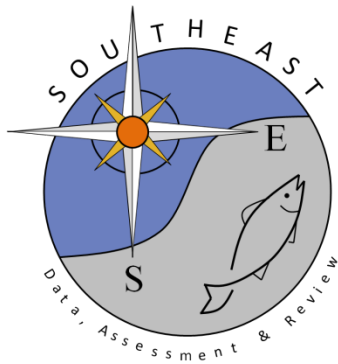


LIFE HISTORY OF JUVENILE GAG, MYCTEROPERCA MICROLEPIS, IN NORTH
CAROLINA ESTUARIES

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ABSTRACT

Gag, *Mycteroperca microlepis*, is the most abundant and widely distributed of the seven grouper species that may occur as juveniles in North Carolina estuaries. Gag larvae migrate from offshore spawning areas to high salinity estuaries and are most common in seagrass beds. Monthly collections (1981-1982) revealed that young gag first appeared in grass beds in mid-late April at 13-16 mm SL (mean = 14.9 mm). They reached maximum abundance by May or June (mean size = 31.6 mm) and by September attained lengths of 99-186 mm (mean = 132.3 mm). With growth, many gag moved from grass beds to other complex estuarine habitats. Most young-of-the-year gag left the estuaries for offshore reefs during mid-late autumn, and cold weather fronts may have precipitated these emigrations. Gag were carnivorous throughout their estuarine period. Fish <70 mm fed mainly on copepods, amphipods, and *Palaemonetes* spp. As they grew, gag fed more on larger crustaceans and other fishes. We determined meristic values of all grouper collected; however, color patterns were most useful for identifying all juvenile groupers. The weight-standard length relationship was: $W = 1.9 \times 10^{-5}(SL)^{3.04}$, $N = 244$, $r^2 = 0.99$. The TL-SL regression was: $TL = 1.03 + 1.22(SL)$, $r^2 = 0.99$.

Epinepheline groupers (Serranidae) are well represented in North Carolina by 21 species whose adult populations are affiliated with offshore reefs/hard bottoms. Groupers are important in the recreational (Huntsman, 1976) and commercial (Rohde and Francesconi, 1992) fisheries of the Carolinas and are consistently listed among the most common hard ground fishes of the southeastern United States (Miller and Richards, 1980; Grimes et al., 1982; Parker and Ross, 1986). Life history and fisheries data have been reported for the adults of several species; however, the early life history of most groupers has not been adequately described (Thresher, 1984; Leis, 1987; Richards, 1990) because young groupers (especially larvae) are difficult to identify, are cryptic, and they occur in habitats that are difficult to sample (Keener et al., 1988).

Groupers spawn along the outer continental shelf of the southeastern United States during late winter through early spring (Powles, 1977; Collins et al., 1987). Larvae and/or juveniles of many species consistently tend to occupy shallow, even estuarine, waters not frequented by the adults (Smith, 1978; Leis, 1987; Keener et al., 1988; Ross, 1988; Hood and Schlieder, 1992; Brule and Canche, 1993). The larvae or juveniles of seven species of groupers have been collected from North Carolina estuaries (Table 1).¹ Young gag (*Mycteroperca microlepis*), black grouper (*M. bonaci*), and red grouper (*Epinephelus morio*) are the most frequently collected in North Carolina estuaries and can be locally abundant.

In this study we describe estuarine recruitment, distribution, growth, and diet of juvenile gag in North Carolina and present evidence supporting Keener et al.'s (1988) hypothesis that gag are dependent on estuarine habitats as nursery areas. Because young groupers are difficult to identify, we also present meristic and color pattern data for all grouper species we collected. Gag occur in continental

¹ A record of larval jewfish (*E. itajara*) from near Beaufort, North Carolina (A. Powell, pers. comm.) was not included because it can not be confirmed.

Table 1. Epinepheline groupers (Serranidae) reported from North Carolina estuaries as juveniles. Abundance categories are relative estuarine rankings within the groupers only. Salinities are the total ranges from all references.

Species	Abundance	Salinity (‰)	References*
<i>Mycteroperca microlepis</i>	abundant	2–36	1, 2, 4, 5, 6
<i>M. bonaci</i>	common	4–36	1, 2, 5
<i>M. phenax</i>	rare	32	1
<i>M. venenosa</i>	rare	polyhaline	2
<i>Epinephelus morio</i>	common	4–25	1, 2, 5
<i>E. nigritus</i>	rare	24–30	3, 5
<i>E. striatus</i>	rare	19	2, 5

* 1 = This study, 2 = Smith (1907), 3 = Turner and Johnson (1973), 4 = Adams (1976a), 5 = Schwartz et al. (1981), 6 = Ross and Epperly (1985).

shelf and estuarine waters from Massachusetts to the Campeche Bank and in Bermuda and Brazil (Briggs, 1958; Smith, 1978), being most common in warm-temperate waters. Distribution, age and growth, diet, reproduction, coloration, and fisheries have been reported for adult gag (McErlean, 1963; McErlean and Smith, 1964; Manooch and Haimovici, 1978; Naughton and Saloman, 1985; Collins et al., 1987; Gilmore and Jones, 1992; McFall, 1992; Hood and Schlieder, 1992). The only detailed life history studies on juvenile gag described ingress, ages, growth, trophic ontogeny and feeding morphology from estuaries near Charleston, South Carolina (Keener et al., 1988; Mullaney, 1991).

METHODS

Most juvenile gag were collected from two polyhaline stations, Phillips Island and northeastern Bogue Sound (Fig. 1), whose sampled areas equalled 656 and 343 m², respectively. These stations were dominated by submerged aquatic grasses, *Zostera marina* and *Halodule wrightii*, with small areas

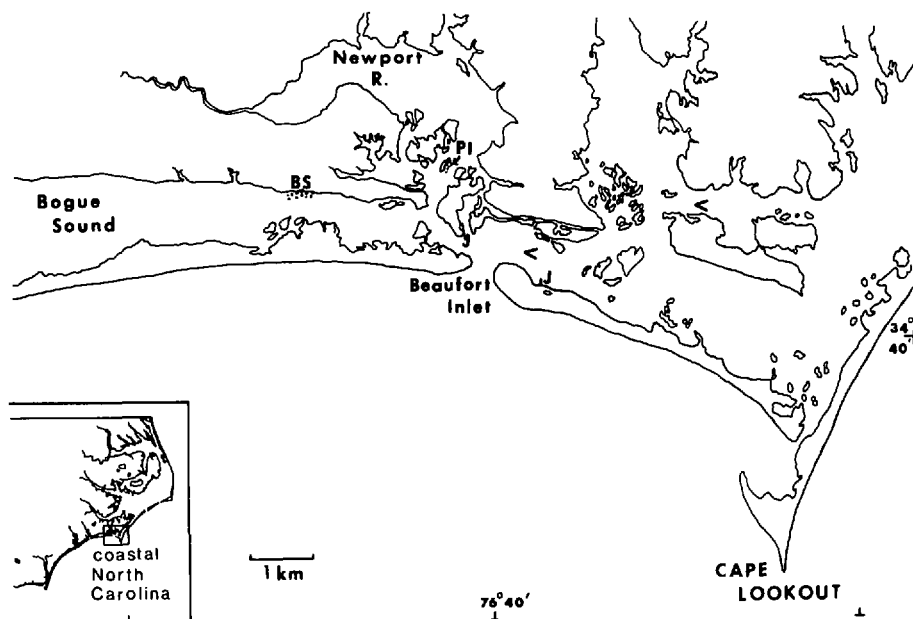


Figure 1. Sampling locations in the Beaufort, North Carolina area. BS = grass bed station in Bogue Sound, PI = grass bed station at Phillips Island, J = estuarine jetties, < = channel net stations.

of sand among the beds and along the shoreward edges of the stations. Tidal range at these stations was about 0.7 m and most collections were made at mid-ebb to low tide (depth \approx 0.2–0.7 m). One (occasionally both) of these stations was sampled monthly from March through October 1981 and from April through September 1982 using either 3 m, 3.2 mm mesh or 18–30 m, 6.4 mm mesh seines. More frequent collections were made during the spring recruitment season (April–early June) in both years. No sampling was conducted during winter because previous sampling indicated that juvenile groupers were absent or rare in the estuaries during that time. At each sampling if no grouper were collected in 6–7 seine hauls, sampling was discontinued. If grouper were collected, seining continued until no grouper were collected in 2–3 successive hauls. Periodically, representative groupers were kept alive and photographed (Kodachrome 64 film) in small aquaria to describe color patterns. Otherwise, all groupers were preserved in 10% formalin solution in the field and later transferred to 40% isopropanol.

Supplemental data were acquired from several sources. Size, distribution, and abundance data were obtained from monthly (March–November 1981–1982) state-wide estuarine trawl surveys (79 stations) conducted by the North Carolina Division of Marine Fisheries (NCDMF). These stations were located in shallow, mostly mud-bottom creeks and bays and were sampled with 1 min (=68.6 m) tows of a 3.2 m, 3.2 mm mesh cod end flat trawl. Two commercial shrimp channel net sets (Fig. 1) were sampled irregularly during the autumn of 1980. These anchored 30 m wide, 4 m deep nets were fished at the surface at night on falling tides, and all groupers collected were saved on ice, then preserved as above for later analyses. The senior author used SCUBA (depths <34 m) and submersibles (23–152 m depths) from 1975 to 1985 to determine distribution and relative abundance of groupers (and other fishes) on North Carolina hard bottoms in the estuary (two jetties near Beaufort, North Carolina; Fig. 1) and in offshore waters (43 locations). Submersible methods were described by Parker and Ross (1986). SCUBA methods consisted of visually categorizing groupers as larvae, juveniles, or adults and recording their relative abundance as rare (<10), common (10–100), or abundant (>100).

Gag stomachs were removed and their contents washed onto a Petri dish marked with a grid of 1 mm squares. All items ingested were identified to the lowest possible taxa. We estimated volume (mm^3) of each food item in the stomach by grouping like items on the Petri dish, flattening them to a uniform height (usually 1 mm), and then counting grid squares occupied by the items. Total food volume contained in each stomach equaled the sum of the volumes of all food items. Volumes of each item were converted to percentages of the total volume of each stomach. Percent frequency of each item equaled the number of times the item occurred divided by the total number of stomachs times 100. Diet data were grouped into four seasonal time periods: April–May = spring, June = early summer, July–August = late summer, and September–October = autumn.

Meristic and color pattern data were used to identify groupers to species. Because these data were not well documented in the literature for juveniles, we initially had difficulty identifying the smallest groupers. Therefore, subsamples ($N = 2\text{--}5$) of groupers (mostly <25 mm SL) representing each color pattern were held in aquaria until they grew to sizes that allowed ready identification to species. Thus, we were able to establish the initial color patterns exhibited by the dominant species. The following meristic counts were recorded for all groupers: dorsal spines and rays, anal spines and rays, pectoral rays, and total first arch gill rakers. Elongated second dorsal, pelvic, and preopercle spines were evidence that individuals had recently recruited (settled) to benthic habitats from the plankton (Thresher, 1984; Keener et al., 1988). Groupers were measured to the nearest mm (total and standard lengths) and weighed to the nearest 0.01 g.

RESULTS

Recruitment, Distribution, and Abundance.—Each year a single cohort of gag, initially covering a range of about 10 mm SL (Fig. 2), recruited to North Carolina estuaries. Gag first appeared in the grass beds as early as mid-April. Most recruitment occurred during May of both years (Table 2) when fish averaged 16.5 mm SL. We assumed these fish had recently settled from the water column because all gag collected in April and May 1981 (all <20 mm, Fig. 2) and most of those from May 1982 (the fish <20 mm, Fig. 2) exhibited recent settlement characteristics (see Methods). Recruitment to benthic habitats was nearly over by early June because only a few fish ($N = 9$, all <20 mm) displayed planktonic characteristics. The earliest collections of young-of-the-year gag by the NCDMF were also in May or June.

For the first 3–4 months of their estuarine phase young-of-the-year gag were most abundant in grass beds in high salinity areas. Gag ($N = 80$) were collected

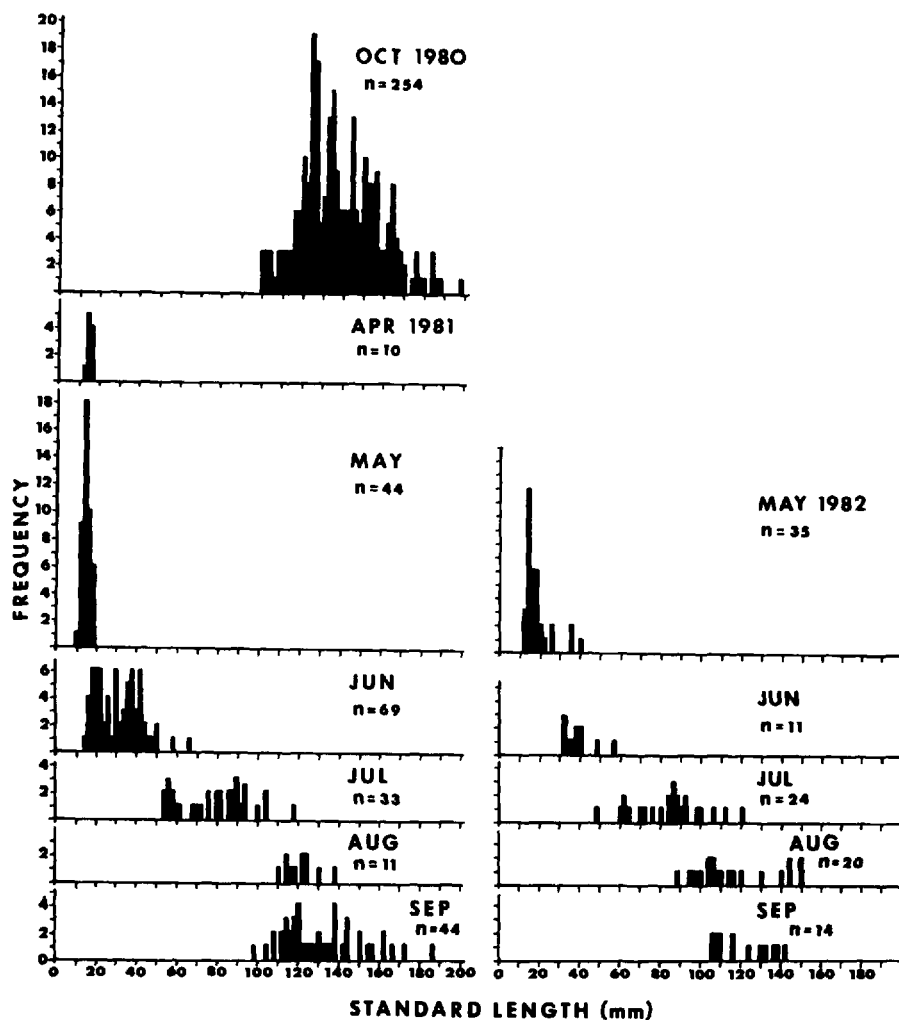


Figure 2. Monthly standard length frequency graphs for gag collected in North Carolina estuaries, October 1980–September 1982.

at only 9 of the 79 NCDMF trawl stations, and most (91%) of these were from four grass bed stations. Despite the variety of environments sampled, all 9 of these gag stations were polyhaline (mean bottom salinity = 26‰) and near inlets. At the two grass bed stations we sampled overall mean bottom salinity was 31.5‰. No juvenile gag were observed on the two estuarine jetties prior to middle July.

Between late June and early July gag abundance in the grass beds declined rapidly (Table 2) as they moved toward other complex substrate estuarine habitats. From late July through early November gag were frequently observed (60% of the dives) around the two estuarine jetties. Extensive surveys of offshore hard grounds (542 combined SCUBA and submersible dives at 43 offshore sites from 10 to 152 m) indicated that small gag (<100 mm TL) were absent or rare throughout the year. Larger juvenile gag appeared on offshore wrecks and rock ledges in

Table 2. Numbers of grouper collected by seine in two North Carolina grass beds (BS = Bogue Sound, PI = Phillips Island) by sample date. Bottom temperature (Btemp, °C) and salinity (Bsal, ‰) are included when available.

Date	Location	Btemp/Bsal	Gag	Black	Red	Scamp
29 Mar 81	BS	14/32				
23 Apr	BS	21/33	6			
28 Apr	BS	22/35	4			
13 May	BS	22/30	20			
25 May	BS	23/32	24	1		
06 Jun	PI	27/32	29	3		
21 Jun	PI	—/—	33		2	
19 Jul	BS	31/32	8			1
26 Jul	BS	31/32	9			
30 Aug	BS	28/28	11			
04 Oct	BS	22/35	2			
17 Apr 82	BS	22/—				
02 May	BS	20/—	3			
03 May	PI	20/26	6	1		
22 May	BS	27/—	6			
26 May	BS	25/—	4			
01 Jun	BS	30/—				
25 Jul	BS	29/—	1			
05 Sep	BS	—/—	1			

depths ≤ 30 m from mid-summer (usually July) through autumn, apparently after emigration from estuaries.

Although uncommon, the juvenile black and red grouper and scamp we collected (Table 2) were distributed similarly to gag. They were collected in grass beds mostly during May or June (Table 2), and they appeared on the estuarine jetties from late summer through autumn. They were absent from offshore hard grounds at sizes < 100 mm, and at larger sizes were observed there only from late summer through autumn. These species were not identified in NCDMF trawl sampling.

Growth.—Nearly identical sigmoidal growth curves, apparent in both years, suggested three distinct estuarine growth phases (Fig. 3). Early growth rates were slow until fish attained ≈ 25 mm SL (early June). After recruitment to benthic habitats ended, growth was quite rapid from June through August (or until ≈ 120 mm SL), with gag reaching 99 to 186 mm by September (Fig. 2). During this 92-day period mean size increased 95 mm (i.e., growth rate = 1.03 mm/da). Growth rates declined during the last months of the cohort's estuarine phase. In three successive autumns, gag attained similar mean sizes of 138 (Oct 80), 132 (Sep 81), and 120 (Sep 82) mm SL. The largest gag observed during our estuarine surveys was 198 mm SL, and records of gag > 200 mm SL are rare from North Carolina estuaries.

Young-of-the-year gag had a typical weight-standard length relationship of the form: $W = 1.9 \times 10^{-5}(\text{SL})^{3.04}$, $N = 244$, $r^2 = 0.99$. The TL-SL regression for all sizes of gag combined was: $\text{TL} = 1.03 + 1.22(\text{SL})$, $N = 244$, $r^2 = 0.99$.

Diet.—We examined 246 gag stomachs of which 96 (39%) were empty. Most empty stomachs ($N = 58$) were from the smallest fish collected during April–May. The highest percentage of stomachs with food (82%) occurred during the period of fastest growth (June–August). Overall, we identified 30 prey items from gag stomachs (Table 3); however, individual gag were not diverse feeders as

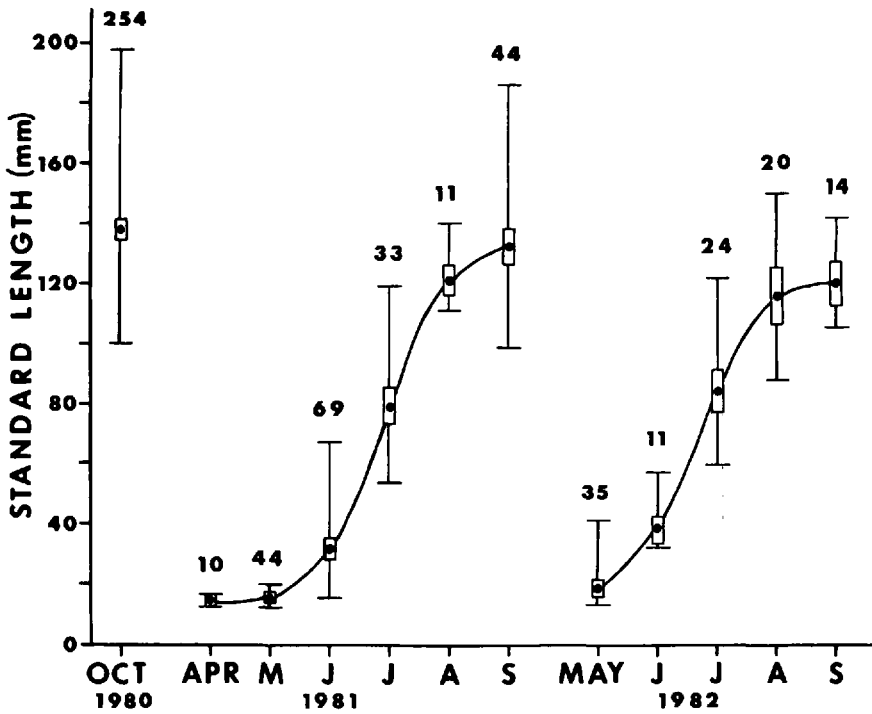


Figure 3. Monthly mean standard lengths (dots) of juvenile gag collected in North Carolina estuaries, October 1980–September 1982. Vertical lines are length ranges and open boxes are \pm one standard error of the mean. Sample sizes are above each line. Curves were fit by eye.

evidenced by the low overall mean number of different items ingested (1.7, range = 1–8, SD = 1.3). Feeding diversity changed seasonally with individual gag eating significantly (t -test, $P < 0.05$) more varieties of food items during late summer (mean = 2.5) than during spring or early summer (combined mean = 1.4). Mean number of different items ingested during autumn (1.8) was statistically similar ($P > 0.05$) to the other seasons.

We grouped all prey items into 7 general categories: Copepods, Amphipods (all tubicolous), Caridean shrimp (mostly *Palaemonetes*), Penaeid shrimp, Fish (mostly *Anchoa*), miscellaneous Crustaceans (mostly various shrimp parts) and Other (Table 3). Overall, caridean shrimp were the dominant food throughout estuarine life, were eaten by nearly 75% of the gag, and contributed 51% to the total volume of food. Penaeid shrimp and fish were nearly equally important in both overall frequency (13 and 15%, respectively) and volume (21 and 16%, respectively). Amphipods and copepods were frequently ingested, but due to their small sizes they contributed only a small percentage to the overall food volume (Table 3). Miscellaneous crustacea was an important general category; however, its largest components, unidentified shrimp and parts, most likely belonged to caridean and/or penaeid shrimp categories. The category Other was omitted from further analysis because of its small contribution to the diet and because it represented a mixture of generally unrelated, infrequently eaten items (Table 3).

With growth, diet shifted from smaller size prey categories (copepods and amphipods) toward larger prey (penaeid shrimp and fish) (Figs. 4, 5). Copepods, the smallest prey, were not eaten after June (gag sizes ≤ 67 mm SL, Fig. 4). Although

Table 3. Overall percent frequency and volume of food items ingested by juvenile gag in North Carolina estuaries, 1981-1982. Percentages are based on the number of stomachs with food (N = 150).

Food item	% Frequency	% Volume
Caridean Shrimp	74.7	51.1
<i>Alpheus normanni</i>	6.0	16.7
<i>Crangon septemspinosa</i>	0.7	0.2
<i>Hippolyte</i> sp.	3.3	0.6
<i>Palaemonetes intermedius</i>	1.3	0.3
<i>P. pugio</i>	18.0	7.2
<i>P. vulgaris</i>	10.0	10.2
<i>P.</i> sp.	20.0	7.9
<i>Periclimenes longicaudatus</i>	6.0	3.2
<i>Tozeuma carolinense</i>	5.3	4.7
Unidentified parts	3.3	<0.1
Penaeid Shrimp	12.7	20.8
<i>Penaeus aztecus</i>	0.7	5.7
<i>P. duorarum</i>	0.7	3.5
<i>P. setiferus</i>	1.3	1.2
Unidentified	10.0	10.4
Amphipods (tubicolous)	24.0	0.7
<i>Ampithoe</i> sp.	6.0	0.2
<i>Jassa falcata</i>	9.3	0.3
Unidentified	9.3	0.2
Copepods	7.3	<0.1
<i>Euterpina acutifrons</i>	1.3	<0.1
<i>Harpacticus</i> sp.	1.3	<0.1
<i>Paracalanus</i> sp.	1.3	<0.1
<i>Pseudodiaptomus coronatus</i>	1.3	<0.1
Unidentified calanoids	0.7	<0.1
Unidentified harpacticoids	1.3	<0.1
Fish	14.7	16.2
<i>Anchoa</i> sp.	2.7	3.6
<i>Bairdiella chrysoura</i>	0.7	<0.1
<i>Orthopristis chrysoptera</i>	0.7	0.2
<i>Syngnathus</i> sp.	1.3	0.4
Unidentified juveniles	8.7	12.0
Unidentified larvae	0.7	<0.1
Miscellaneous crustacea	29.3	10.6
<i>Callinectes sapidus</i>	1.3	2.1
<i>Clibanarius vittatus</i>	0.7	1.0
<i>Mysidopsis</i> sp.	2.0	1.4
<i>Squilla empusa</i>	0.7	<0.1
Unidentified shrimp	14.0	3.2
Unidentified hermit crab	0.7	0.2
Unidentified crab	0.7	0.1
Unidentified parts	9.3	2.5
Other	11.3	0.6
<i>Cyathura</i> sp.	0.7	0.1
<i>Erichsonella attenuata</i>	0.7	<0.1
<i>Nereis</i> sp. + polychaete bristles	1.3	0.1
Sand	2.0	<0.1
Seagrass	5.3	0.2
Unidentified organic matter	1.3	0.3

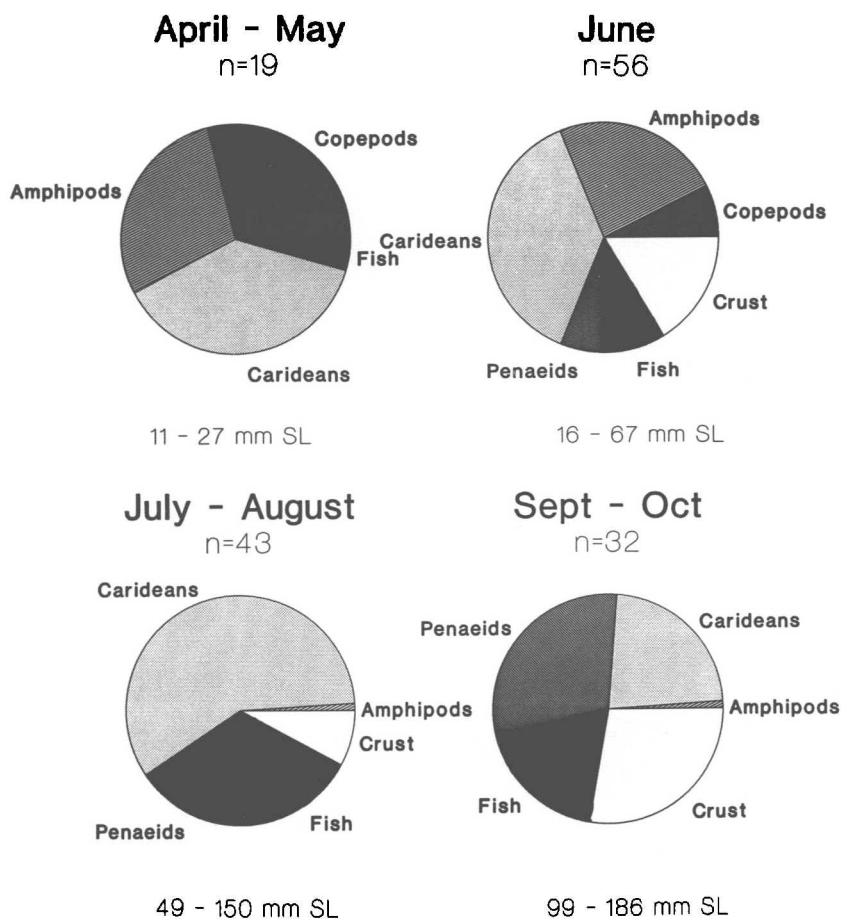


Figure 4. Percent frequencies of major food categories eaten by juvenile gag in North Carolina estuaries by season, 1981-1982. Crust = crustaceans.

caridean shrimp were an important food throughout the estuarine phase in both percent frequency (Fig. 4) and volume (Fig. 5), they were not dominant in the largest gag (>99 mm SL, September and October). They were largely replaced in the diet by fish and penaeid shrimp.

Emigration.—Movement of gag out of the estuary in autumn appeared to be accelerated by rapid decreases in water temperature caused by passage of cold fronts. Prior to 30 September 1980 catches from the channel net we sampled near Beaufort Inlet contained very few grouper or other fishes. Catches from two other channel nets also set near Beaufort Inlet had similar low species richness during this time (T. Credle and M. Hooper, pers. comm.). Between 27-28 September a cold front, accompanied by strong northerly winds, passed through the area, causing water temperatures to decline from 27° to 22°C over a 2-3 day period (W. F. Hettler, pers. comm.). The channel net fish catches increased abruptly on 30 September (L. Davidson, pers. comm.) and peaked on 1 and 2 October (for gag see Fig. 2). Only 6 h of total fishing time on the two peak nights produced 44 total fish species. In addition to gag (N = 267), one black grouper and one red grouper were the only other groupers captured during these samples. Because the net

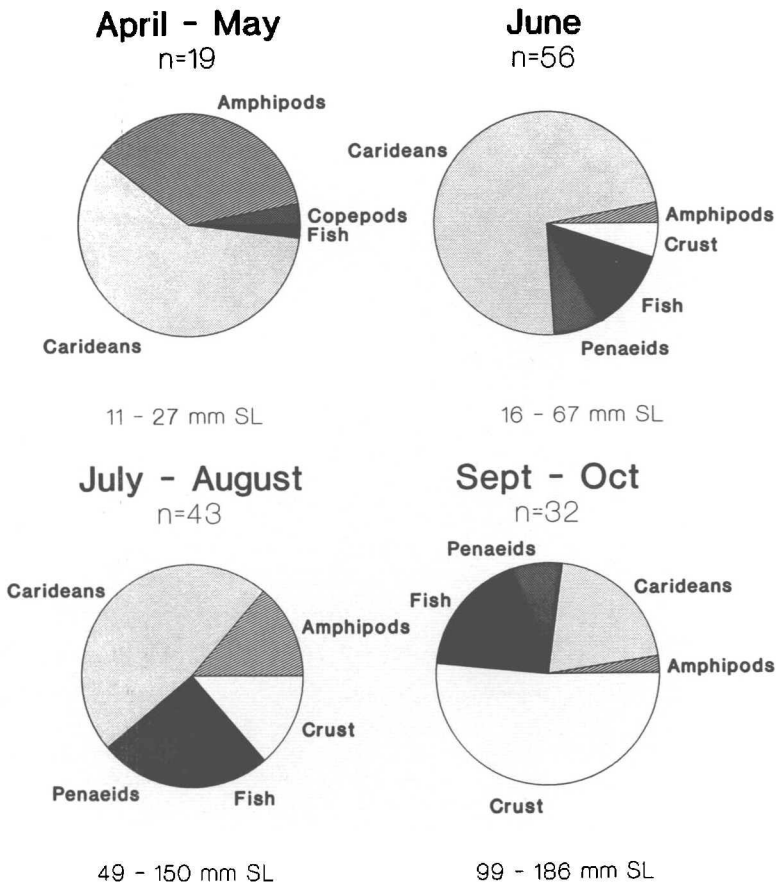


Figure 5. Percent volumes of major food categories eaten by juvenile gag in North Carolina estuaries by season, 1981–1982. Crust = crustaceans.

sampled was within 1 km of the inlet and because these fishes were moving with the strong ebbing current, we assumed that they were leaving the estuary. Corresponding with this emigration and the apparent decline in overall estuarine abundance of gag, we observed on 11 October and 1 November 1980 increased numbers of young-of-the-year gag (classified as abundant and common, respectively), black grouper, red grouper, and scamp on nearshore wrecks (7–24 km from Beaufort Inlet) compared to observations earlier in the year (before September). Juvenile groupers were observed on estuarine jetties until early November, but none were ever collected or observed there from mid-November through March.

Identifications: Meristics and Color Patterns.—The meristics we measured overlapped considerably (Table 4) and thus, were generally not useful for separating grouper species. However, red grouper could be identified by a low anal ray count (9–10, Table 4) when small (<30 mm SL) and when larger by a uniform reddish brown color. Gag and black grouper, overlapping in all counts (Table 4), were the most difficult to separate. Recently settled gag (11–20 mm SL) had a uniform coloration (Fig. 6), which varied from nearly transparent (often with a reddish tint) at early settlement to a greenish brown. By about 25–30 mm SL gag displayed a mottled, reticulated pattern of light and dark patches (Fig. 7), which they

Table 4. Selected meristic frequencies of juvenile groupers collected in North Carolina estuaries, 1981-1982

	Dorsal spines			Dorsal rays			
	X	XI	XII	15	16	17	18
Gag	10	203	2	1	47	128	38
Black		5			1	4	
Red		2			2		
Scamp		1					1

	Anal rays					Left + right pectoral rays						
	9	10	11	12	13	30	31	32	33	34	35	36
Gag		7	191	17	1	4		15	19	162	7	7
Black				4	1				2	3		
Red	1	1						1				1
Scamp			1							1		

	Total first arch gill rakers									
	18	19	20	21	22	23	24	25	26	27
Gag	2	10	26	43	36	30	19	42	8	1
Black		2	1	2						
Red					2					
Scamp										1

generally retained throughout estuarine residency. In contrast, small, recently settled black grouper (15-31 mm SL) displayed a distinct color pattern of large, dark, rectangular blocks separated by thin pale spaces (Fig. 6). They retained this pattern (Fig. 7), although it became somewhat less distinct with growth. All scamp we collected or observed were large juveniles distinguishable by coloration alone. For the sizes we collected (10-198 mm SL) color patterns were adequate to identify most groupers even after they were preserved.

Gag gill raker counts exhibited a wide range and bi-modality (Table 4) because they increased with increasing fish size. Total gill raker (GR) count was significantly correlated ($r^2 = 0.57$) with SL and was described by the nonlinear relationship: $GR = 16.23 + 3.95(\log SL)$.

DISCUSSION

Early, post-settlement juvenile gag occur predominantly in estuaries. While they are frequently reported from a wide variety of estuaries (e.g., Adams, 1976a; Gilmore, 1977; Ross and Epperly, 1985; Hood and Schlieder, 1992), there are few records of small (<50 mm SL) juvenile gag on offshore benthic habitats. We agree with Keener et al. (1988), that young-of-the-year gag are estuarine dependent, in the same manner as many other offshore winter-spring spawned fishes of the southeastern United States (e.g., *Leiostomus xanthurus*, *Micropogonias undulatus*, *Lagodon rhomboides*, *Orthopristis chrysoptera*). Gag larvae may be transported across the shelf to estuaries by the mechanisms proposed for other estuarine dependent fishes (Miller et al., 1984); however, they consistently recruit to estuarine benthic habitats over a shorter period than these fishes.

Although collected less frequently, juvenile black and red groupers may also be estuarine dependent. They are consistently reported from estuaries (Wang and Raney, 1971; Gilmore, 1977; Mullaney, 1991), but have not been reported from offshore benthic habitats at small sizes. Complex habitats need to be more extensively sampled to document areas that are critical to early life history stages of cryptic reef fishes.

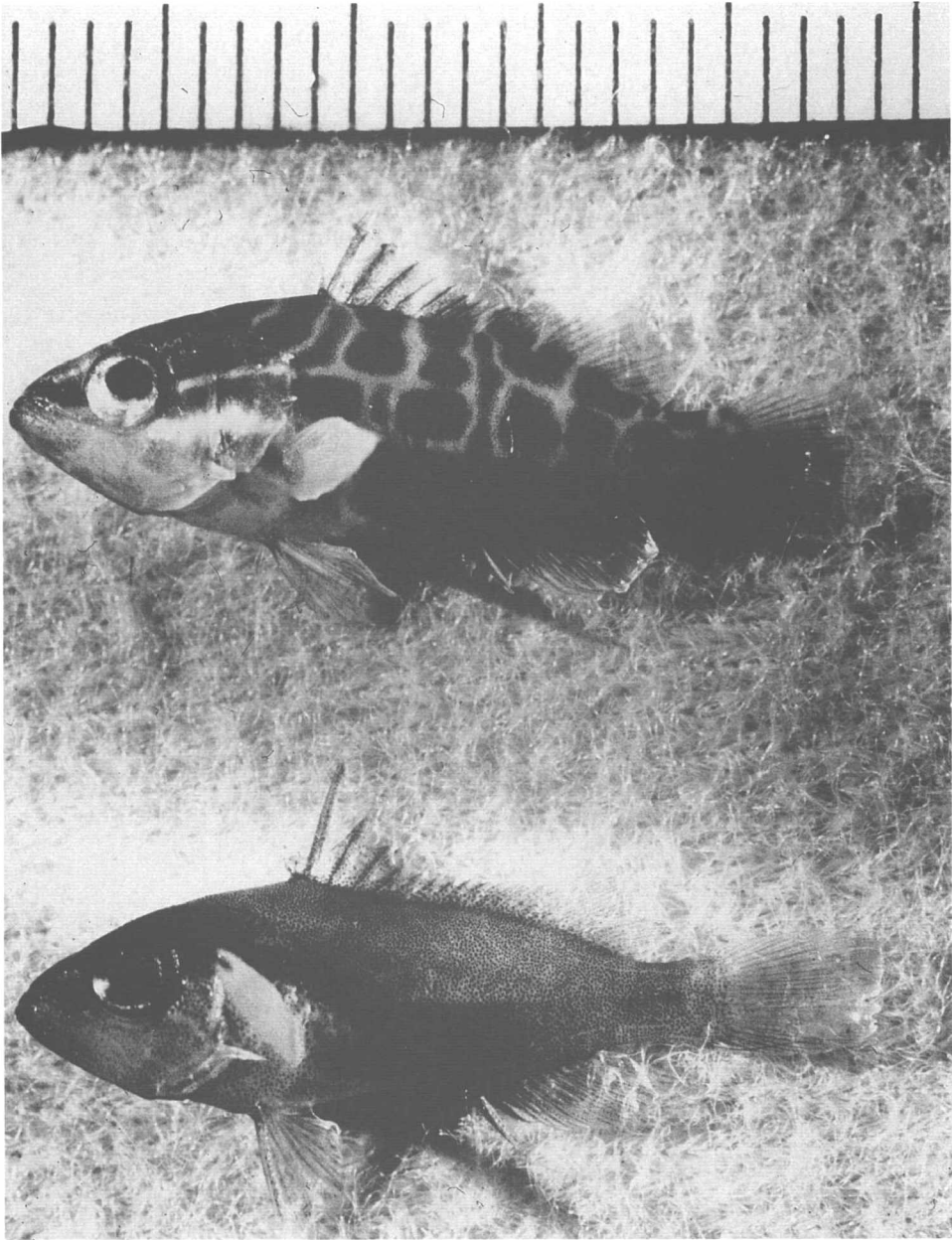


Figure 6. Recently settled black (top) and gag (bottom) groupers collected in the Phillips Island grass bed, 6 June 1981. Each scale mark at the top of the figure = 1 mm.

We propose that young gag initially prefer settlement (or survive better) in high salinity estuarine grass beds, and that in the absence of grass beds they occupy other complex habitats. In North Carolina gag were most abundant in polyhaline grass beds from first settlement (April–May) through mid-summer. Commercial long-haul seine fishermen reported that gag can be extremely abundant (late sum-



Figure 7. Juvenile black (top) and gag (bottom) groupers collected in the Phillips Island grass bed, 6 June 1981. Each scale mark at the top of the figure = 1 mm.

mer-fall) in hauls made near or over grass beds in eastern Pamlico Sound (B. Foster, pers. comm.). In other studies where diverse estuarine habitats were sampled, juvenile gag were most common in polyhaline grass beds (Wang and Raney, 1971; Gilmore, 1977; Heck and Thoman, 1984; Ross and Epperly, 1985); however, all available reef-like habitats were not sampled in most of these studies. Mullaney (1991) found that in South Carolina estuaries gag preferred to settle on oyster rocks, the only abundant reef-like habitat, rather than on adjacent soft bottoms. We did not sample oyster rocks during this study, and gag may use this habitat, or other hard substrates, during early recruitment in North Carolina. Oyster rocks are generally undersampled; nevertheless, juvenile gag seem to be less common in estuarine systems that lack grass beds but that do have extensive oyster reefs such as those of the Cape Fear River, North Carolina (Schwartz et al., 1981) and Georgia (Dahlberg, 1972). Whether gag prefer grass beds to other available complex habitats or whether they grow or survive better in grass beds is unknown.

As the season progressed juvenile gag moved from grass beds to other complex habitats (jetties, pilings) and open water areas. An indication of their late season move to more open waters was their consistent appearance during or after August (1982–1985) in the Pamlico Sound commercial long-haul seine fishery (Ross et al., 1986; Moyer and Strasser, 1989). As reported for other estuarine dependent

fishes (Suttkus, 1955; Ogren and Brusher, 1977), mass emigration of gag from estuaries may be precipitated by changes in weather patterns and/or rapid changes in water temperatures. The sudden cold fronts and associated north winds that occur in autumn are called "Mullet Blows" in North Carolina because they seem to cause mass schooling and rapid movement of fishes, like *Mugil* spp., out of estuaries. A few juvenile gag were observed on nearshore wrecks during late summer and early fall (prior to the cold front described in the Results), and we assume that these fish represented early emigrants from the estuaries.

Juvenile gag consistently grew slower at the beginning and end of the estuarine phase. Continued immigration of small gag during the early recruitment period may have caused us to underestimate individual growth rates. However, Keener et al. (1988) and Mullaney (1991), using age specific data, also documented slow early growth rates which increased rapidly after settlement. The decline in growth rates by autumn could be explained by early emigration of faster growing individuals; however, juvenile gag occurring offshore during late summer through autumn did not appear to be larger than those in the estuaries. By autumn, McErlean's (1963) mean gag SL's were similar to those of this study, exhibiting the same decline in growth. The autumn decline in gag growth rates may be caused by the decreasing water temperatures and, perhaps, by reduced feeding efficiency during their movements into more open waters. Rapid growth may resume after gag reach offshore hard grounds, as suggested by the growth data of Manooch and Haimovici (1978).

Rapid growth appears to be characteristic of gag during the period after settlement (early June) until emigration from estuaries. Juvenile gag from Tampa Bay and Charlotte Harbor, Florida (McErlean, 1963; Wang and Raney, 1971; Hood and Schlieder, 1992) and from Virginia (Hoese et al., 1961) also grew rapidly. The Florida gag were larger during May–July than North Carolina specimens, while the Virginia July–August specimens were smaller. Latitudinal differences in water temperatures may explain the summer differences in mean gag sizes between areas.

The rapid growth of juvenile gag in grass beds is complemented by reports that they are carnivorous and voracious predators (Adams, 1976b; Nelson, 1979a; Mullaney, 1991) with relatively high ecological efficiencies (Adams, 1976c). Like other juvenile fishes from North Carolina estuaries (Currin et al., 1984; Ross, 1992), Adams (1976c) also proposed that eelgrass fishes were not food limited even though they may significantly alter the prey community (Nelson, 1979a; Fulton, 1985).

During residency in grass beds gag seemed to feed opportunistically on the most abundant invertebrates, prey items that are prevalent in most grass bed predators (Heck and Weinstein, 1989). Caridean shrimp dominated the gag diet (Adams, 1976b; this study), and carideans, like other principal foods, were abundant in grass beds when gag were there (Fulton, 1984; Fonseca et al., 1990; pers. obs.). The trophic ontogeny evident in gag (i.e., shift from small crustacean prey to larger decapod crustacean and fish prey with growth, Mullaney, 1991; this study) may be partially related to changes in food availability. The decline in the importance of amphipods in the diet as the season (and gag size) advanced is correlated with the seasonal decline in amphipod abundance in North Carolina grass beds (Nelson, 1979b). Diet shifts were probably facilitated by ontogenetic changes in gag's feeding apparatus (Mullaney, 1991). On offshore habitats, adult gag were mainly piscivorous, feeding mostly on schooling, pelagic fishes (Naughton and Saloman, 1985; McFall, 1992). The increasing tendency toward piscivory and feeding on larger prey with increasing gag size is characteristic of grouper (Brule

and Canche, 1993). Such dietary changes probably help maintain rapid estuarine growth rates because of the general increase in energy content of these larger prey (Thayer et al., 1973).

Identification of groupers <10–15 mm SL to species is difficult (Johnson and Keener, 1984; Leis, 1987). Keener et al. (1988) indicated that pre-settlement post-larvae of black grouper and gag could be separated with 80% accuracy based on anal ray counts. Our frequency distributions of anal fin ray counts also indicated a high (92%) separation probability between gag and black grouper; however, all of the post-settlement gag and black grouper we collected were distinguishable based on color patterns alone. Mullaney indicated (pers. comm.) that coloration differences between gag and black grouper were not as distinct in Charleston Harbor as those we describe for North Carolina; therefore, the success of using color alone to identify juvenile groupers may vary by area and/or habitat. We agree with Smith (1971) that the opercular angle difference should not be used to separate *Mycteroperca* spp. smaller than 75 mm.

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