontogeny, overall stomach content particle size does not change. Increase in relative intestinal length in large mullet may be correlated with its herbivorous feeding habit and not a change that results in the ontogenetic dietary shift. It appears that ontogenetic dietary change is associated with a change in feeding behavior from browsing on to grazing in the sediment. Blaber (1987) found that diet of Mugilidae changed upon entering estuaries. Transitions in diet were closely linked with the mechanism for migration into estuaries and a change from a pelagic to benthic mode of life. The fact that the mullet of this study were caught well into an estuarine system suggest that the mechanism for migration (i.e. salinity and turbidity gradients) and feeding behavior may have synergistic effects on diet.

In conclusion, an ontogenetic dietary shift in *Mugil cephalus* occurs. Three distinct stages of feeding are observed (20–30 mm, 30–40 mm and > 40–100 mm SL) and the contribution of sand and organic matter are primarily responsible for the change in diet. Small mullet (< 40 mm SL) are found to feed exclusively on the sediment by browsing. Large mullet (> 40 mm SL) had: (1) a high similarity between their stomach contents and the contents of the sediment subsamples, (2) increasing proportions of sand in the diet, and (3) been observed to graze in laboratory experiments. This suggests that mullet of this size are grazers on the sediment. Feeding location is not responsible for

the ontogenetic dietary change in mullet because both feeding location and intra-habitat location were similar. Morphological measurements such as interraker distances, interspine distances, gill raker lengths, intestinal length and mouth width and height appear not to contribute to the shift in diet.

### Acknowledgements

We would like to thank several people that helped us extensively during this project. Committee members Susan Bell and Clinton Dawes were very helpful throughout this project and offered support and encouragement throughout. Special thanks go to those who trudged through the muck and mud to assist us in the field collections: Jim Daly, Kari Clifton, and Diana Eggold. SEM micrographs and figures were completed with the help of Betty Lorrann and John Tsibris. The financial support was provided by the University of South Florida to Philip Motta, Sigma Xi research grant and a Lerner-Gray Fund for Marine Research Grant. This paper is drawn from a thesis submitted to the University of South Florida by the senior author in partial fulfillment of the requirements for the M.S. Degree in Zoology.

### References cited

- Bell, J.D., J.J. Burchmore & D.A. Pollard. 1978a. Feeding ecology of a scorpaenid fish, the fortessave, *Centropogon australis* from a *Posidonia* seagrass habitat in New South Wales. *Aust. J. Mar. Fresh. Res.* 29: 175-185.
- Bell, J.D., J.J. Burchmore & D.A. Pollard. 1978b. Feeding ecology of three sympatric species of leatherjackets (Pisces Monacanthidae) from a *Posidonia* seagrass habitat in New South Wales. *Aust. J. Mar. Fresh. Res.* 29: 631-643.
- Bison, P.A. 1978. Diel food selection by two sizes of rainbow trout (*Salmo gairdneri*) in an experimental stream. *J. Fish. Res. Board Can.* 35: 971-975.
- Blaber, S.J.M. 1976. The food and feeding ecology of Mugilidae in the St. Lucia Lake system. *Biol. J. Linn. Soc.* 8: 267-277.
- Blaber, S.J.M. 1987. Factors affecting recruitment and survival of Mugilids in estuaries and coastal waters of Southeastern Africa. *American Fisheries Society Symposium* 1: 507-518.
- Blaber, S.J.M. & A.K. Whitfield. 1977. The feeding ecology of juvenile mullet (Mugilidae) in south-east African estuaries. *Biol. J. Linn. Soc.* 9: 277-284.
- Brooks, J.L. & S.I. Dodson. 1965. Predation, body size and composition of plankton. *Science* 150: 28-35.
- Carr, W.E.S. & C.A. Adams. 1972. Food habits of juvenile marine fishes evidence of the cleaning habit in the leather jacket, *Oligoplites saurus*, and the spottail pinfish, *Diplodus holbrooki*. *U.S. Fish. Bull.* 70: 1111-1120.
- Chao, L.N. & J.A. Musick. 1977. Life history, feeding habit and functional morphology of juvenile sciaenid fishes in the York River Estuary, Virginia. *U.S. Fish. Bull.* 75: 657-702.
- Comp. G.S. & W. Seaman. 1988. Estuarine habitat and fishery resources of Florida. pp. 337-435. *In: W. Seaman, Jr. (ed) Florida Aquatic Habitat and Fishery Resources*, Florida Chapter of the American Fisheries Society, Florida.
- Darnell, R.M. 1961. Trophic spectrum of an estuarine community, based on studies of Lake Pontchartrain, Louisiana. *Ecology* 43: 553-568.
- Das, N.G. & Z.A. Chowdhury. 1983. Food and feeding habit of 3 grey mullet from the Matamuhury river estuary (Bangladesh). *Chittagong Univ. Stud. Part II Science* 7: 57-68.
- Dauer, D.M. & J.L. Simon. 1975. Lateral or along-shore distribution of the polychaetous annelids of an intertidal sand habitat. *Mar. Biol.* 31: 363-370.
- De Silva, S.S. 1980. Biology of juvenile grey mullet. A short review. *Aquaculture* 19: 21-36.
- De Silva, S.S. & M.J.S. Wijeyaratne. 1977. Studies on the biology of young grey mullet, *Mugil cephalus* L. II. Food and feeding. *Aquaculture* 12: 157-167.
- Drenner, R.W., J.R. Mummert, F. deNoyelles & D. Kettel. 1984. Selective particle ingestion by a filter feeding fish and its impact on phytoplankton community structure. *Limnol. Oceanogr.* 29: 941-948.
- Drenner, R.W., J.R. Strickler & W.J. O'Brien. 1978. Capture probability: the role of zooplankton escape in the selective feeding of a planktivorous fish. *J. Fish. Res. Board Can.* 35: 1370-1373.
- Ebeling, A.W. 1957. The dentition of eastern Pacific mullet with special reference to adaptation and taxonomy. *Copeia* 1957: 173-180.
- Feller, R.J. & V.W. Kaczynski. 1975. Size selection predation on juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. *J. Fish. Res. Board Can.* 32: 1419-1422.
- Field, J.G. & G. McFarlane. 1968. Numerical methods in marine ecology. 1. A quantitative similarity analysis of rock shore samples in False Bay, South Africa. *Zool. Africana* 119-137.
- Findley, J.S. & H. Black. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology* 64: 625-630.
- Galbraith, M.G. 1967. Size selective predation on *Daphnia* rainbow trout and yellow perch. *Trans. Amer. Fish. Soc.* 96: 1-10.
- Gatz, A.J. 1979. Ecological morphology of freshwater stream fishes. *Tulane Studies in Zoology and Botany* 21: 18-123.
- Grant, G.S. & A.V. Spain. 1975. Reproduction, growth and allometry of *Mugil cephalus* L. (Pisces; Mugilidae) from

- North Queensland inshore waters. *Aust. J. Zool.* 23: 181-201.
- Grossman, G.D. 1986. Food resource partitioning in a rocky intertidal fish assemblage. *J. Zool. Lond.* 1: 317-355.
- Harmelin-Vivien, M.L. & Y. Bouchon-Navaro. 1983. Feeding diets and significance of coral feeding among chaetodontid fishes in Moorea (French Polynesia). *Coral Reefs* 2: 119-127.
- Harmelin-Vivien, M.L., R.A. Kaim-Malka, M. Ledayer & S.S. Jacob-Abraham. 1989. Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. *J. Fish Biol.* 34: 715-734.
- Heffernan, J.J. & R.A. Gibson. 1982. Seagrass productivity in Tampa Bay: a comparison with other subtropical communities. p. 247. *In: S.F. Treat (ed.) Proceedings Tampa Bay Area Scientific Information Symposium.* Bellwether Press, Minneapolis.
- Hiatt, R.W. 1944. Food chains and the food cycle in Hawaiian fish ponds. Part II. The food and feeding habits of mullet (*Mugil cephalus*), milkfish (*Chanos chanos*) and the ten pounder (*Elops machnata*). *Trans. Amer. Fish. Soc.* 74: 250-261.
- Hiatt, R.W. & D.W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. *Ecol. Monog.* 30: 65-127.
- Hickling, C.F. 1970. A contribution to the natural history of the English grey mullets (Pisces: Mugilidae). *J. Mar. Biol. Assoc. U.K.* 50: 609-633.
- Hobson, E.S. 1968. Predatory behavior of some shore fishes in the Gulf of California. *U.S. Fish Wildl. Serv., Res. Rept.* 73: 1-92.
- Hobson, E.S. 1974. Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *U.S. Fish. Bull.* 72: 915-1031.
- Hubbs, C.L. & K.F. Lagler. 1958. *Fishes of the Great Lakes Region.* University of Michigan Press, Ann Arbor. 213 pp.
- Huh, S.H. & C.L. Kitting. 1985. Trophic relationships among concentrated populations of small fishes in seagrass meadows. *J. Exp. Mar. Biol.* 92: 29-43.
- Johansson, J.O.R., K.A. Steidinger & D.C. Carpenter. 1982. Primary production in Tampa Bay, Florida: a review. pp. 279-298. *In: S.F. Treat (ed.) Proceedings Tampa Bay Area Scientific Information Symposium.* Bellwether Press, Minneapolis.
- Karr, J.R. & F.C. James. 1975. Eco-morphological configurations and convergent evolution in species and communities. pp. 258-291. *In: M.L. Cody & J.M. Diamond (ed.) Ecology and Evolution of Communities.* Belknap Press, Cambridge.
- Keast, A. 1985. Development of dietary specializations in a summer community of juvenile fishes. *Env. Biol. Fish.* 13: 211-224.
- Keast, A. & L. Welsh. 1968. Daily feeding periodicities, food uptake rates and dietary changes with the hour of day in some lakes. *J. Fish. Res. Board Can.* 25: 1133-1144.
- Lewis, R.R., M.J. Durako, M.D. Moffler & R.C. Phillips. 1982. Seagrass meadows of Tampa Bay - a review pp. 210-246. *In: S.F. Treat (ed.) Proceedings Tampa Bay Area Scientific Information Symposium.* Bellwether Press, Minneapolis.
- Lewis, V.P. & D.S. Peters. 1984. Menhaden-a single step vascular plant to fishery harvest. *J. Exp. Mar. Biol. Ecol.* 84: 95-100.
- Liem, K.F. 1980. Adaptive significance of intra- and interspecific differences in the feeding repertoires of cichlid fishes. *Amer. Zool.* 20: 245-314.
- Livingston, R.J. 1980. Ontogenetic trophic relationships and stress in coastal seagrass system. pp. 423-435. *In: U.A. Kennedy (ed.) Estuarine Perspectives.* Academic Press, New York.
- Livingston, R.J. 1982. Trophic organization of fishes in a coastal seagrass system. *Mar. Ecol. Prog. Ser.* 7: 1-12.
- Livingston, R.J. & A.W. Stoner. 1984. Ontogenetic patterns of diet and feeding morphology in sympatric sparid fishes from seagrass meadows. *Copeia* 1984: 174-187.
- Loftus, W.F., J.A. Kushlan & S.A. Voorhees. 1983. Status of the mountain mullet in southern Florida. *Flor. Sci.* 47: 257-263.
- Love, M.S. & A.W. Ebeling. 1978. Food and habitat of three switch-feeding fishes in the kelp forests off Santa Barbara, California. *U.S. Fish. Bull.* 76: 257-271.
- MacNeill, D.B. & S.B. Brandt. 1990. Ontogenetic shifts in gill raker morphology and predicted prey capture efficiency of the alewife, *Alosa pseudoharengus*. *Copeia* 1990: 164-170.
- Marais, J.F.K. 1980. Aspects of food intake, food selection and alimentary canal morphology of *Mugil cephalus* L., *Liza tricuspidens* Smith, *L. richardsoni* Smith, and *L. dumerili* Steindachner. *J. Exp. Mar. Biol. Ecol.* 44: 193-210.
- Marais, J.F.K. & T. Erasmus. 1977. Chemical composition of alimentary canal contents of mullet (Teleostei Mugilidae) caught in the Swartkops estuary near Port Elizabeth, South Africa. *Aquaculture* 10: 263-273.
- Minkley, W.L. 1982. Tropic interrelations among introduced fishes in the lower Colorado River, Southeastern U.S. *California Fish and Game* 68: 78-89.
- Motta, P.J. 1985. Functional morphology of the head of Hawaiian and Mid-Pacific butterflyfishes (Perciformes, Chaetodontidae). *Env. Biol. Fish.* 13: 253-276.
- Moyle, P.B. & F.R. Senanayake. 1984. Resource partitioning among the fishes of rainforest streams in Sri Lanka. *J. Zool. Lond.* 202: 195-223.
- Odum, W.E. 1968. The ecological significance of fine particle selection by the striped mullet *Mugil cephalus*. *Limnol. Oceanog.* 13: 92-97.
- Odum, W.E. 1970. Utilization of the direct grazing and plant detritus food chains by the striped mullet, *Mugil cephalus*. pp. 222-240. *In: J.H. Steele (ed.) Marine Food Chains.* Oliver and Boyd, Edinburgh.
- Pillay, T.V.T. 1953. Studies on the food, feeding habits and alimentary tract of the grey mullet, *Mugil tade* Forskal. *Proc. Natn. Inst. Sci. India.* 19: 777-827.
- Robertson, A.I. & R.K. Howard. 1978. Diel trophic interactions between vertically-migrating zooplankton and their fish predators in an eelgrass community. *Mar. Biol.* 48: 207-213.
- Robotham, P.W.J. 1982. An analysis of a specialized feeding mechanism of the spined loach, *Cobitis taenia* (L.), and a description of the related structures. *J. Fish Biol.* 20: 173-181.

- Romer, G.S. & A. McLachlan. 1986. Mullet grazing on surf diatom accumulations. *J. Fish Biol.* 28: 93-104.
- Rosen, R.A. & D.C. Hales. 1981. Feeding of paddlefish, *Polyodon spathula*. *Copeia* 1981: 441-455.
- Smith, C.L. 1978. Coral reef fish communities: a compromise view. *Env. Biol. Fish.* 3: 109-128.
- Stoner, A.W. 1980. The feeding ecology of *Lagodon rhomboides* (Pisces Sparidae) variation and functional responses. *U.S. Fish. Bull.* 78: 337-352.
- Tosi, L. & P. Torricelli. 1988. Feeding habits of mullet fry in the Arno River (Tyrrhenian coast). II. The diet. *Boll. Zool.* 3: 171-177.
- Vallet, F., J. Berhout, C. Leray, B. Bonnet & P. Pic. 1970. Preliminary experiments on the artificial feeding of Mugilidae. *Helgol. Wiss. Meeresunters* 20: 610-619.
- Weisel, G.F. 1973. Anatomy and histology of the digestive system of the paddlefish (*Polyodon spathula*). *J. Morphol.* 140: 243-251.
- Wiens, J.A. & J. Rotenberry. 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. *Ecol. Monogr.* 50: 287-308.
- Wijeyaratne, M.J.S. & H.H. Costa. 1986. On the biology of an estuarine population of grey mullet, *Mugil cephalus* L., in Negombo Lagoon, Sri Lanka. *Cybium* 10: 351-363.
- Wijeyaratne, M.J.S. & H.H. Costa. 1987. The biology of grey mullets in a tropical lagoon in Sri Lanka. I- Age and growth. *Bull. Nat. Inst. Oceanogr.* 20: 163-170.
- Wood, E.J.F. 1953. Heterotrophic bacteria in marine environments of Eastern Australia. *Aust. J. Mar. Fresh. Res.* 4: 166-200.
- Wright, D.I. & W.J. O'Brien. 1984. The development and field test of a tactical model of the planktivorous feeding of white crappie (*Pomoxis annularis*). *Ecol. Monogr.* 54: 65-98.