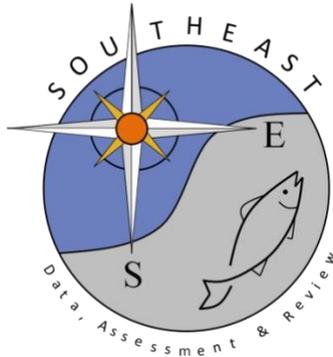


Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae)

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SEDAR68-RD27

August 2019



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INGRESS OF POSTLARVAL GAG,
MYCTEROPERCA MICROLEPIS (PISCES: SERRANIDAE),
THROUGH A SOUTH CAROLINA BARRIER ISLAND INLET

*Paula Keener, G. David Johnson, Bruce W. Stender,
Edward B. Brothers and Howard R. Beatty*

ABSTRACT

Postlarval gag, *Mycteroperca microlepis*, collected with fixed neuston nets at Price Inlet, South Carolina, entered the barrier island inlet during late spring-early summer. The mean age of *M. microlepis* collected during 5 years of sampling was 43 days; mean standard length was 15 mm. Postlarvae were most abundant in near-surface waters during night flood tides and generally did not leave the inlet on subsequent ebb tides. Analysis of back-calculated fertilization dates, as determined from presumed daily growth increments in lapilli from postlarvae, indicated that putative peaks in spawning were correlated with lunar phase. Estimates of the magnitude of ingress and the extremely rare occurrence of young of the year offshore suggest that estuarine ingress and residence is probably a consistent and integral part of the early life history of *M. microlepis* off South Carolina.

The gag, *Mycteroperca microlepis* (Goode and Bean, 1880), is a large (up to 1,200 mm TL) epinepheline serranid found in coastal waters of the western Atlantic from New York to Brazil, including the Gulf of Mexico, Cuba, and Bermuda (Smith, 1971; Hardy, 1978). Along the southeastern coast of the United States and the Gulf of Mexico, the gag is often an important component of recreational and commercial fisheries. Although certain aspects of the biology of the adults have been examined (McErlean, 1963; McErlean and Smith, 1964; Huntsman and Dixon, 1976; Manooch and Haimovici, 1978; Collins et al., 1987), little is known of the early life history of *M. microlepis* or, for that matter, other grouper species (Hardy, 1978; Leis, 1986). Characters useful for generic and specific identification of American grouper larvae have been described only recently (Johnson and Keener, 1984) and the larvae of many species, particularly those of *Mycteroperca*, remain indistinguishable. Although the Serranidae has been reported to be one of the most abundant families taken in ichthyoplankton collections from the southeastern coast of the United States, the Gulf of Mexico, and the Caribbean (Powles and Stender, 1976; Finucane et al., 1979; Houde et al., 1979; Richards, 1984; McGowan, 1985), the subfamily Epinephelinae is nowhere abundant in the plankton (Houde, 1982; Leis, 1986), and it is therefore difficult to make valid, meaningful comparisons of their distribution and relative abundance. Newly settled young of most species are cryptic inhabitants of structurally complex bottoms and are rarely collected by conventional sampling methods.

Off the southeastern coast of the United States, adult *M. microlepis* are most frequently found in association with live bottom (sponge-coral) habitats (Struh-saker, 1969; Wenner, 1979; 1983; Powles and Barans, 1980) in depths from 25 to 100 m from 40 to 70 km offshore. Small juveniles, presumably young of the year, have been collected in estuarine waters (Hoese et al., 1961; McErlean, 1963; Adams, 1976; Manooch and Haimovici, 1978) but the generality and extent of their estuarine association has not been investigated. McErlean (1963) reported that young gag occur inshore in the Gulf of Mexico 3 to 4 months after the time of spawning and noted that "a vigorous collecting program aimed at obtaining

newly transformed larvae or a tagging program would give valuable information in this regard."

The central question is this: Are the small juvenile gag occasionally reported from estuarine waters merely strays that for some reason failed to settle offshore with the rest of their cohort, or does the magnitude of the ingress indicate that a period of estuarine residence is a consistent and integral part of the early life history of gag? In the summer of 1979, reports of the occurrence of juvenile *M. microlepis* in high salinity estuaries along the coast of South Carolina led us to initiate a study that would begin to answer this question. This paper summarizes the results of a five-year study that was designed to investigate the estuarine ingress of *M. microlepis*.

MATERIALS AND METHODS

From 1980 to 1984, sampling for postlarval *M. microlepis* took place as early as 2 April 1981 to as late as 5 July 1983 in Price Inlet, a high salinity barrier island inlet north of Charleston, South Carolina, between Capers and Bull Island (Fig. 1). The term postlarva, as used here, is defined as a late pre-settlement larva that has not yet developed the juvenile pigmentation pattern. Based on preliminary sampling in 1979, sampling encompassed what we believed to be the major period of estuarine ingress and generally occurred every week. From 1982–1984, we attempted to maximize the catch by sampling up to 7 days in a week when large numbers of specimens were taken in a collection. A fixed Boothbay neuston net (1 × 2 m frame, 947 μm or 2 mm mesh) was buoyed at the 0 to 1-m depth-interval and fished during night flood tides from the R/V ANITA, which was anchored inside the inlet about 625 m from the entrance in a depth of 5 m. The width of the inlet at this location was approximately 273 m. In 1981, sampling took place slightly closer to the entrance of the inlet; width of the inlet at this point was 230 m. In addition to this standard sampling design, other sampling procedures were attempted and modified from year to year based on their relative success (Table 1). Samples for diel-depth comparisons were collected with surface and subsurface nets fished simultaneously during different diel periods. The two nets were mounted on a single frame, and the subsurface net could then be raised or lowered to the desired position below the surface net. Five depth intervals were sampled—surface (0 to 1 m), 1 to 2 m, 2 to 3 m, 3 to 4 m, and near-bottom (4 to 5 m). Sequential surface flood and ebb tides were also sampled. Samples were classified to diel period and tidal stage based on whether most of the sampling period occurred during day, night, dusk (1 h before and after sunset), or dawn (1 h before and after sunrise), and early, maximum, or late flood, or early, maximum, or late ebb tide. From 1980 to 1981, sampling duration was approximately 2 h during the mid-portion of each flood or ebb tide. Nets were fished for the entire duration of the flood tide from 1982 to 1984.

$$\text{Standardized catch} = \frac{\text{Number of individuals collected}}{\text{Volume strained}} \times 1,000.$$

Only data from standard samples (as described above) were used in yearly comparisons of dates of capture and standardized catch.

In 1981, supplementary to the ingress sampling, settled juveniles were collected in tidal creeks in the vicinity of Price Inlet by a variety of methods, including seines, trawls, traps, rotenone, and hook and line. Details of methods of collection were given in a preliminary data report.¹

Postlarval groupers were large enough at the time of ingress (Fig. 2) to allow visual sorting of all samples in the field. Specimens were fixed in 95% ethanol to ensure preservation of otoliths for aging. Standard length (SL) was measured to the nearest millimeter and lapilli were taken from 733 postlarvae and 21 settled juveniles. A series of length measurements made before and after preservation in 95% ethanol indicated that shrinkage was minimal (0–3.6%). Lapilli were examined from specimens collected from 1981–1983 and otolith preparation generally followed the methods of Brothers and McFarland (1981). Lapilli were removed, cleaned, then placed on a glass slide and examined in immersion oil with a compound microscope equipped with a video viewing system, monitor, and polarized light source (1,000–2,700×). Observations of ground and polished lapilli, along with comparisons of increment counts between sagittae and lapilli, indicated that we were unable to detect the

¹ Johnson, G. D. and H. R. Beatty. 1981. Preliminary report on ingress of postlarval *Mycteroperca microlepis* at Price Inlet, South Carolina, 1981. S.C. Wildl. and Mar. Resour. Dept., Charleston, South Carolina, Unpubl. MS, 17 pp.

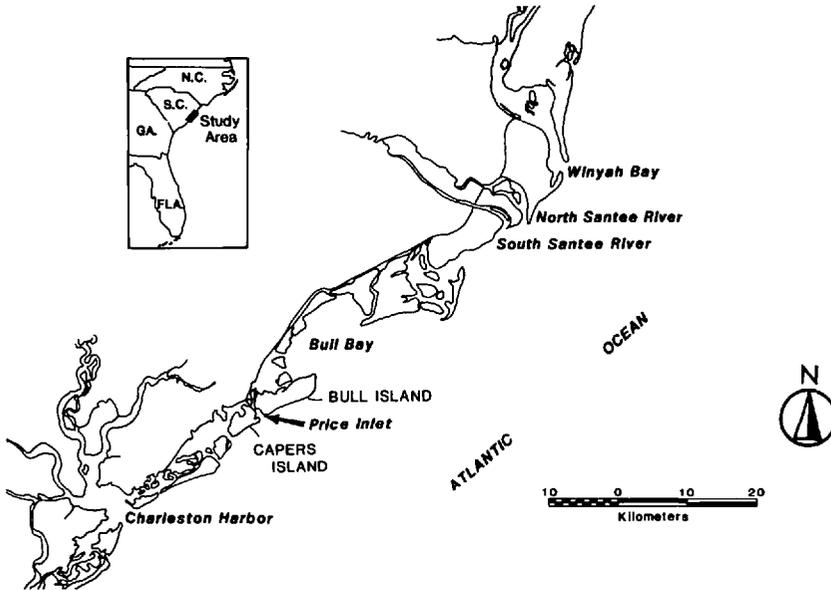


Figure 1. Sampling location, Price Inlet, South Carolina.

first few increments in lapilli under normal preparation procedures, i.e., without grinding and polishing. In addition, there is an expected lag of 2 to 3 days between fertilization and the initiation of increment deposition. Accordingly, a correction factor of 6 days was added to the total lapillus increment counts in order to establish the presumed daily age of an individual. With only two exceptions in 1982, ages were assigned to the majority of specimens throughout a complete size range in a collection. Lengths of specimens that were assigned ages were proportional to the sample length-frequency. Discrepancies between numbers of individuals collected and numbers of individuals aged and measured on any given day are the result of damaged specimens, damaged lapilli, or in the case of large samples, subsamples based on length-frequencies of individuals in a collection. Back-calculated fertilization dates were then analyzed with respect to lunar periodicity. To enhance detection of possible relationships between lunar phase and spawning, data on fertilization dates for *M. microlepis* from 1981 to

Table 1. Collection information for moored plankton net samples taken at Price Inlet, South Carolina, from 1980 to 1984. Codes are defined as follows: Gear 2N2 (1 × 2 m neuston net—4.9 m, 2 mm-mesh); 2N6 (1 × 2 m neuston net—4.9 m, 600- μ m mesh); 2N9 (1 × 2 m neuston net—4.9 m, 947- μ m mesh); BO7 (1 × 2 m neuston net—8.5 m, 947- μ m mesh). Tidal stage—0, entire flood tide; 1, early flood; 2, maximum flood; 3, late flood; 4, slack before ebb; 5, early ebb; 6, maximum ebb; 7, late ebb. Diel period—1, day; 2, night; 3, dawn; 4, dusk

Year	Date	Gear	Depth (m)	Tidal stage	Diel period
1980	14–29 May	2N6, BO7	0.0, 6.7 7.6, 7.9 9.1, 10.1	1, 2, 3, 5, 7	1, 2
1981	2 Apr–19 Jun	2N9, BO7	0.0, 4.0 4.3, 6.1 7.3	1, 2, 3, 5, 6, 7	1, 2, 3, 4
1982	22 Apr–26 May	2N9, BO7	0.0, 1.0 2.0, 3.0	0, 2	1, 2, 4
1983	7 Apr–5 Jul	2N2, 2N9 BO7	0.0, 3.0	0	1, 2, 4
1984	5 Apr–12 Jun	2N2, 2N9	0.0	0, 2	1, 2, 3, 4

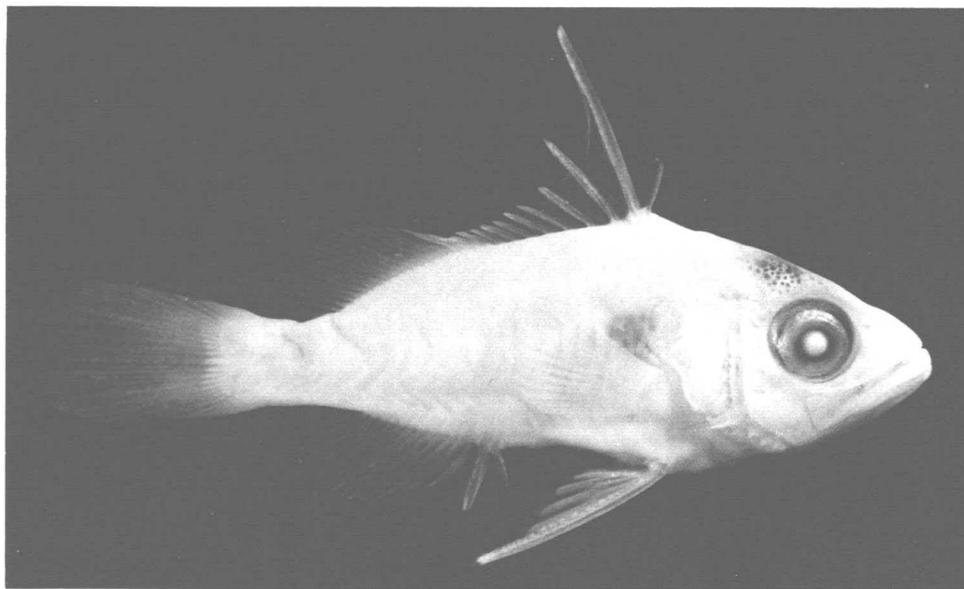


Figure 2. *Mycteroperca microlepis* postlarva, 14.4 mm SL.

1983 were pooled and analyzed over a single lunar cycle, with respect to the number of days on either side of the full moon (McFarland et al., 1985).

Identification.—Based on previous records (Shealy, 1974; 1975; Shealy et al., 1974; Poole, 1978; Wenner et al., 1982) and our own sampling, juveniles of four grouper species occur in estuarine waters of South Carolina: *M. microlepis* (by far the most abundant), *M. bonaci*, *Epinephelus morio*, and *E. itajara*. Postlarval specimens were assigned to one of these species based on dorsal and pelvic fin-spine morphology and/or fin-ray counts (Johnson and Keener, 1984). *Mycteroperca* is separable from *Epinephelus* by a higher number of anal soft rays (10–13 vs. 8–9) and dorsal and pelvic fin-spine morphology. Based on the frequency distribution data of Smith (1971), specimens with 10–11 anal soft rays were identified as *M. microlepis* and those with 12 anal soft rays were identified as *M. bonaci*. Specimens with damaged anal fins or on which anal-fin rays were not counted were identified only to genus (*Mycteroperca* sp.); however, for reasons discussed below, we believe that the vast majority of these specimens were *M. microlepis*. Postlarval *E. morio*, taken occasionally in our samples, were identified by a low anal-fin ray count and diagnostic dorsal and pelvic fin-spine morphology (Johnson and Keener, 1984). Because so few specimens of *E. morio* were collected, they were not included in the analyses. Postlarval *E. itajara* are separable from other species of *Epinephelus* by fin-ray counts and diagnostic dorsal and pelvic fin-spine morphology. We know of only four records of juvenile *E. itajara* in estuarine waters of South Carolina (P. Keener, pers. obs.) and none were collected during the course of this study.

Besides *M. microlepis*, which accounted for over 80% of the total commercial landings by weight of *Mycteroperca* species in 1985, *M. phenax* (commonly called scamp) is the most abundant species of *Mycteroperca* in offshore waters of the Carolinas, and accounted for approximately 20% of the total commercial landings by weight of *Mycteroperca* species in 1985 (D. Theiling, South Carolina Wildlife and Marine Resources Department, Charleston, South Carolina, pers. comm., 1986). *M. interstitialis* and *M. venenosa* also occur in offshore waters of South Carolina. These two species are rare in commercial finfish catches and generally comprise between 0.01–0.2% of total commercial landings by weight of *Mycteroperca* species (D. Theiling, pers. comm., 1986). We are unable to distinguish the larvae of these four species, but settled juveniles are easily distinguished by color pattern (C. L. Smith, American Museum of Natural History, New York, New York, pers. comm., 1986). With the exception of *M. microlepis*, there are no confirmed records of juveniles of these four species in estuarine waters of South Carolina (Shealy, 1974; 1975; Shealy et al., 1974; Wenner et al., 1982), nor were any taken in trawls, traps, or rotenone collections in the small tidal creeks of Price Inlet that consistently produced specimens of *M. microlepis*, and less commonly, *M. bonaci* and *E. morio*.¹ Consequently, we were confident that postlarval *M. phenax*, *M. interstitialis*, and *M. venenosa* were absent or extremely rare in our ingress samples.

Table 2. Kinds, total numbers, percentages, and dates of collection of postlarval groupers at Price Inlet, South Carolina 1980 to 1984. (Figures enclosed in parentheses represent standard samples)

Year	<i>Mycteroperca microlepis</i>		<i>Mycteroperca</i> sp.	
1980	—	(—)	98 100% 14 Apr–29 May	(65) (100%) 15–29 May
1981	318 58.89% 2 Apr–4 June	(212) (50.84%) 3 Apr–4 June	201 37.22% 23 Apr–5 June	(187) (44.84%) 15–28 May
1982	300 37.78% 22 Apr–26 May	(111) (37.12%) 22 Apr–18 May	493 62.09% 22 Apr–20 May	(187) (62.54%) 22 Apr–20 May
1983	291 76.78% 7 Apr–10 June	(115) (84.56%) 21 Apr–10 June	4 1.05% 3–14 May	(—)
1984	228 67.26% 5 Apr–2 June	(108) (93.10%) 5 Apr–10 May	95 28.02% 11 Apr–2 June	(1) (0.86%) 7 May
Total	1,137 52.88% 2 Apr–10 June	(546) (52.86%) 3 Apr–10 June	891 41.44% 11 Apr–5 June	(440) (42.59%) 22 Apr–29 May

M. bonaci accounted for <0.01% of total commercial landings by weight of *Mycteroperca* species in 1986 (D. L. Stubbs, South Carolina Wildlife and Marine Resources Department, Charleston, South Carolina, pers. comm., 1986). Although much less abundant than *M. microlepis*, juveniles do occur in estuarine waters (Poole, 1978; and several were reported from trap and trawl samples¹) and postlarvae were present in our ingress samples. Based on frequency distributions of anal-fin ray counts (Smith, 1971), *M. bonaci* can be separated from *M. microlepis* with ~80% accuracy by a higher number of anal-fin rays (12 vs. 11). In 1980, we were unaware of the potential presence of *M. bonaci* in our samples and did not make anal-fin ray counts on those specimens. Assuming that the ratio of *M. microlepis* to *M. bonaci* remained approximately the same during the five years of our sampling, the majority of specimens assigned to *Mycteroperca* sp. from 1980 to 1983 were almost certainly *microlepis* (Table 2). This is corroborated by the fact that only seven juvenile *M. bonaci* were collected in the vicinity of Price Inlet by trawls or traps from 1979 to 1982 whereas 142 settled *M. microlepis* were collected there in 1981 alone.¹

Estimates of Numbers of Postlarval Gag Entering Price Inlet.—In 1983 and 1984, estimates of the total number of postlarval *Mycteroperca microlepis* entering Price Inlet over a 10-week period were made. Calculations were based on number of individuals collected during surface flood tides at night. Because sampling did not extend throughout the entire flood tide in 1981 and sampling was sporadic in 1982, data from these years were omitted from the calculations. For reasons discussed above, the majority of specimens assigned to *Mycteroperca* sp. were believed to be *M. microlepis*; thus, they were included in calculations for estimates of the numbers of postlarvae that entered Price Inlet. To ensure conservative estimates, the following assumptions were made: (1) since postlarvae were rare in near-bottom samples, concentrations in the upper 3 m of the water column were assumed to represent the majority of individuals entering the inlet, and concentrations between three meters below the surface and the bottom were excluded from the calculations, and (2) Price Inlet was approximately 273 m wide at the sampling site and current velocities did not differ substantially across the central 100 m of inlet width at the sampling site. Although preliminary sampling in 1983 with nets positioned across the width of the inlet² at the sampling site indicated that distribution of postlarvae across the middle 150 m of the inlet was not random on any given day, there were no consistent temporal trends in distribution patterns across this distance throughout the sampling period, and the apparent "patchy" distribution of postlarvae seemed to occur randomly in the middle 150 m of the inlet. Thus, in the following calculations, concentrations at the sampling site were projected across 150 m.

² Stender, B. W. 1983. Preliminary cruise report—1983 grouper ingress survey. S.C. Wildl. and Mar. Resour. Dept., Charleston, South Carolina. Unpubl. Rep., 11 pp.

Table 2. Continued

<i>M. bonaci</i>		<i>Epinephelus morio</i>	
—	(—)	—	(—)
20	(18)	1	(—)
3.70%	(4.32%)	0.18%	
17 Apr–28 May	17 Apr–28 May	23 Apr	
1	(1)	(—)	(—)
0.13%	(0.33%)		
22 Apr	22 Apr		
68	(18)	16	(3)
17.94%	(13.24%)	4.22%	(2.02%)
2 May–10 June	7 May–10 June	11–15 May	11–12 May
14	(6)	2	(1)
4.13%	(5.17%)	0.59%	(0.86%)
5 Apr–29 May	5 Apr–1 May	5 Apr–20 May	5 Apr
103	(43)	19	(4)
4.79%	(4.16%)	0.88%	(0.39%)
5 Apr–10 June	5 Apr–10 June	5 Apr–20 May	5 Apr–12 May

Total number of postlarval *M. microlepis* collected during a single flood tide (N/t) was multiplied by 75 to expand the sampling concentration across 150 m of Price Inlet. Because our comparative depth sampling indicated that grouper postlarvae were evenly concentrated in the upper 3 m of the water column, N/t was multiplied by three to expand estimates of ingress to the upper 3 m of the water column. Mean number of postlarval *M. microlepis* entering Price Inlet per day (N/d) was then calculated by averaging all N/t values for a single year. N/d was multiplied by 70 to give an estimate of the number of postlarval gag entering the inlet over a 10-week period.

RESULTS

Catches. — A total of 2,150 postlarval groupers was collected in 262 samples taken at Price Inlet from 1980 to 1984 (Table 2). Data from standard samples (as defined in Materials and Methods) were used in the following yearly comparisons of dates of capture and standardized catch. We collected postlarval groupers from as early as 2 April 1981 to as late as 10 June 1983. In 1981, highest standardized catch values for all three taxa occurred on 15 May (Fig. 3). In 1982, highest standardized catches for *M. microlepis* occurred on 28 April and 18 May, and for *Mycteroperca* sp., on 28 April. In 1983, highest standardized catches for *M. microlepis* occurred on 6 and 12 May, and for *M. bonaci*, on 9, 12, and 13 May. In 1984, highest standardized catches for both *M. microlepis* and *M. bonaci* occurred on 9 April. Standardized catches generally decreased toward the end of the sampling period and no postlarvae were collected on the last day of sampling in 1981, 1983, and 1984 (in 1982, one specimen of *M. microlepis* was collected on the last day of sampling). Mean yearly standardized catches for *M. microlepis*, *Mycteroperca* sp., and *M. bonaci* were highest in 1981 (Table 3).

We observed no distinct separation with respect to times of ingress for *M. microlepis* and *M. bonaci*. In 1981 and 1983, *M. microlepis* were taken in early April, whereas *M. bonaci* did not appear in our samples until mid-April (1981) and early May (1983). In 1984, however, both species were taken in early April and both were taken during all years until late May and early June. Length and

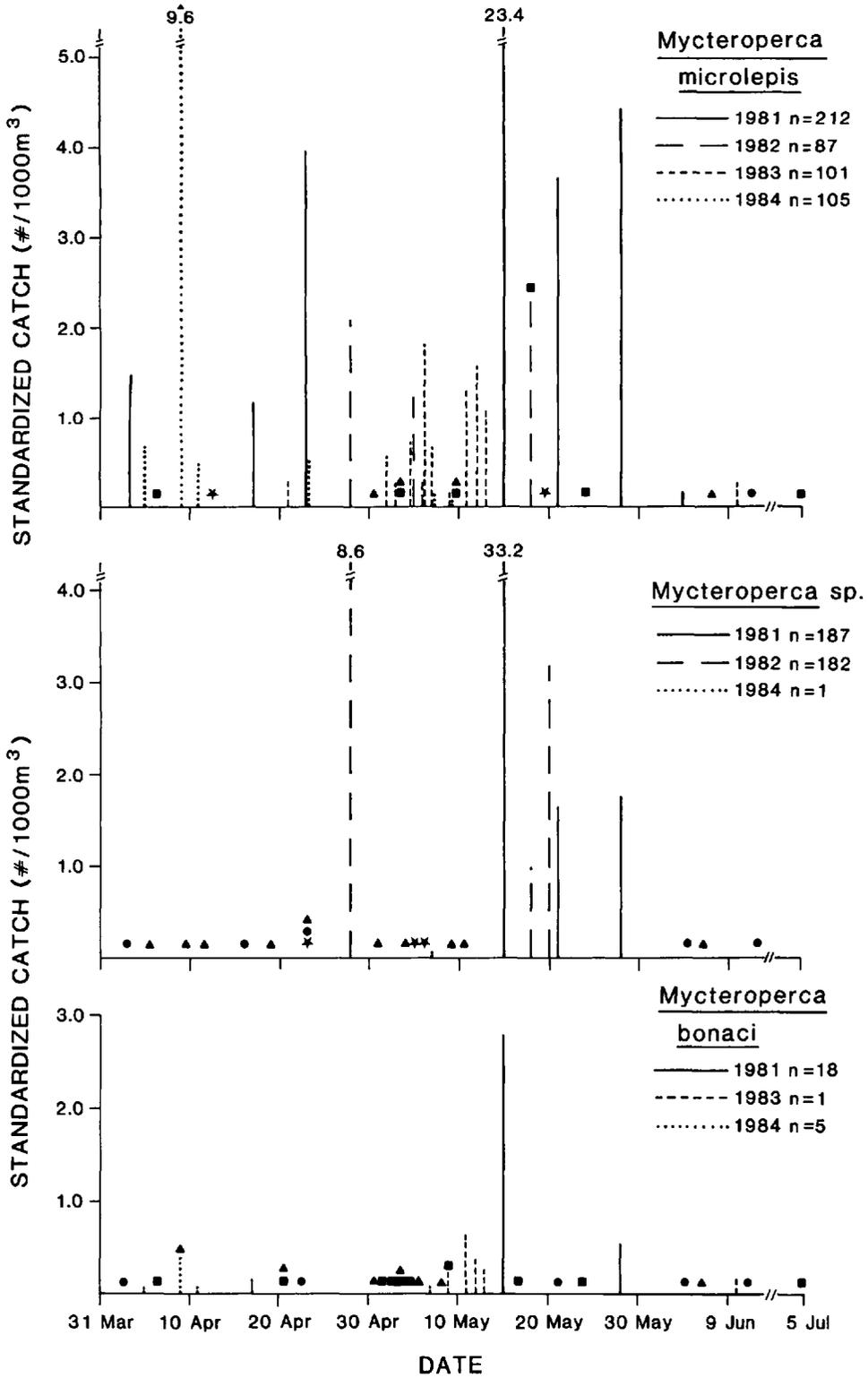


Table 3. Standardized catches (#/1,000 m³) for postlarval *Mycteroperca microlepis*, *Mycteroperca* sp. and *M. bonaci* collected by standard sampling at Price Inlet, South Carolina, from 1981 to 1984

Year	Total volume strained (m ³)	<i>Mycteroperca microlepis</i>		<i>Mycteroperca</i> sp.		<i>M. bonaci</i>	
		Standardized catch	%	Standardized catch	%	Standardized catch	%
1981	56,022	4.861	26.7	12.213	67.0	1.144	6.3
1982	77,554	1.458	25.6	4.243	74.4	—	—
1983	195,048	0.873	69.5	—	—	0.198	15.7
1984	172,666	1.914	88.6	0.029	1.3	0.163	7.5

age at ingress (as will be discussed later) were also similar, and it appears that individuals of these two species spawn during the same time of year.

Diel-depth Comparisons.—Data from 35 diel surface and subsurface samples (Fig. 4) indicated that significantly more postlarvae were collected at the surface during night than day (Mann Whitney *U*-test, $P < 0.05$; Siegel, 1956). Significant differences in day-night catches were not detected for any other depth interval (data for the 1 to 2 m depth-interval were excluded from analyses due to low sample sizes). Significant differences were not detected among day catches from the 0 to 1 m, 2 to 3 m, and 3 to 4 m depth-intervals but collections from each of these depth intervals produced significantly greater catches during the day than the 4 to 5 m interval (Kruskal-Wallis test, $P < 0.05$; Siegel, 1956). No significant differences were detected in night catches from the 0 to 1 m and the 2 to 3 m depth-intervals; however, significantly greater catches of postlarvae were found in the 0 to 1 m depth-interval than both the 3 to 4 m and 4 to 5 m depth-intervals (Kruskal-Wallis test, $P < 0.05$; Siegel, 1956).

Flood-ebb Comparisons.—Sequential surface flood and ebb tide collections ($N = 29$) taken in 1981 indicated that there was a striking difference in the mean standardized catch of postlarvae collected at the surface on flood tides versus ebb tides (Fig. 5). Although we have no data on sequential near-bottom (4–5 m) flood and ebb tide collections, surface and near-bottom ebb tide collections during day and night rarely produced specimens; thus, we believe that if postlarvae were vertically migrating in response to changes in diel periods, the effect of these migrations on ebb tide catches was insignificant.

Size and Age at Ingress.—*M. microlepis* ranged in length from 9 to 20 mm SL, with a mean of 15 mm, and in age from 33 to 66 days, with a mean of 43 days (Table 4). Specimens identified as *Mycteroperca* sp. had a mean SL of 15 mm (range: 12–18 mm), and a mean age of 47 days (range: 43–58 days). *M. bonaci* averaged 15 mm SL (range 11–18 mm) and were from 31 to 57 days old ($\bar{x} = 41$ days). Although a one-way ANOVA and Scheffe's multiple comparison test, $P < 0.05$ (Sokal and Rohlf, 1969) occasionally showed significant differences for both mean SL and mean ages among date of collection, no consistent temporal patterns were evident among the significantly different values. Furthermore, low r^2 values for the ANOVA indicated that most of the variance could not be explained by

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Figure 3. Standardized catches expressed as #/1,000 m³ by date for *Mycteroperca microlepis*, *Mycteroperca* sp., and *M. bonaci*, from 1981 to 1984. Dates when sampling occurred but no specimens were collected are indicated by ● in 1981, ★ in 1982, ■ in 1983, and ▲ in 1984.

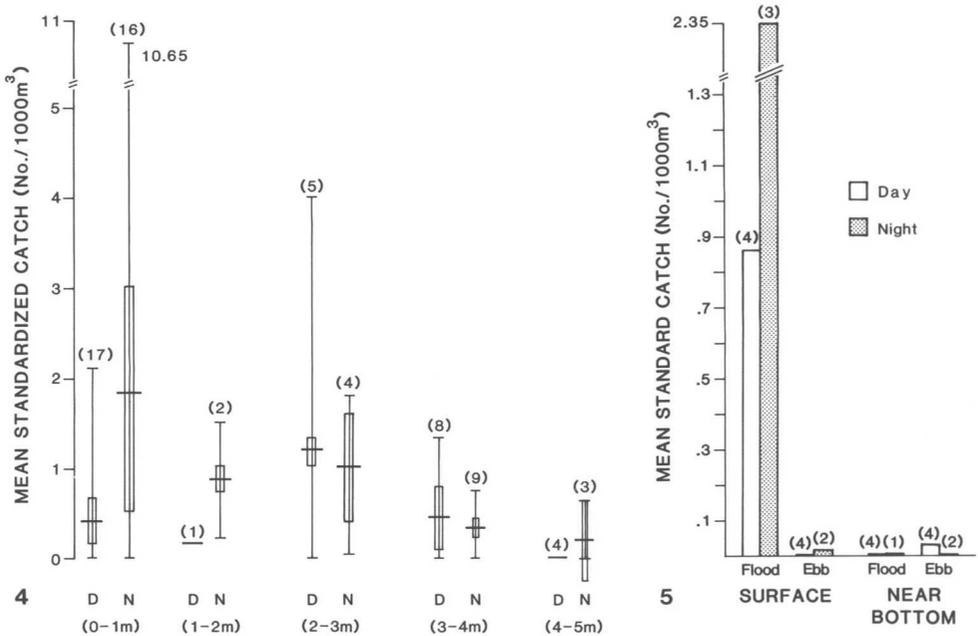


Figure 4. (Left) Diel-depth comparisons of standardized catches (mean, range, and two standard deviations on either side of the mean) of postlarval groupers at five depth intervals. D denotes day, N denotes night, and figures enclosed in parentheses represent numbers of samples.

Figure 5. (Right) Comparison of standardized catches of postlarval groupers collected in surface and near-bottom waters during day, night, flood, and ebb tides. Figures enclosed in parentheses represent numbers of samples.

mean SL of postlarval *M. microlepis* at ingress did not vary considerably within or among years (Fig. 6), mean age at ingress in 1982 and 1983 showed trends toward lower mean ages at ingress as the sampling period progressed (Fig. 7). Standard lengths of *M. microlepis*, when plotted against age, showed a strong upward inflection in rate of growth upon entrance into the estuarine habitat (Fig. 8). Included in Figure 8 are larval specimens taken from offshore ichthyoplankton collections and settled juveniles collected at Price Inlet.¹

Daily growth increments in lapilli from 21 settled juvenile gag (SL range: 16–186 mm; range in age: 41–182 days) showed a transition in optical density and spacing of the increments at a mean otolith age of 35.6 days (range in otolith age: 26–44 days) (Fig. 9). The addition of the correction factor of 6 days to the mean otolith age at transition for *M. microlepis* (N = 637) gave an average age of 41.6 days at the time of formation of the transition mark in the lapillus.

Based on back-calculated fertilization dates from 1981 to 1983, *M. microlepis* began spawning in mid-February to early March, and *M. bonaci* spawning was initiated slightly later (Table 5). Numbers of postlarval *M. microlepis* collected in 1981, 1982, and 1983, when plotted against back-calculated fertilization dates, indicated that individuals from a spawn on any given day entered Price Inlet from 1 to 29 days apart, with a mean period of 11.3 days between the first and last entrance (Figs. 10, 11, and 12). Standardized catches (as calculated from data taken not only from standard samples, but also from data taken by additional sampling procedures as defined in Materials and Methods) neither increased when

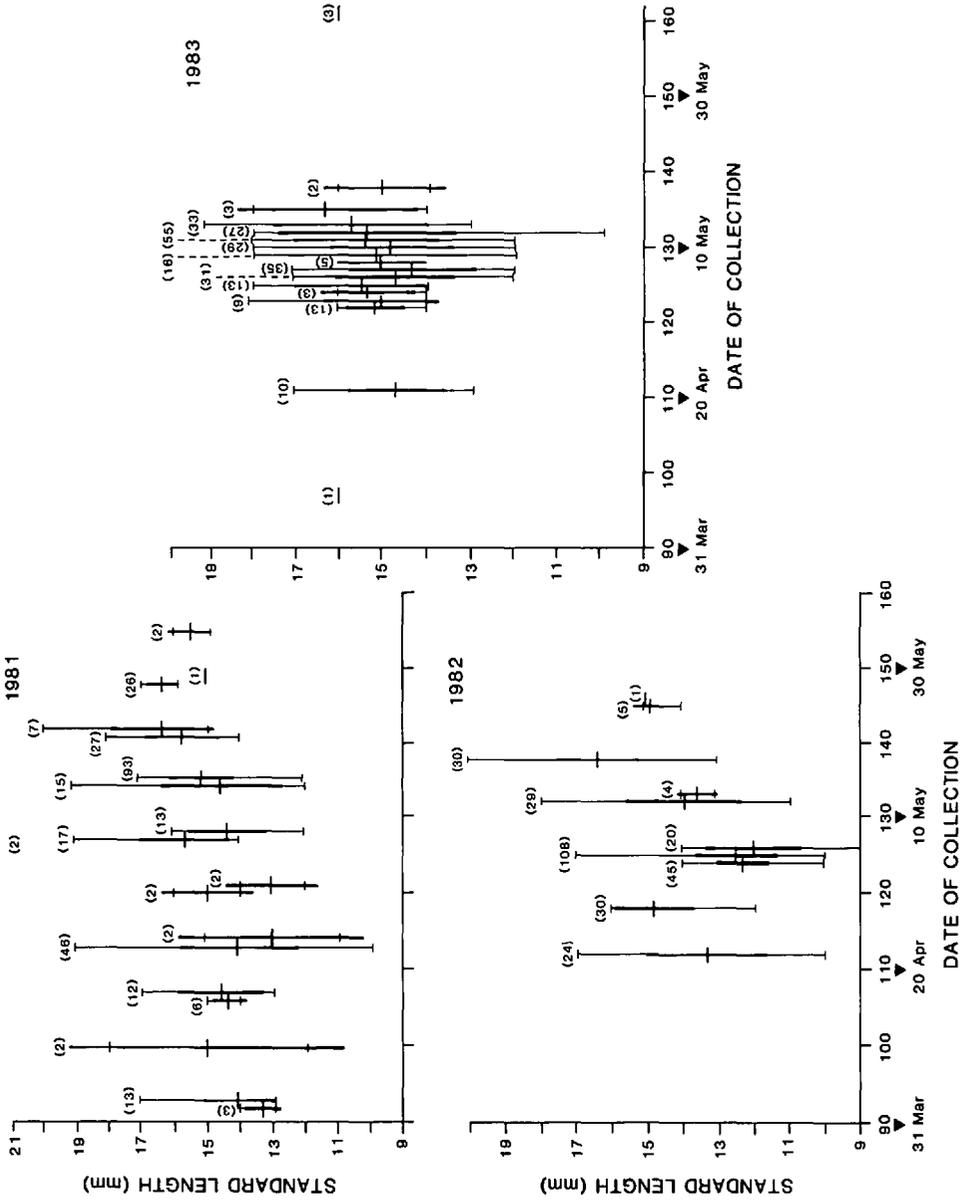


Figure 6. Standard lengths (mm) of postlarval *Mycteroperca micropalepis* by date of collection, from 1981 to 1983. Dates of collection are expressed as consecutive days of the year, i.e., January 1 = Day 1. Figures enclosed in parentheses represent numbers of individuals.

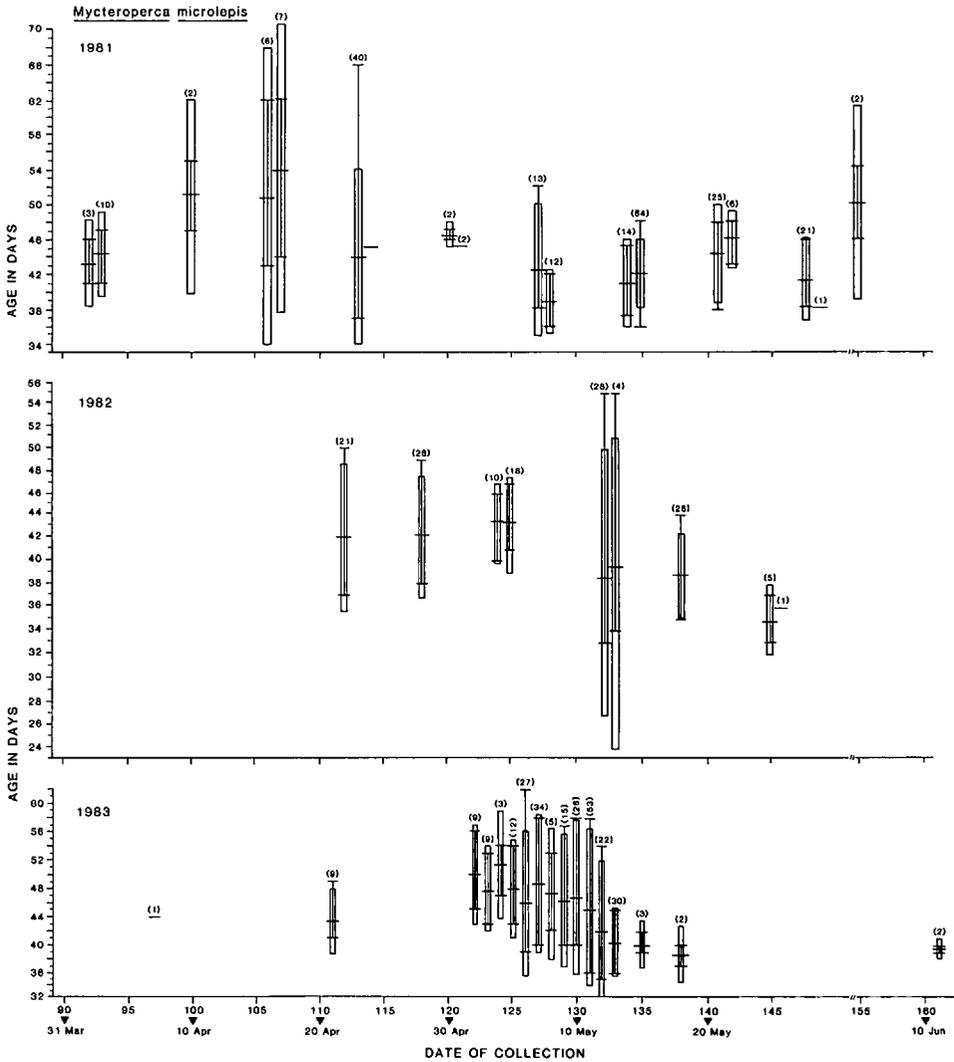


Figure 7. Age, in days, of postlarval *Mycteroperca microlepis* by date of collection, from 1981 to 1983. Dates of collection are expressed as consecutive days of the year, i.e., January 1 = Day 1. Figures enclosed in parentheses represent numbers of individuals.

current rates increased nor during times of full moons. Standardized catches did show, however, that temporal variability in the relative abundance of postlarval gag corresponded to the temporal patterns of back-calculated fertilization dates (Figs. 10, 11, and 12). Furthermore, in all 3 years, peaks in fertilization date plots were shifted back from standardized catch plots by a mean of 44 days, which corresponded closely to the mean age of postlarval *M. microlepis* at ingress (43.3 days).

We were unable to identify a clear relationship between lunar phase and back-calculated fertilization dates for *M. microlepis* collected within a single year (Figs. 10, 11, and 12). However, when data in fertilization dates from 1981 to 1983 were pooled and analyzed over a single lunar cycle (Fig. 13), it was clear that

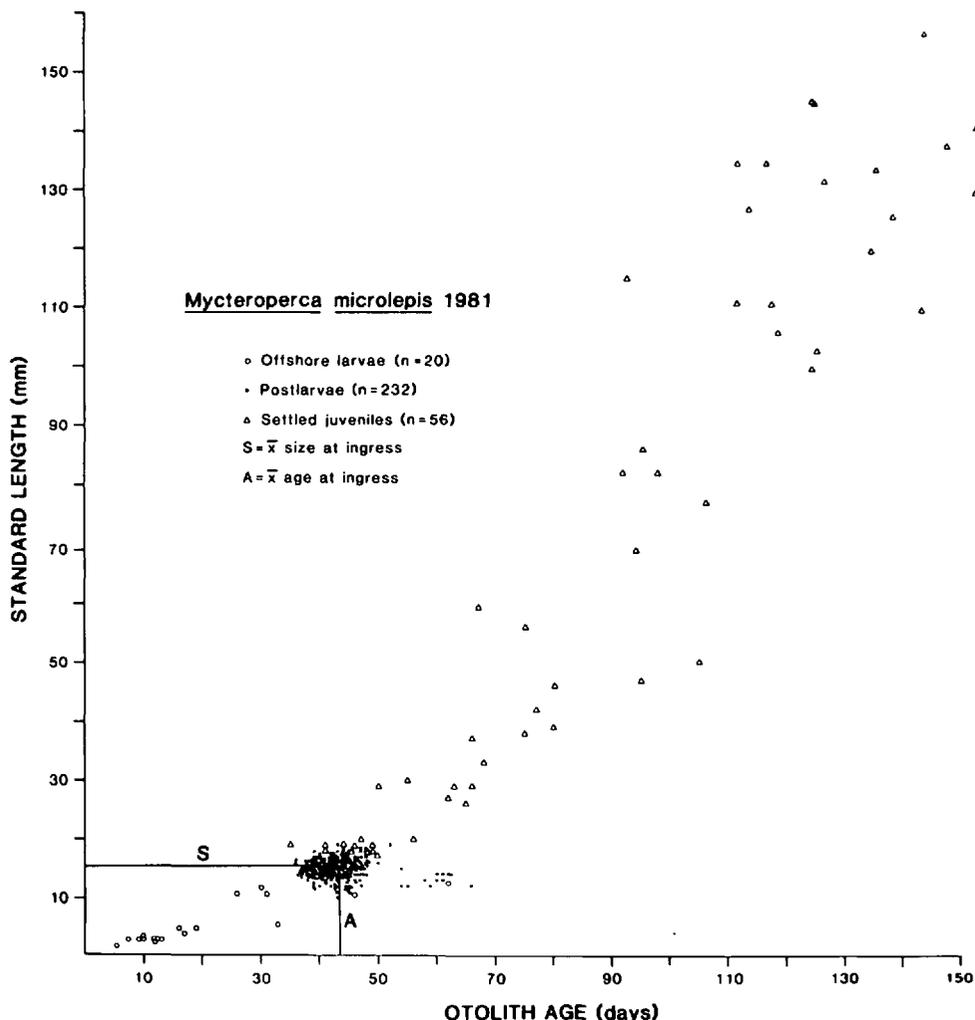


Figure 8. Growth curve based on standard lengths (mm) and ages (in days) of *Mycteroperca microlepis* collected in 1981.

although spawning occurred throughout the lunar cycle, putative peaks in spawning activity were evident and were predominantly associated with times of new or full moons.

Magnitude of Ingress.—The estimate of total number of postlarval *M. microlepis* that entered Price Inlet over a 10-week period in 1983 was 365,400 (3 April to 11 June). In 1984, an estimated 904,050 postlarval gag entered Price Inlet over a 10-week period (1 April to 9 June). Estimates of total number of postlarval gag entering Price Inlet over a 10-week period during 1981 were presented in a preliminary data report¹ and were projected to be 294,000 to 900,970. However, these estimates were based on only 4 h of a flood tide and were expanded to only the top 2 m of the water column.

Table 4. Means, ranges, and standard deviations of standard length (mm) and age (days) at ingress for postlarval *Mycteroperca microlepis*, *Mycteroperca* sp., and *M. bonaci* from 1981 to 1984

	<i>Mycteroperca microlepis</i>			<i>Mycteroperca</i> sp.			<i>M. bonaci</i>		
	SL (mm)	Age (days)	SL (mm)	Age (days)	SL (mm)	Age (days)	SL (mm)	Age (days)	
1981	\bar{x} = 15.0 10-20 mm SL s = 1.30 N = 289	\bar{x} = 43.6 36-66 days s = 3.59 N = 232	\bar{x} = 15.0 12-18 mm SL s = 2.14 N = 15	\bar{x} = 46.9 43-58 days s = 4.94 N = 12	\bar{x} = 15.7 13-18 mm SL s = 0.83 N = 15	\bar{x} = 41.0 39-45 days s = 2.30 N = 13			
1982	\bar{x} = 13.3 9-20 mm SL s = 1.20 N = 296	\bar{x} = 40.6 33-56 days s = 3.62 N = 143	—	—	\bar{x} = 14 14 mm SL s = 0 N = 1	\bar{x} = 38 38 days s = 0 N = 1			
1983	\bar{x} = 15.1 10-19 mm SL s = 1.59 N = 288	\bar{x} = 45.3 35-62 days s = 4.67 N = 262	—	—	\bar{x} = 14.5 11-18 mm SL s = 1.69 N = 68	\bar{x} = 41.6 31-57 days s = 4.89 N = 58			
1984	\bar{x} = 15.2 12-20 mm SL s = 1.54 N = 80	—	—	—	\bar{x} = 14 14 mm SL s = 0 N = 1	—			
Total	\bar{x} = 15.1 9-20 mm SL s = 1.8 N = 953	\bar{x} = 43.3 33-66 days s = 5.2 N = 637	\bar{x} = 15.0 12-18 mm SL s = 2.1 N = 15	\bar{x} = 46.9 43-58 days s = 4.9 N = 12	\bar{x} = 14.7 11-18 mm SL s = 1.7 N = 85	\bar{x} = 41.4 31-57 days s = 5.6 N = 72			

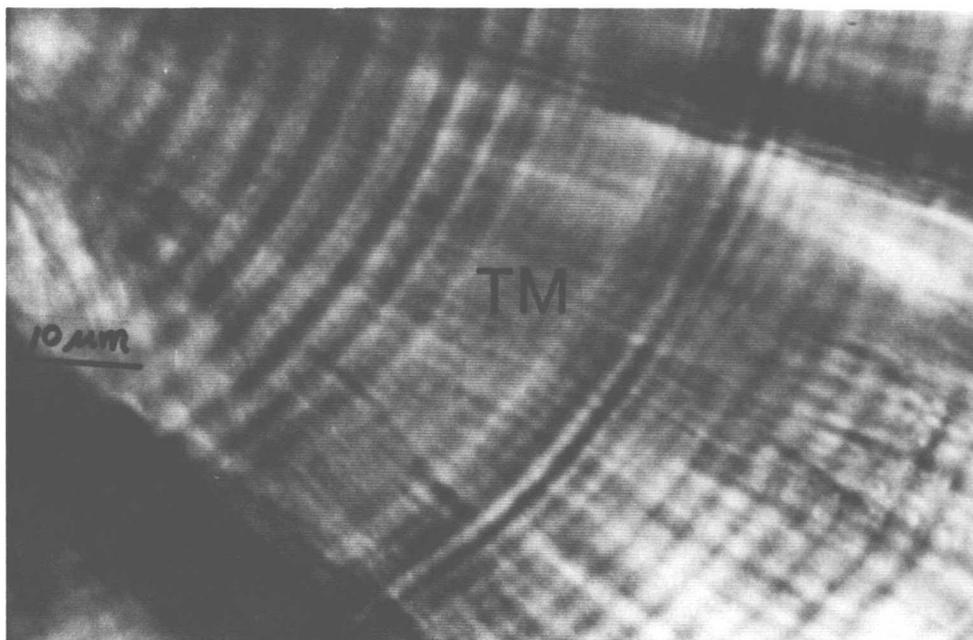


Figure 9. Photomicrograph of the lapillus from a 75-mm SL *Mycteroperca microlepis* settled juvenile. TM denotes transition mark.

DISCUSSION

Previous knowledge of the early life history of *M. microlepis* was limited to occasional reports of small juvenile gag in estuarine waters (Hoese et al., 1961; McErlean, 1963; Adams, 1976; Manooch and Haimovici, 1978). Based on our studies and estimates of the number of postlarval gag entering Price Inlet each year, we believe that a period of estuarine ingress and residence in high salinity barrier island inlets is a consistent and integral part of the life history of this species. Although *M. microlepis* is by far the most abundant species of grouper off South Carolina, we know of only one diver observation of a small juvenile gag (estimated length of 80 to 100 mm TL) in an offshore habitat off Little River, South Carolina (S. B. VanSant, South Carolina Marine Resources Research Institute, Charleston, South Carolina, pers. comm., 1986). Furthermore, collections from offshore habitat traps have consistently yielded young of the year of virtually every grouper species known to occur off South Carolina, but *M. microlepis* has never been taken in any of these collections.

Although some ingress probably occurred prior to April during all years, we believe our sampling encompassed the major period of ingress of postlarval groupers into Price Inlet each year. This is corroborated by Collins et al. (1987), who reported, based on histological examination of gonads, that adult *M. microlepis* spawn off the southeastern coast of the United States during late winter–early spring, with a peak in spawning activity occurring in late March–early April.

During ingress, postlarvae appeared to be evenly concentrated in the upper three meters of the water column during day and night, and were rarely encountered in near-bottom (4 to 5 m) depths. Significantly higher catches near the surface at night could have reflected migration towards the surface and/or reduced net avoidance.

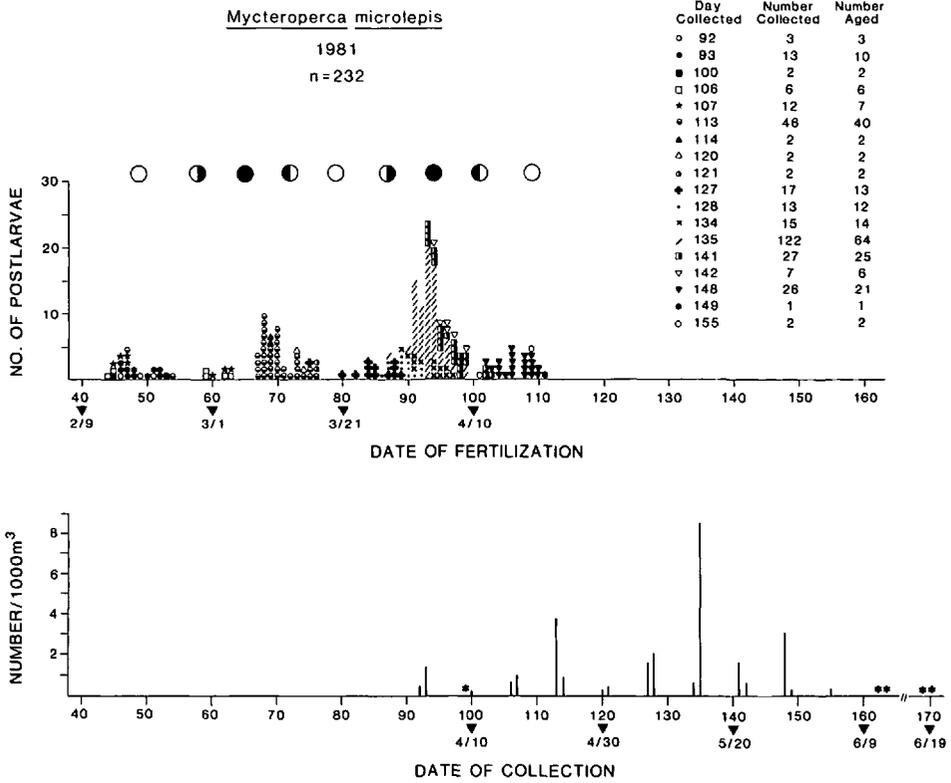


Figure 10. Back-calculated fertilization dates and corresponding standardized catches by date for individual postlarval specimens of *Mycteroperca microlepis* collected in 1981. Dates of collection are expressed as consecutive days of the year, i.e., January 1 = Day 1. Dates when sampling occurred but no specimens were collected are denoted by *.

Postlarval groupers, like other fishes that utilize estuaries as nursery grounds, entered inlets on flood tides and were not swept seaward on subsequent ebb tides. Studies of the retention of postlarval *Leiostomus xanthurus*, *Micropogonias undulatus*, and *Paralichthys* spp. in a Cape Fear River estuary showed that postlarvae were able to remain in preferred locations in the estuary by varying their behavior, primarily in response to changes in tidal stage and diel period, thereby preventing their transport seaward on ebb tides (Weinstein et al., 1980). Weinstein et al. (1980) reiterated Bousfield's (1955) observations that the mechanisms by which postlarvae avoid seaward transport on ebb tides may be species-specific, and involve vertical migrations, non-tidal drift, and behavioral changes associated with the stage of the tide. In the case of the relatively large postlarval gag, avoidance of seaward transport on ebb tides is probably simply a matter of immediate settlement to the bottom, where they assume residence in oyster beds or other areas affording cryptic habitation.¹ There is probably also a behavioral change upon settling, so that the transforming postlarvae orient and maintain position relative to bottom features.

Although we did not attempt age validation, we believe that the microstructural features counted in lapilli represented daily growth increments since they were structurally analogous to validated daily growth increments observed in lapilli

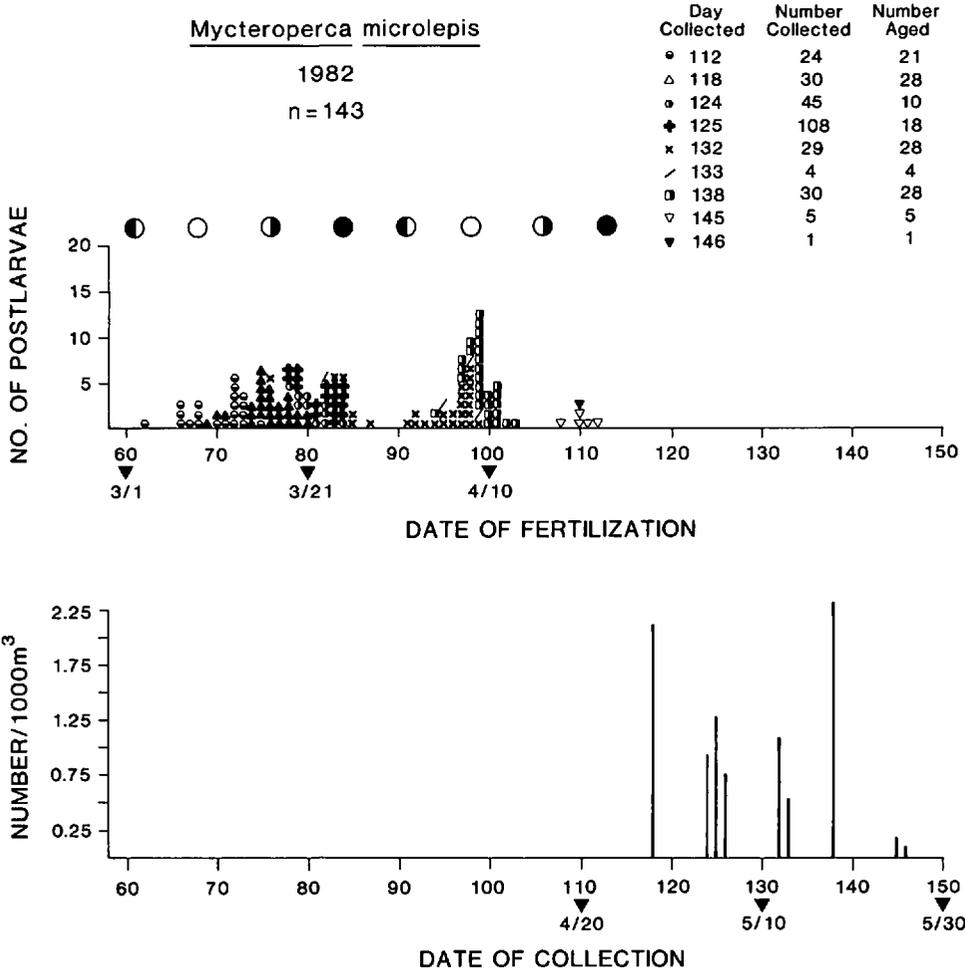


Figure 11. Back-calculated fertilization dates and corresponding standardized catches by date for individual postlarval specimens of *Mycteroperca microlepis* collected in 1982. Dates of collection are expressed as consecutive days of the year, i.e., January 1 = Day 1.

from larvae of many different species. Recent studies on groupers (*Epinephelus* spp.) from the Arabian Gulf (Brothers and Mathews, in press) have validated the existence of daily growth increments in both sagittae and lapilli by comparison of increment counts with the known age of cultured fish of up to 1 year of age. The increments observed in the *Mycteroperca* and *Epinephelus* species studied here were identical in appearance to those of Arabian Gulf groupers. Back-calculated fertilization dates for postlarval groupers collected during our study coincided with the reported spawning season for *M. microlepis* off the southeastern coast of the United States (Collins et al., 1987), and consequently lend supporting evidence to our assumption that the increments were formed on a daily basis.

The relatively long pelagic duration of *Mycteroperca microlepis* (43.3 days) may be related to the distance (at least 60 km) from offshore spawning areas to estuarine nursery grounds; however, we have no data for pelagic duration of other grouper

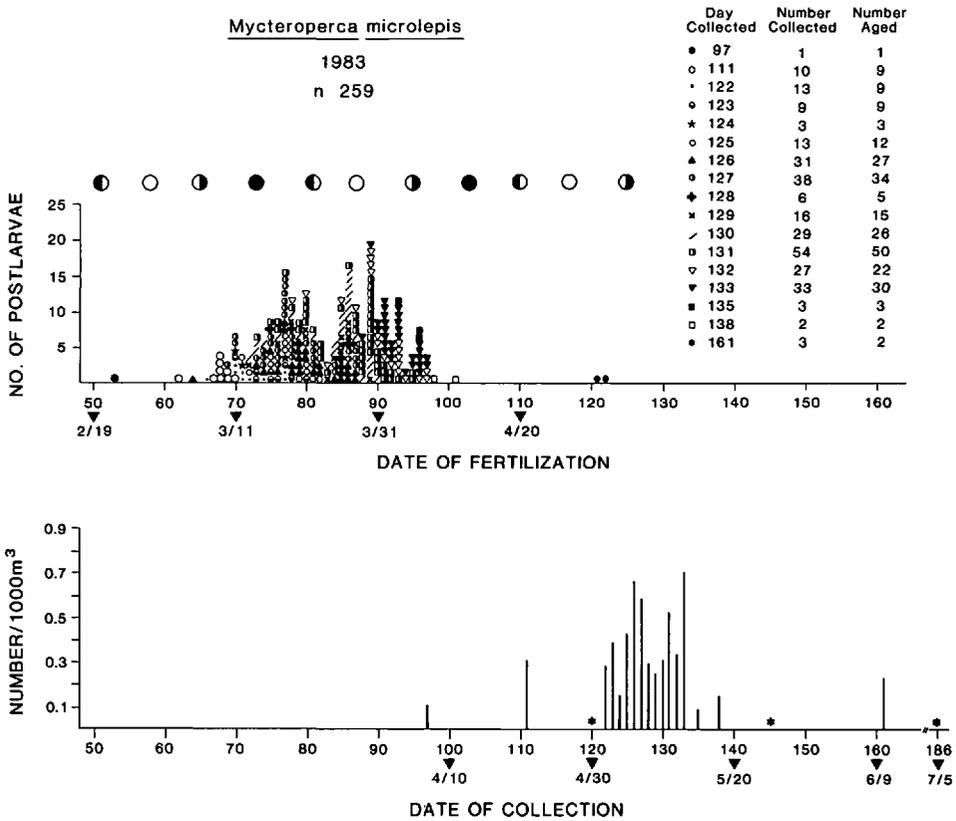


Figure 12. Back-calculated fertilization dates and corresponding standardized catches by date for individual postlarval specimens of *Mycteroperca microlepis* collected in 1983. Dates of collection are expressed as consecutive days of the year, i.e., January 1 = Day 1. Dates when sampling occurred but no specimens were collected are denoted by *.

species that settle offshore. McFarland et al. (1985) reported that the short pelagic existence of *Haemulon flavolineatum* indicated that larval dispersal did not take place over large distances, because postlarvae settled on coral reefs at about 2 weeks of age (Brothers and McFarland, 1981). Reported settling times for other reef-associated species range from 15 to 85 days (Brothers et al., 1983; Brothers and Thresher, 1985; McFarland et al., 1985).

Trends toward lower mean ages at ingress suggest that postlarval *M. microlepis*

Table 5. Ranges of back-calculated fertilization dates for *Mycteroperca microlepis*, *Mycteroperca* sp., and *M. bonaci*, from 1981 to 1983, as determined from daily ages

Year	<i>Mycteroperca microlepis</i>	<i>Mycteroperca</i> sp.	<i>M. bonaci</i>
1981	13 Feb–21 Apr (N = 232)	24 Feb–8 Apr (N = 12)	7 Mar–20 Apr (N = 13)
1982	3 Mar–22 Apr (N = 143)	—	15 Mar (N = 1)
1983	22 Feb–2 May (N = 262)	—	13 Mar–5 May (N = 58)

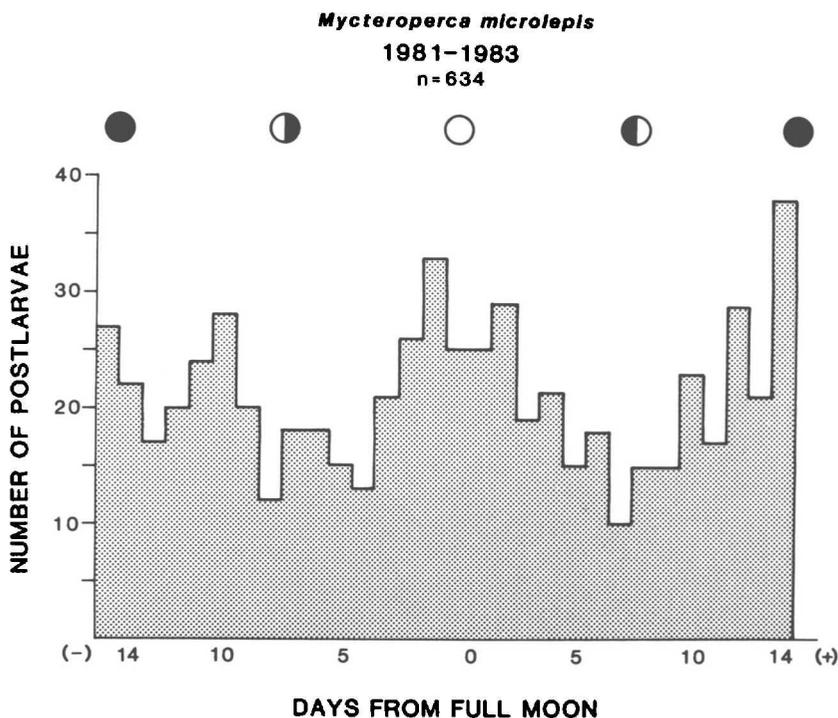


Figure 13. Back-calculated fertilization dates for postlarval *Mycteroperca microlepis* from 1981 to 1983, plotted over a single lunar cycle with respect to number of days on either side of the full moon.

reach estuarine nursery grounds faster towards the end of the sampling period. Because there was little variation in mean SL at ingress, individuals entering the inlet later in the sampling period apparently grew faster than those individuals entering several weeks earlier. This apparent increase in growth rate later in the sampling period corresponds with higher rates of primary productivity during this time of year (Atkinson, 1985), and may reflect increased prey availability. Major fluctuations in factors affecting the success of transport should also be reflected in ages and standard lengths of postlarvae upon entry to the estuarine habitat, and it is possible that significant annual differences in planktonic duration could provide a test for hypotheses for the mechanism of transport, when correlated with specific annually fluctuating physical factors.

Our observations of lapilli from settled juvenile *M. microlepis* indicated that the transitions in daily growth increments in lapilli may be correlated with physiological, morphological, and/or environmental changes associated with transformation to a different developmental stage (Brothers and McFarland, 1981; Pannella, 1980; Victor, 1982). Small sizes of some of these specimens (16–20 mm SL) and retention of the characteristic elongate, serrated second dorsal and pelvic fin-spines suggested that these juveniles were newly settled. Furthermore, increases in the amount of pigment indicated that these individuals were in the initial stages of developing juvenile pigmentation patterns. The mean age of these small (<20 mm SL) settled juveniles (47.1 days, ranging from 41–56 days) indicated that they had only recently entered the inlet, since the mean age at ingress was 43.3 days. The mean age at which transition marks were formed in the lapilli of these small settled juveniles (41.6 days) corresponded closely to the mean age at ingress (43.3

days), indicating that transition marks were only recently formed in the lapilli. Since transition marks were formed in lapilli shortly before postlarvae actually settled out of the plankton, this mark may reflect the initiation of physiological, morphological, and/or environmental changes that immediately precede settlement.

Periodicity in the relative abundance of postlarval gag was indicated by variation in standardized catches throughout the sampling period. One would expect back-calculated daily ages for these specimens to reflect a similar periodicity, presumably a periodicity in the spawning activity of the adults. Johannes (1978) reported that 51 species of fishes worldwide (45 of which are tropical) are known to exhibit lunar spawning periodicities (spawning on new or full moons). Putative peaks in spawning activity of *M. microlepis* were associated with times of new or full moons and Johannes' (1978) list of species demonstrating lunar spawning periodicities included four species of epinepheline serranids—*E. merra*, *E. tauvina*, *E. striatus*, and *Plectropomus leopardus*.

Although putative fertilization peaks may actually represent peaks in reproductive activity, they alternatively could reflect peaks in survivorship and/or efficiency of larval transport, resulting from fluctuations in environmental factors. McFarland et al. (1985) discussed the problem that results from back-calculating fertilization dates based only on ages of postlarvae that have survived to the time of sampling and have successfully migrated or been transported to the sampling area. More detailed information is needed on the reproductive activity of adults and factors affecting survivorship of the larvae, and, perhaps more importantly, the mechanism(s) (and associated parameters) by which the postlarvae are transported shoreward to the areas where they settle.

Differences in estimates of the magnitude of ingress for postlarval *M. microlepis* for 1983 and 1984 are difficult to interpret, and may simply reflect variability in the extent and coverage of sampling from year to year. However, these differences could also reflect yearly fluctuations in general fecundity, as related to the physical condition of the adults, the success of spawning, early larval mortality, and parameters affecting the mechanism(s) of transport. As with yearly fluctuations in age and length at ingress, significant differences in estimates of the magnitude of ingress from year to year could provide a means of testing proposed hypotheses of the mechanism(s) of transport by correlating estimates of ingress with variability in various factors thought to be associated with transport to the estuarine habitat.

Our estimates of the magnitude of annual ingress of postlarval gag into Price Inlet during our study are substantial, particularly when one considers the potential contribution to recruitment of adult stocks offshore. Preliminary data collected at 11 other inlets, as far north as Little River, South Carolina (33°51.4'N) and as far south as Calibogue Sound, South Carolina (32°07.3'N), in 1983 indicated that similar ingress of postlarval gag was occurring in tidal passes all along the coast and our estimates apply to ingress at only one of the many barrier island inlets of South Carolina. Postlarval gag are relatively large at ingress and are certainly beyond the major periods of larval mortality; the estuarine habitat offers an abundance of food and probably some haven from predation, both of which could enhance growth rates (as evidenced by the inflection in the growth curve for *M. microlepis*) and survival rates relative to that characteristic of offshore habitats. Unfortunately, no data are available on the early growth of grouper species that typically settle offshore.

Further research into spawning periodicities and environmental and/or behavioral factors driving the transport-migration mechanisms would broaden our understanding of estuarine ingress of *M. microlepis*. This, in turn, could provide

important early life history information that might be utilized in the development of spawner-recruit models for fisheries management.

ACKNOWLEDGMENTS

Many individuals participated in collection and laboratory processing of data during the course of this study. We thank personnel of the MARMAP (Marine Resources Monitoring, Assessment, and Prediction) program at the South Carolina Marine Resources Research Institute and Capt. V. Taylor of the R/V ANITA for their assistance in data collection. C. B. Olmi assisted in reading daily growth increments. M. R. Collins, G. R. Sedberry, C. A. Wenner, and E. L. Wenner provided information on statistical analysis procedures. M. J. Clise and W. P. Coon, III provided invaluable assistance in data processing. The South Carolina Sea Grant Consortium provided funds for sampling during 1980 and partially funded the study during 1981. This research was also sponsored by the National Marine Fisheries Service (Southeast Fisheries Center) under Contract No. 50-WCNF-7-06-004 and the South Carolina Wildlife and Marine Resources Department (SCWMRD Contribution No. 231).

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DATE ACCEPTED: July 7, 1987.

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