

**Ontogenetic Shifts in the Diet of Gag,
Mycteroperca microlepis, (Goode and Bean),
(Pisces: Serranidae)**

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ABSTRACT

The gag, *Mycteroperca microlepis*, is an epinepheline serranid found in the live-bottom habitats of the western Atlantic and the Gulf of Mexico. Gag are known to be piscivorous as adults; however, little is known of the feeding habits and other aspects of their early life history. Larval gag enter inlets into estuaries of South Carolina in the early spring, settling in oyster reef environments until emigrating to offshore reefs in the fall as juveniles. Results of stomach content analysis of postlarval and juvenile gag demonstrate that distinct trophic stages exist, and that the trend toward piscivorous feeding habits in this species is apparent prior to their offshore emigration.

KEY WORDS: Gag, Trophic ontogeny, Oyster shell habitat.

INTRODUCTION

The gag, *Mycteroperca microlepis* (Goode and Bean) is an epinepheline serranid occurring in temperate and tropical habitats in the western Atlantic, including the Gulf of Mexico (Smith, 1971; Collins *et al.*, 1987). Adult gag are found in association with live-bottom sponge and coral habitats at depths of 20 to 100 m (Powles and Barans, 1980; Sedberry and Van Dolah, 1984) and are an important component of commercial and recreational fisheries along the southeastern coast of the United States and the Gulf of Mexico (Huntsman and Dixon, 1976).

The biology of adult gag is comparatively well known. Naughton and Salomon (1985) determined the feeding habits of adult *M. microlepis* from North Carolina and Florida. They reported gag to be highly piscivorous; invertebrates never exceeded five percent of total food volume in the stomachs they examined. Age and growth studies have been conducted on offshore adults (McErlean, 1963; Manooch and Haimovici, 1978). The reproductive biology of gag, a protogynous hermaphrodite, has also been studied (McErlean and Smith, 1964; Collins *et al.*, 1987).

Little is known, however, of the early life history of gag or indeed of any other grouper species (Leis, 1986). Postlarval gag are carried on swift surface

flood tides in the spring into barrier island inlets along coast lines bordering the western Atlantic and Gulf of Mexico (Hoese *et al.*, 1961; Adams, 1976; Johnson, 1981; Keener *et al.*, 1988). Postlarvae, late pre-settlement larvae that have not yet developed the juvenile pigmentation pattern (Keener *et al.*, 1988), then settle in cryptic environments within the estuaries, which presumably serve as nursery grounds (Miller *et al.*, 1985) affording developing grouper with abundant prey and reduced predation. In a five-year study designed to estimate the magnitude of estuarine ingress of postlarval gag, Keener *et al.* (1988) used a fixed neuston net to collect gag entering a barrier island inlet north of Charleston, South Carolina. Based on the large number of postlarval gag collected, they concluded that estuarine ingress is "a consistent and integral part of the early life history of *M. microlepis* off South Carolina."

Ontogenetic change in the diet of fishes has been documented in numerous species (Chao and Musick, 1977; Livingston, 1980; Magnan and FitzGerald, 1984; Schmitt and Holbrook, 1984; Stoner and Livingston, 1984; Leucke, 1986). In this paper, I describe the trophic ontogeny of postlarval and juvenile *M. microlepis* occupying the oyster shell habitats in high salinity creeks of the Charleston Harbor, South Carolina estuary. Some of the information provided may be useful in evaluating the patterns of resource utilization in gag and in assessing the role of this species in the estuarine ecosystem.

MATERIAL AND METHODS

Collection

Gag (N = 200) were collected from May 1987 until mid-December of 1988 in the high salinity tidal creeks landward of barrier inlets north of the Charleston Harbor estuary. Gears employed were a 3.7 m x 0.64 cm otter trawl equipped with a tickler chain and with open-topped habitat trays of various sizes. Trawling was done at high tide over oyster shell habitats. The habitat trays, which were placed over oyster reefs and adjacent mud-bottom habitats, were filled with oyster shell and inspected at low tide. Seines and gill nets were unsuccessfully employed, apparently failing to sample the cryptic habitat of settled gag. An additional 30 specimens were captured at Breach Inlet 10 km east of Charleston by the South Carolina Wildlife and Marine Resources Department (SCWMRD) with a 1 m x 2 m neuston net (2 mm mesh). The total number of specimens examined for feeding habits was therefore 230.

Juvenile black grouper (*Mycteroperca bonaci*) and red grouper (*Epinephelus morio*) were occasionally captured. Gag were easily distinguished from red grouper by differences in coloration and were separated from black grouper by anal soft-ray counts (10 to 12, usually 11 in *M. microlepis* versus 12 or 13 in *M. bonaci*) (Keener *et al.*, 1988), preopercular angle (Smith, 1971), and by relative scale size.

Stomachs of specimens were injected with formalin (100%) in the field in order to fix the contents. An effort was made to collect at dawn and dusk; crepuscular feeding activity was reflected in the smaller degree of digestion of prey items found in the stomachs of specimens collected at those times.

Stomach Content Analysis

Standard lengths (SL) and total lengths (TL) of gag were measured in the laboratory to the nearest 0.1 mm using either dial calipers or a dissecting microscope equipped with an ocular micrometer. All specimens were weighed to the nearest g. The entire gastrointestinal tracts were then removed, individually labelled, and preserved in 10 percent seawater-buffered formalin.

Each stomach was cut open and its contents identified to the lowest possible taxon and enumerated. Volume displacement of larger food items was measured using appropriately sized graduated cylinders. For smaller prey items, volume displacement was estimated using a 0.1 cm² grid (Windell, 1971). Because many methods of quantifying feeding habits include inherent bias (Pinkas *et al.*, 1971; Sedberry, 1983), the relative contribution of food items to the diet of gag was determined using the following methods: (1) percentage frequency of occurrence (F)—indicating the proportion of specimens per size class in which a particular prey item was present, (2) percentage numerical abundance (N)—the proportion a prey category composed of the total number of prey items within each size class, and (3) percentage volumetric displacement (V). These measurements were calculated both for specific and higher taxonomic categories of prey.

From these measurements, an index of relative importance (Pinkas *et al.*, 1971) was calculated as follows: $IRI = (N + V)F$, where: IRI = index of relative importance, N = numerical percentage, V = volumetric percentage, and F = frequency of occurrence percentage. This index has been used previously to determine the relative importance of prey taken by fishes (Pinkas *et al.*, 1971; McEachran *et al.*, 1976; Sedberry and Musick, 1978; Sedberry, 1983). In the present study, the IRI was used to describe the ontogeny of feeding.

For analysis of trophic ontogeny, gag were placed into 10-mm size classes up to 60 mm SL; 20-mm size classes from 60-100 mm SL; and in 25-mm size classes for specimens larger than 100 mm SL. Specimens within size classes were treated as collections and were grouped on the basis of similarity of prey. For all specimens, total volume of prey items was divided by number of prey items to examine ontogenetic shifts in average volume of food items taken by postlarvae and juveniles. The cumulative number of prey types was plotted against randomly pooled numbers of stomachs for each size class to evaluate adequacy of sample sizes (Singer, 1985).

RESULTS

Habitat preference of gag was consistent for both years of collection. Gag, as well as black and red grouper, apparently prefer structurally complex habitats during their estuarine residence. Habitat trays placed on oyster beds were very successful in capturing grouper (N = 72), but those placed on muddy bottoms adjacent to oyster beds failed to capture any grouper.

Of the 230 stomachs analyzed, 209 contained food, and at least 44 prey items were represented (Table 1). The principal prey items of estuarine gag were calanoid copepods, mysids, gammaridean amphipods, grass shrimp (*Palaemonetes* spp.), penaeid shrimp, and fishes (Figure 1). Sufficient sample sizes were indicated for all size classes by the asymptotic levelling of plots of cumulative numbers of prey types versus randomly pooled numbers of stomachs.

The diet of gag in the smallest size class (10.1 – 20.0 mm SL) was composed primarily of calanoid copepods and gammaridean amphipods, these prey accounting for over 90 percent of the total Index of Relative Importance (IRI) for that size class (Figure 2). A drastic reduction in the relative importance of copepods in the diet of gag larger than 20.0 mm SL was apparent; copepods accounted for less than 3 percent of the total IRI in the 20.1 – 30.0 mm SL size class (Figure 2).

The diet of 20.1-50.1 mm SL individuals was dominated by amphipods, decapods, and mysids (Figure 2). Decapods were the most important prey for individuals 50.1-80.1 mm SL (Figure 2). Small *Palaemonetes* spp. (grass shrimp) were predominant in the diets of 50.1 – 60.1 mm gag, whereas larger *Penaeus* spp. composed a major part of the diets of gag from 60.1 to 125 mm SL.

As the importance of decapods in the diet of the larger size classes (> 100 mm SL) decreased, a concomitant increase in the importance of fishes occurred (Figures 1 and 2). In the largest juveniles, approximately 68 percent of the total volume of stomach contents was composed of fishes (Figure 1), accounting for 60 percent of the total IRI (Figure 2).

The average volume of individual prey items of gag from 10 to 50 mm SL was consistently very small, but gradually increased from 50 to 125 mm SL as gag preyed primarily on decapods (Figure 3). This was then followed by a pronounced increase when fishes became the predominant prey of large juveniles (125 – 150 mm SL).

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Table 1. Percentage of frequency occurrence (F), percentage of number (N), percentage of volume (V), and Index of Relative Importance (IRI) of prey items and higher taxonomic groups of food in the diet of gag, *Mycteroperca microlepis*.

Taxon Prey item	F	N	V	IRI
Algae				
Rhodophyta	0.48	0.12	0.01	0.06
Annelida				
Polychaeta				
<i>Nereis</i> sp.	0.48	0.12	0.01	0.06
Mollusca				
Cephalopoda				
<i>Lolliguncula brevis</i>	0.96	0.36	4.06	4.24
Arthropoda				
Crustacea				
Harpacticoida	0.48	0.49	<0.01	0.23
Calanoida	7.66	14.84	0.08	114.24
Cyclopoida	1.91	0.49	<0.01	0.94
Total Copepoda	7.66	15.80	0.09	121.58
Mysidacea				
<i>Mysidopsis almyra</i>	1.91	0.49	0.09	1.11
<i>Mysidopsis bahia</i>	6.70	2.80	0.45	21.78
<i>Mysidopsis bigelowi</i>	1.44	0.49	0.28	1.10
<i>Mysidopsis</i> sp.	3.35	3.16	0.16	11.21
Mysidacea undetermined	5.26	1.82	0.06	9.94
<i>Neomysis americana</i>	8.13	2.31	0.65	24.06
Total Mysidacea	21.53	11.07	1.69	274.46
Isopoda				
<i>Mesanthura</i> sp.	1.91	0.61	0.02	1.19
Amphipoda				
<i>Caprella</i> sp.	0.48	0.12	0.01	0.06
<i>Dulichella appendiculata</i>	20.10	12.41	0.93	268.00
<i>Gammarus mucronatus</i>	6.22	7.42	0.28	47.87
<i>Gammarus palustris</i>	13.40	11.4	0.48	159.69
<i>Gammarus</i> sp.	8.13	5.35	0.13	44.63
<i>Lembos hypacantha</i>	3.35	1.34	0.06	4.67
<i>Leucothoe spinicarpa</i>	0.96	0.24	0.10	0.33
<i>Leucothoe</i> sp.	1.44	0.49	0.01	0.71
<i>Listriella</i> sp.	1.44	0.61	0.03	0.91
<i>Stenothoe</i> sp.	0.48	0.12	0.01	0.06
Amphipoda undetermined	0.48	0.12	<0.01	0.06
Total Amphipoda	33.01	39.66	2.05	1374.73
Decapoda				
<i>Alpheus heterochaelis</i>	2.87	0.85	1.87	7.81
<i>Hippolyte pleuracanthus</i>	0.48	0.24	0.09	0.16
<i>Lysmata wurdemanni</i>	0.48	0.12	0.32	0.21
<i>Lysmata</i> sp.	0.48	0.12	0.01	0.06
<i>Neopontonides beaufortensis</i>	0.96	0.24	0.02	0.25
<i>Palaemonetes intermedius</i>	0.96	0.24	0.46	0.67

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<i>Palemonetes pugio</i>	20.10	8.03	8.78	337.71
<i>Palemonetes vulgaris</i>	5.26	1.82	1.10	15.39
<i>Palemonetes</i> sp.	14.35	4.87	4.27	131.13
<i>Panopeus herbstii</i>	0.48	0.12	0.07	0.09
<i>Panaeus aztecus aztecus</i>	1.91	0.73	2.63	6.44
<i>Panaeus setiferus</i>	4.31	1.58	19.32	90.88
<i>Panaeus</i> sp.	0.96	0.36	0.49	0.81
<i>Uca minax</i>	0.96	0.36	0.11	0.46
<i>Uca pugnax</i>	0.96	0.24	1.58	1.75
<i>Uca</i> sp.	1.44	0.36	0.05	0.60
<i>Upogebia affinis</i>	0.48	0.12	0.86	0.47
<i>Upogebia</i> sp.	0.48	0.12	0.32	0.21
<i>Panaeidae</i> undetermined	0.48	0.12	0.01	0.06
<i>Natantia</i> undetermined	3.35	0.85	0.03	2.96
<i>Reptantia</i> undetermined	0.48	0.12	0.01	0.06
Total Decapoda	54.55	21.58	42.62	3504.5
Chordata				
Vertebrata				
Pisces				
<i>Anchoa</i> sp.	1.91	0.49	1.96	4.68
<i>Bathygobius soporator</i>	4.31	1.95	2.45	18.94
<i>Chasmodes bosquianus</i>	0.96	0.24	1.74	1.90
Elopidae	0.48	0.12	0.02	0.07
Engraulidae	0.48	0.12	0.41	0.25
<i>Fundulus heteroclitus</i>	4.78	1.34	13.47	70.88
<i>Fundulus majalis</i>	1.44	0.36	1.39	2.51
<i>Gobiosoma bosci</i>	0.96	0.36	0.59	0.92
<i>Gobiosoma</i> sp.	0.48	0.12	0.83	0.45
<i>Hypsoblennius hentzi</i>	1.44	0.36	2.58	4.23
<i>Lagodon rhomboides</i>	0.48	0.12	0.01	0.07
<i>Lutjanus griseus</i>	1.44	0.36	17.21	25.23
<i>Opsanus tau</i>	0.96	0.24	1.97	2.12
<i>Prionotus</i> sp.	0.96	0.24	2.12	2.26
Osteichthyes undetermined	10.53	2.68	2.63	55.90
Total Pisces	28.71	9.11	49.39	1679.55

Number of stomachs examined: 230

Number of stomachs with food: 209

DISCUSSION

Upon settlement in the estuary, postlarvae remain quiescent for a short while (B. W. Stender, SCWMRD, pers. comm.). Once settled in the oyster beds, transformed juveniles assume general epibenthic feeding habits. Subsequent ontogenetic shifts in diet may be the result of increasing metabolic requirements associated with development. Most investigators into optimal foraging theory have assumed that predators choose diets that maximize the net yield of energy per unit foraging time; that is, predators are efficient in their feeding activities (Charnov, 1976; Estabrook and Dunham, 1976; Pyke *et al.*, 1977; Werner and

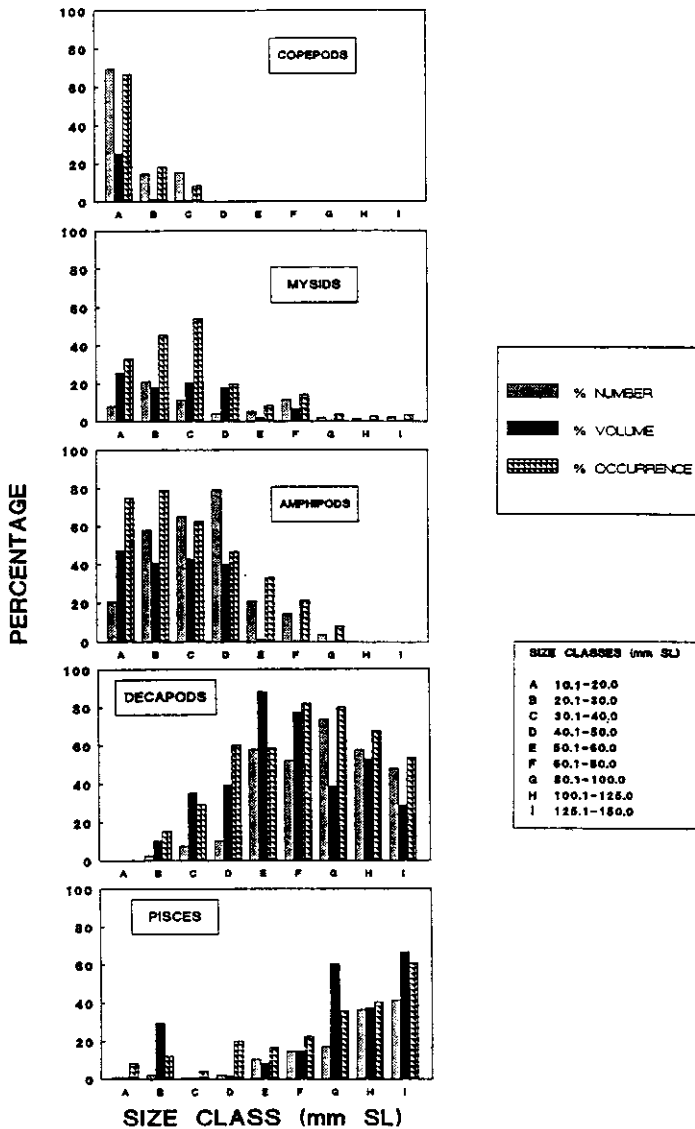


Figure 1. Numerical percentage, volumetric percentage, and frequency of occurrence percentage of higher taxonomic groups of prey items for size classes (A thru I) of *Mycteroperca microlepis*.

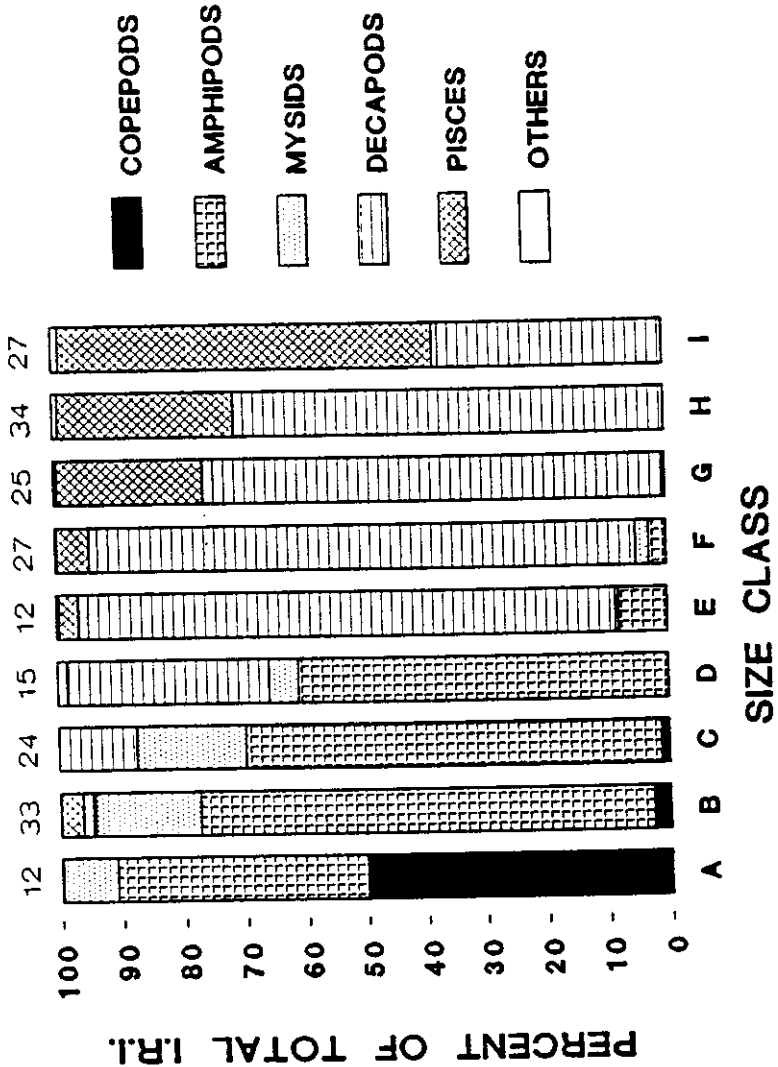


Figure 2. Ontogenetic changes in the diet of *Mycteroperca microlepis*. Bars represent relative proportions of major dietary components (percentage of total Index of Relative Importance) for each size class. See Figure 1 for description of size classes. Numbers above bars indicate the number of stomachs containing food in each respective size class.

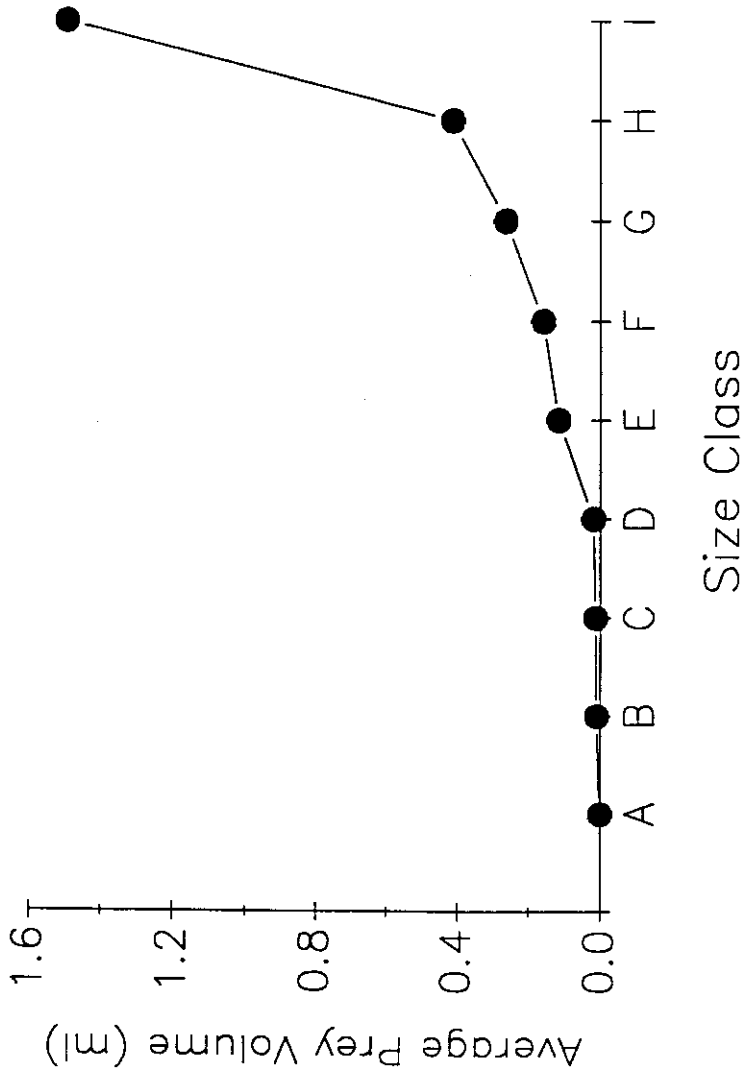


Figure 3. Relationship between size of *Mycteroperca microlepis* and average volume of prey consumed. See Figure 1 for description of size classes.

Hall, 1979). Wankowski (1979) showed that the optimum prey size for maximum growth of Atlantic salmon, *Salmo salar*, increases in direct proportion to fish length.

It is possible that comparison of the average length of prey items might have delineated the ontogeny of prey-size selection in gag better than comparison of shifts in prey volumes. In general, however, the trophic ontogeny of gag represents a sequence of size-dependent shifts from a diet composed mainly of microcrustaceans, to one of larger epibenthic invertebrates, and finally to one of even larger fishes. The caloric content per gram live weight of amphipods, decapods, and fishes from a shallow water estuarine system near Beaufort, North Carolina was shown by Thayer *et al.* (1973) to increase in that order. The increased pursuit and handling time incurred by piscivorous feeding habits (Werner, 1974) of large juvenile gag is apparently compensated for by the increased energetic profitability associated with piscivory.

According to Winemiller (1989), two main causes of size-related feeding shifts among piscivores are as follows: 1) juvenile fishes are constrained by their small sizes to exploit small food items; and 2) shifts from feeding on invertebrates to other fishes often coincide with changing food availabilities. In fish that ingest their prey whole, such as *M. microlepis*, mouth size obviously limits the maximum size of prey that can be handled (Brooks and Dodson, 1965; Werner, 1974). Many piscivorous fishes must therefore undergo a period of initial growth before initiation of their terminal feeding mode (Winemiller, 1989). This may partly account for the lag in the onset of piscivory observed in juvenile gag from 30-125 mm SL, and indicates that some alterations in the diet (and feeding mode) may be imposed by morphometric limitations of the mouth.

Prey availability most likely plays a role in the trophic ontogeny of *M. microlepis* in the Charleston harbor estuary as well. Trophic ontogeny of gag generally follows seasonal trends in abundance of invertebrate organisms in the oyster reef habitat in the high salinity tidal creeks of the Charleston Harbor estuary (Fox and Ruppert, 1987). Switches from predation on amphipods and grass shrimp to penaeid shrimp roughly coincide with seasonal peaks in abundance of those organisms. Most fishes utilized as prey by gag, however, are year-round residents of the estuary (*e.g.*, *Fundulus heteroclitus*, *Bathygobius soporator*, *Opsanus tau*), and commonly occur in the oyster reef habitats of South Carolina estuaries (Ogburn *et al.*, 1988). One fish species of major dietary importance, *Lutjanus griseus*, is presumably recruited from the plankton and utilizes the estuary as a nursery ground in much the same way as gag. *Lutjanus griseus* was commonly captured along with gag in habitat trays placed in oyster beds.

Ontogeny of feeding in *Mycteroperca microlepis* proceeds as a series of gradual changes rather than by distinct progressions, and results in acquisition of

the terminal feeding mode. Piscivory is initiated prior to estuarine egression in the fall, and likely prepares juvenile gag for their second major ecological transition, that to offshore live-bottom habitats.

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LITERATURE CITED

- Adams, S.M. 1976. Feeding ecology of eelgrass fish communities. *Trans. Am. Fish. Soc.* 4:514-519.
- Brooks, J.L. and S.J. Dodson. 1965. Predation, body size, and composition of the plankton. *Science* 150:28-35.
- Chao, L.N. and J.A. Musick. 1977. Life history, feeding habits, and functional morphology of juvenile sciaenid fishes in the York River estuary, Virginia. *U.S. Fish. Bull.* 75:657-702.
- Charnov, E.L. 1976. Optimal foraging: Attack strategy of a mantid. *Am. Nat.* 110:141-151.
- Collins, M.R., C.W. Waltz, W.A. Roumillat and D.L. Stubbs. 1987. Contribution to the life history and reproductive biology of gag, *Mycteroperca microlepis* (Serranidae), in the South Atlantic Bight. *Fish. Bull., U.S.* 85:648-653.
- Estabrook, G.E. and A.E. Dunham. 1976. Optimal diet as a function of absolute abundance, relative abundance, and relative value of available prey. *Am. Nat.* 110:401-413.
- Fox, R.S. and E.E. Ruppert. 1987. *Shallow-water marine benthic macroinvertebrates of South Carolina: Species identification, community composition, and symbiotic associations*. Belle W. Baruch Library in Marine Science, No. 14. University of South Carolina Press.
- Hoese, H.D., C.E. Richards and M. Castagna. 1961. Appearance of the gag, *Mycteroperca microlepis* in coastal waters of Virginia. *Chesapeake Sci.* 2:104-105.

Non-Peer Reviewed Section

- Huntsman, G.R. and R.L. Dixon. 1976. Recreational catches of four species of grouper in the Carolina headboat fishery. *S. 29th Ann. Conf. Southeast Assoc. Game Fish Comm.* pp.185-194.
- Johnson, G.D. 1981. Habitat identification of juvenile snappers and groupers, p. 18 in South Carolina Sea Grant Consortium. Bi-annual Report.
- Keener, P., G.D. Johnson, B.W. Stender, E.B. Brothers and H.R. Beatty. 1988. Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae), through a South Carolina barrier island inlet. *Bull. Mar. Sci.* 42(3):376-396.
- Leis, J.M. 1986. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae), p. 189-237 in *Tropical Snappers and Groupers: Biology and Fisheries Management*, J.J. Polovina & S. Ralston (eds.), Westview Press, Inc., Boulder, Colorado.
- Leucke, C. 1986. Ontogenetic changes in feeding habits of juvenile cutthroat trout. *Trans. Am. Fish. Soc.* 115: 703-710.
- Livingston, R.J. 1980. Ontogenetic trophic relationships and stress in a coastal seagrass system in Florida, p. 423-435 in *Estuarine Perspectives*, V.A. Kennedy (ed.), Academic Press, New York.
- Magnan, P. and G.J. FitzGerald. 1984. Ontogenetic changes in diel activity, food habits and spatial distribution of juvenile and adult creek chub, *Semotilus atromaculatus*. *Environ. Bio. Fish.* 11:301-307.
- Manooch, C.S. III and M. Haimovici. 1978. Age and growth of the gag, *Mycteroperca microlepis*, and size-age comparison of the recreational catch off the Southeastern United States. *Trans. Am. Fish. Soc.* 107 (2):234-240.
- McEachran, J.D., D.F. Boesch and J.A. Musick. 1976. Food division within two sympatric species-pairs of skates (Pisces: Rajiidae). *Mar. Biol. (Berl.)* 35:301-307.
- McErlean, A.J. 1963. A study of the age and growth of the gag, *Mycteroperca microlepis* Goode and Bean (Pisces: Serranidae) on the west coast of Florida. *Fla. Board Conserv. Mar. Lab. Tech. Serv.* 41:1-29
- and C.L. Smith. 1964. The age of sexual succession in the protogynous hermaphrodite *Mycteroperca microlepis*. *Trans. Am. Fish. Soc.* 93:301-302.
- Miller, J.M., L.B. Crowder and M.L. Moser. 1985. Migration and utilization of estuarine nurseries by juvenile fishes: an evolutionary perspective. in *Migration: Mechanisms and Adaptive Significance*, M.A. Rankin (ed.), Marine Sci. Inst., Univ. of Texas, Austin Contrib. in Mar. Sci. 27.
- Naughton, S.P. and C. H. Salomon. 1985. *Food of gag (Mycteroperca microlepis) from North Carolina and three areas of Florida*. NOAA Technical Memorandum MNFS-SEFC-160. p. 1-36.

- Ogbum, M.V., D.M. Allen and W.K. Michener. 1988. *Fishes, shrimps, and crabs of the North Inlet Estuary, S.C.: A four-year seine and trawl survey*. Baruch Institute Tech. Rept. No. 88-1. 299pp. University of South Carolina, Columbia.
- Pinkas, L., M.S. Oliphant and I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California waters. *Calif. Dept. Fish Game Fish. Bull.* 152. 105 p.
- Powles, H. and C.A. Barans. 1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. *Mar. Fish. Rev.* 42:21-35.
- Pyke, G.H., H.R. Pulliam and E.L. Charnov. 1977. Optimal foraging: A selective review of theory and tests. *Quart. Rev. Biol.* 52:137-154.
- Schmitt, R.J. and G.J. Holbrook. 1984. Ontogeny of prey selection by black surfperch (*Embiotoca jacksoni*): The roles of fish morphology, foraging behavior, and patch selection. *Marine Ecology Progress Series.* 18:225-239.
- Sedberry, G.R. 1983. *Food habits and trophic relationships of a community of fishes on the outer continental shelf*. NOAA Tech. Rept. NMFS-SSRF-773. 56 pp.
- and J.A. Musick. 1978. Feeding strategies of some demersal fishes of the continental slope and rise off the mid-Atlantic coast of the U.S.A. *Mar. Biol. (Berl.)* 44:357-375.
- and R.F. Van Dolah. 1984. Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the U.S.A. *Env. Biol. Fish.* 11(4):241-258.
- Singer, M.M. 1985. Food habits of juvenile rockfishes (Sebastes) in a central California kelp forest. *Fish. Bull.* 83(4):531-541.
- Smith, C.L. 1971. A revision of the American groupers: Epinephelus and allied genera. *Bull. Mus. Nat. Hist.* 146: 67-242.
- Stoner, A.W. and R.J. Livingston. 1984. Ontogenetic patterns in diet and feeding morphology in sympatric Sparid fishes from seagrass meadows. *Copeia* 1:174-187.
- Thayer, G.W., W.E. Schaaf, J.W. Angelovic and M.W. Lacroix. 1973. Caloric measurements of some estuarine organisms. *U.S. Fish. Bull.* 71:289-296.
- Wankowski, J.W.J. 1979. Morphological limitations, prey size selectivity, and growth response of juvenile atlantic salmon, *Salmo salar*. *J. Fish. Biol.* 14:89-100.
- Werner, E.E. 1974. The fish size, prey size, handling time in several sunfishes and some implications. *J. Fish. Res. Board Can.* 30:787-797.
- and J.F. and D.J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. *Ecology* 60:256-264.

Non-Peer Reviewed Section

- Windell, J.T. 1971. Food analysis and rate of digestion. p. 215-266 in *Methods for Assessment of Fish Production in Fresh Waters*, W.E. Ricker (ed.), Int. Biol. Programme (IBP) Handb. 3.
- Winemiller, K.O. 1989. Ontogenetic diet shift and resource partitioning among piscivorous fishes in the Venezuelan llanos. *Env. Biol. Fish.* **26**:177-199.