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Partial Life History of Southern Hogchokers, *Trinectes maculatus fasciatus*, in the Back Bay of Biloxi, Mississippi

TANYA L. PETERSON-CURTIS

To address life history variation between hogchoker subspecies, length–weight relationships, length conversion factors, back-calculated lengths at age, and female age at maturity were determined for a southern hogchoker population in the northern Gulf of Mexico. Length–weight relationships of female and male hogchokers differed ($P < 0.05$) only when the regression was based on total lengths. The standard length (SL)–weight equation was $W = 0.000022 \cdot L^{3.136}$. Individuals of the southern population are more robust than those of the northern form, yet have similar SL–TL conversion factors. Otolith annuli were validated, with annuli forming between June and July. The age structure ranged from 1 to 5 yr, with the average SL at age 1 being 21.14 mm. Growth rates appear relatively constant over these 5 yr, with only slight decreases seen in the fourth and fifth year. Females are mature by age 3 or 4. This age structure is different from that reported for mid-Atlantic coast populations with both fewer age classes and lower lengths at age found in the Gulf specimens. The age at maturity for this population is intermediate between values for the northern subspecies in New York and Maryland. Southern hogchokers are smaller and possibly shorter lived than northern hogchokers, suggesting an altered life history in warmer environments.

Hogchokers, *Trinectes maculatus* (Achiridae), are small estuarine flatfish with populations documented in coastal Atlantic waters from Maine to the Yucatan Peninsula (Hildebrand and Cable, 1938; Bigelow and Schroeder, 1953; Gilbert and Kelso, 1971). Two subspecies, *T. m. maculatus* and *T. m. fasciatus*, are currently recognized, being distinguished based on blind side body coloration. The range of *T. m. maculatus* (northern hogchoker) extends southward to approximately the South Carolina coast, with the southern form's (*T. m. fasciatus*) range continuing throughout the remainder of the species range (Hubbs and Allen, 1943). Hogchokers are summer estuarine spawners and the larvae migrate up river into low-salinity habitats. The following spring, these fish move back downstream into more saline habitats. This downstream distance is extended progressively each year until maturity (Dovel et al., 1969). In Mississippi, spawning occurs in salinities of 15–17 ppt (Peterson, 1996). Each fall, the fish return to lower salinities to overwinter.

Both biotic and abiotic factors affect life history patterns. Because juvenile and adult hogchokers have few natural predators and are benthic food generalists (Hildebrand and Schroeder, 1928; Reid, 1954; Castagna, 1955; Wockley, 1968; Carr and Adams, 1973; Smith et al., 1984), any differences in life histories among populations would most likely be the

result of abiotic influences and available genetic variation. Although habitat availability and food limitation are potentially important forces, environmental conditions are probably the main influences. Various aspects of hogchoker life history have been investigated (Hildebrand and Schroeder, 1928; Hildebrand and Cable, 1938; Mansueti and Pauly, 1956; Wockley, 1968; Dovel et al., 1969; Koski, 1978; Smith, 1986), but there is substantial disagreement on the life span, age structure, and reproductive development of this species. For example, life span estimates have ranged from 5–6 (Dovel et al., 1969) to 12 (Wockley, 1968) yr. Most work with *T. maculatus* has been on the northern subspecies, and the few studies investigating the southern form have dealt only with Atlantic coast populations.

The objectives of this study were to: (1) determine the length–weight relationships, length conversion factors, and back-calculated lengths at age of the Back Bay of Biloxi hogchoker population, (2) determine female age at maturity for a Gulf of Mexico population of southern hogchokers, (3) address life history variation between hogchoker subspecies, potentially as a latitudinal gradient of characters, and (4) comment on the developmental progress of field-caught juvenile hogchokers.

MATERIALS AND METHODS

The specimens used in these analyses were collected during 1993 from a monthly fishery

survey along a salinity gradient from the Back Bay of Biloxi offshore to Horn Island by personnel of the Gulf Coast Research Laboratory (GCRL), Ocean Springs, Mississippi (Fig. 1). The survey samples consisted of standardized 10-min tows with a 4.9-m flat otter trawl. Deeper trawls, at stations 83 and 84, required 30-min tows with a 12.2-m flat otter trawl. Both trawls consisted of a 19.1-mm stretch mesh body with a 6.4-mm mesh cod end liner. Each specimen was weighed (0.1 mg), measured [standard length (SL) and total length (TL); 0.01 mm], and then dissected to remove the otoliths. Gender was determined and females were assigned a reproductive classification following Smith (1986).

Least-squares regressions were generated by the SPSS statistical package (version 4.1) and the slopes were compared with hand-calculated t-tests [see Peterson (1994) for details]. All other statistics were calculated with Quattro Pro (version 4.0) software.

The sagittal otoliths were embedded in Ciba Geigy® media and sectioned with a Buehler® Isomet Saw in 1.0–2.0-mm increments. The sections were hand-ground to a 0.20–0.50-mm thickness using 600 and 1,500 grit sandpaper and then polished (Buehler® Alpha Micropolish II). The otoliths were aged by three independent readers at $\times 640$ using transmitted light, and were only included in the analysis if at least two of the three readings agreed. Measurements used for annuli validation, asymmetry validation, and back-calculations were taken with the Java Imaging System at GCRL. The measurements for back-calculations and annuli validation were taken at $\times 640$ as the maximum distance between annuli. To address the possibility of asymmetrical growth of the otoliths, measurements of maximum total width of the otolith and the maximum core-edge distance along this axis were taken at $\times 400$.

Two additional samples of young-of-the-year (YOY) hogchokers were collected at the mouths of the Tchoutachabouffa River and Old Fort Bayou by seining in Aug. and Sep. 1993, respectively. Since the YOY otoliths were too small to section, yet unreadable without processing, they were slightly ground on each side with 1,500 grit sandpaper and mounted on microscope slides with Crystal Bond®. Both otoliths of these fish were read by three independent readers at $\times 400$ and required the same criteria as the survey samples. Only core position measurements were taken from the YOY otoliths to assess the possibility of asymmetrical growth at this stage.

Frequency distributions of the distance measurements were compiled to evaluate asymmetry and annuli validation. The core position (% of total width) frequencies showed a normal distribution for both the survey and YOY samples, validating the assumption of symmetrical otolith growth. An additional collection of hogchokers from the Pearl River, Mississippi (USM #15664), was also examined to validate annuli. The annular formation of rings was validated because only a single peak occurred in the monthly distribution of average ring-to-edge distances, with annular formation occurring between June and July.

RESULTS

During 1993, 142 hogchokers were collected at stations 34, 36, 37, and 32, with no fish collected at stations 83 and 84 (Fig. 1). The length–weight relationships of female and male hogchokers were significantly different ($P < 0.05$) only when the regression was based on TL. The slopes of the TL–weight regressions were 3.250 and 3.177 for females and males, respectively (Fig. 2). The resulting combined SL–weight equation was $W = 0.000022 \cdot L^{3.136}$ (Fig. 3). The length conversion factors were 1.246 for standard-to-total-length and 0.801 for total-to-standard-length conversions.

In the otolith readings, 87% agreement occurred among observers, resulting in 96 specimens, ranging from 25–100 mm SL, being included in the final analysis. The age varied from 1 to 5 yr, with the average SL at age 1 being 21.14 mm. Hogchokers showed a relatively consistent growth rate throughout their lives, with only small decreases seen during the fourth and fifth years (Fig. 4). There was a wide range of SLs at each age (Fig. 5), with overlap occurring among the age classes. This is probably an artifact of their long spawning season, with the largest difference being between the first and last spawned individuals of each year.

Females began maturing at age 2, but did not reach sexual maturity until age 3 or 4 (Table 1). One spent female was collected, but was not included in the aging procedure due to inconsistent readings.

The YOY samples contained 139 specimens, of which 23 were processed for otolith work. The size distribution of the entire sample ranged from 9.3 to 29.9 mm SL, with the mode at 18 mm SL. All specimens were fully metamorphosed into their asymmetrical form and only one fish (14.8 mm SL) still retained pec-

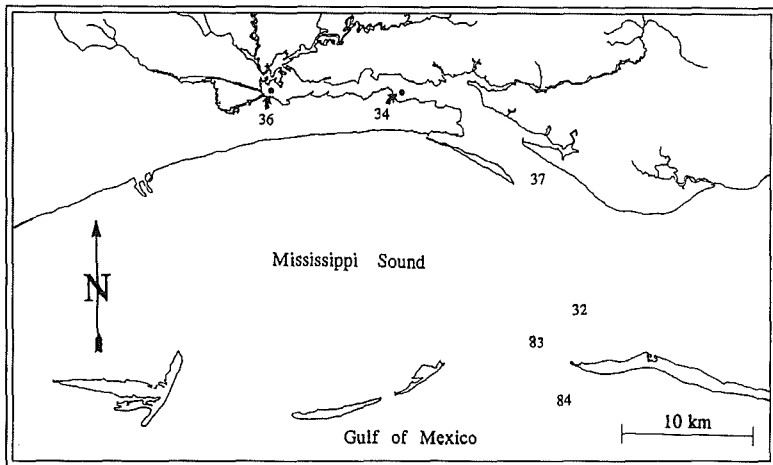


Fig. 1. Distribution of sampling localities for the GCRL survey program in the Back Bay of Biloxi, Mississippi.

toral fin rudiments. All of the 23 preserved fish (12–25 mm SL) were sexually immature. Fifteen pairs of otoliths were suitable for measuring core–edge distances (asymmetry validation), but none were readable for daily age estimates. Rings were clearly visible on several otoliths. However, even with generally clear specimens, the center and outer rings were not visible. If the otoliths were ground enough to clear the center and edges, the intermediate rings were lost. Other processing techniques may be more successful at producing readable “daily” increments.

DISCUSSION

Although the data on YOY hogchoker development presented here are somewhat anecdotal, documentation is warranted, considering that development after the onset of metamorphosis is unknown. Previous studies on hogchokers have reported that newly hatched larvae range from 1.7 to 1.9 mm and the yolk sac is absorbed after approximately 16 h at lengths of 2.2–2.4 mm. Pectoral fin folds are present at the time of yolk sac absorption (Hildebrand and Cable, 1938). At 4 mm in length,

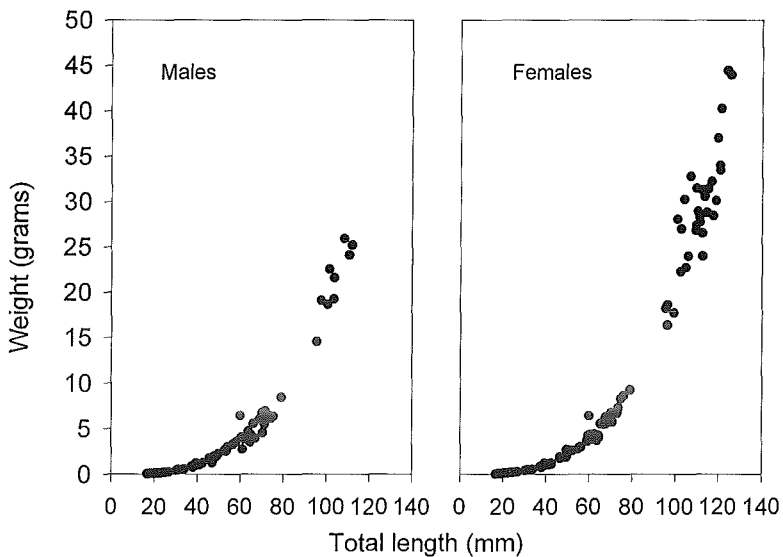


Fig. 2. Total length–weight regressions for (a) male and (b) female hogchokers in the Back Bay of Biloxi.

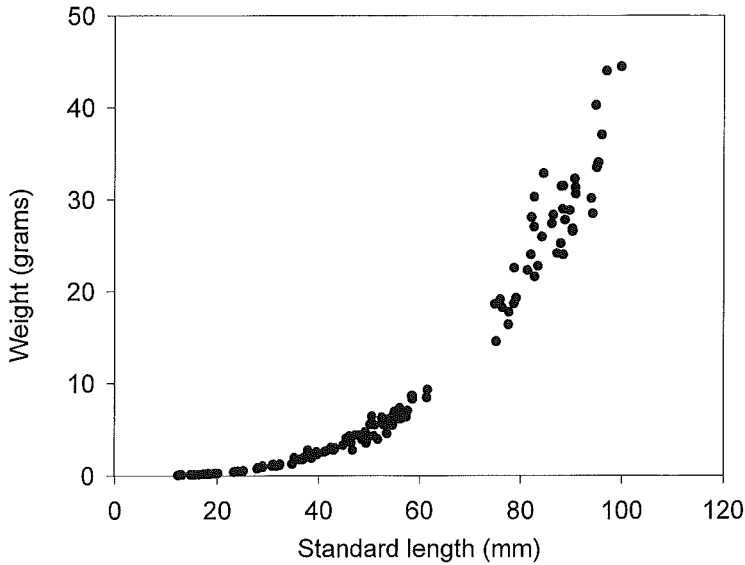


Fig. 3. Standard length–weight regression ($W = 0.000022 \cdot L^{3.136}$) for a Gulf population of southern hogchokers.

the fin rays are clearly differentiated and the body is still symmetrical and heavily pigmented (Pearson, 1941). The eyes begin to migrate at day 34 (5.0–6.0 mm), but no larvae have been observed past this beginning stage (Hildebrand and Cable, 1938). The new data presented here indicate that metamorphosis is completed and pectoral fin rudiments are generally lost by at least 9.3 mm SL. However, the daily aging attempted here does not provide

additional insight as to when these transformations are completed.

Reported slopes for length–weight regressions of northern hogchokers vary from 2.66 (SL; Dawson, 1962) to 3.14 (TL; Wockley, 1968). The values (3.14 SL, 3.25 TL) for this Gulf population of southern hogchokers suggest that these individuals are more robust than those of mid-Atlantic populations. The differences found in the weight–length relationships between males and females when using TL suggest sexual dimorphism in caudal morphology, with females having slightly longer caudal fins. This dimorphism becomes apparent only at larger body sizes (>70 mm SL). Sexual caudal dimorphism has not been reported elsewhere; however, Smith (1986) found that females hogchoker were 9 mm (TL) longer than males at a given age. This occurrence could be a result of differential growth rates between sexes, or an indication of caudal dimorphism as reported in this study. Mansueti and Pauly (1956) and Dawson (1962) reported length conversion factors for Maryland and South Carolina populations that are similar to those reported here. For comparative purposes only, the length conversion factors were calculated with all data combined. However, for accurate application of these values, they should be calculated separately for males and females due to the difference in caudal lengths.

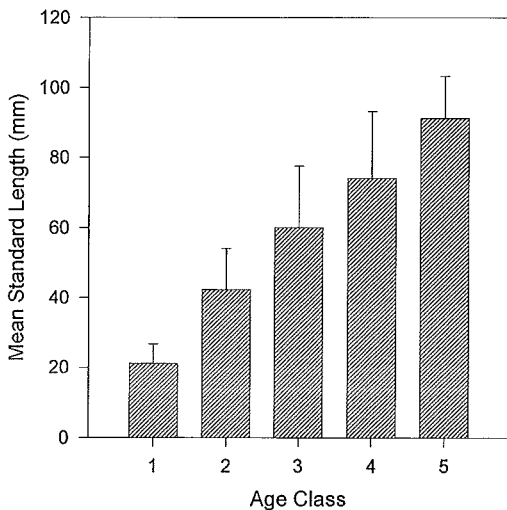


Fig. 4. Mean standard length at each age of southern hogchokers sampled during 1993. Error bars represent 1 SD.

Scale annulus formation occurred in June

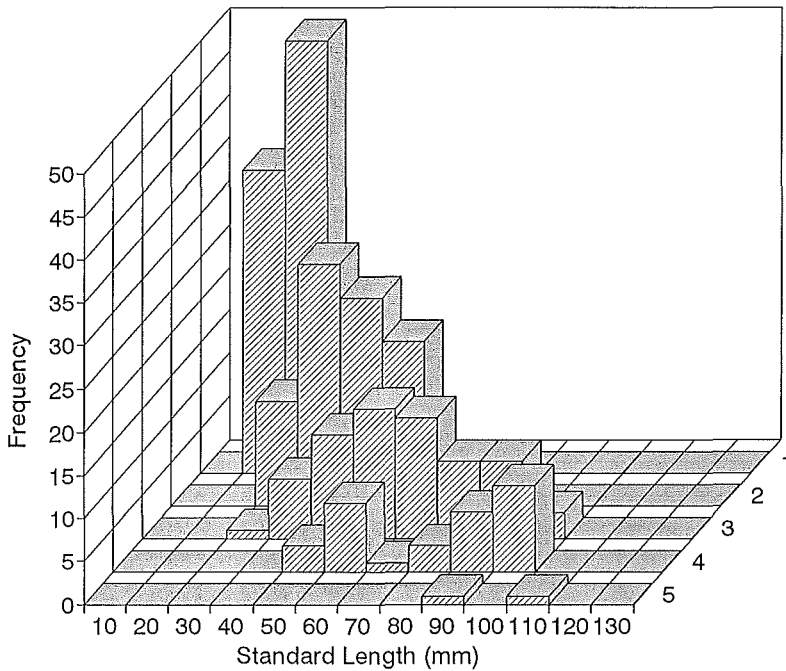


Fig. 5. Frequency distributions of standard lengths of southern hogchokers in each age class collected during 1993.

for a New York population (Koski 1978), indicating similarity in annulus formation between subspecies and between the timing of scale and otolith annulus formation. Maximum ages reported for northern hogchokers vary from 6 (Dovel et al., 1969) to 12 yr. (Wockley, 1968), with average SL at first annulus formation ranging from 40 to 60 mm. However, Hildebrand and Cable (1938) reported that individuals of 18–100 mm SL were all YOY specimens. The maximum TL of specimens examined in these studies ranged from 150 to 200 mm. Castagna (1955), who investigated the partial life history of a Florida population of the southern subspecies, could only distinguish between the YOY age class and all other classes using

monthly length-frequency distributions. During June of the next year, this YOY class had standard lengths of approximately 20–30 mm. His larger age class ranged from 30 to 68 mm SL. Therefore, the Back Bay of Biloxi population differs from the mid-Atlantic populations with both fewer age classes and smaller lengths at age.

The largest specimen collected during the present study was a ripe female of 124.1 mm TL. Larger specimens are not represented in regional fish collections (USM and GCRL Museums; GCRL FAM Survey), suggesting that this Gulf population only reaches sizes of 62–83% of the northern subspecies. The relatively linear growth rate of the Biloxi population, which is different from the normal, asymptotic growth curve of northern hogchokers (Mansueti and Pauly, 1956), raises the question of whether larger specimens were merely “missed” in our collecting efforts. This probably was not the case, as larger fish surely would have been documented in this area over the last century if they indeed existed. Other fishery surveys conducted in the Gulf of Mexico either report an absence of hogchokers in the samples (Miller, 1965; Chittenden and McEachran, 1976; Chittenden and Moore, 1977; Bass and Guillory, 1979), do not report

TABLE 1. Matrix of female southern hogchokers at each age and developmental stage. The values represent the number of females sampled during 1993 in each category.

	Age class				
	1	2	3	4	5
Resting	0	9	10	1	0
Developing	0	2	1	5	1
Ripe	0	0	9	12	1
Spent	0	0	0	0	0

any hogchoker length information (Gunter, 1936, 1961; Hildebrand, 1954; Springer and Bullis, 1956; Bullis and Thompson, 1965; Ogren and Brusher, 1977), or report maximum hogchoker sizes within the range of 94–149 mm TL (Gunter, 1945; Christmas and Waller, 1973; Perret and Caillouet, 1974; Swingle and Bland, 1974). The absence of larger specimens from historical records suggests that southern hogchokers are engaging in an intensive growth pattern throughout their lives. The similarity between the age and size structure reported here and in a Florida population of southern hogchokers, as well as the discrepancy with the northern hogchoker populations, suggests different age structures between hogchoker subspecies.

Female age at maturity for populations of northern hogchokers ranges from 2 (Koski, 1978) to 4 yr. (Mansueti and Pauly, 1956; Dovel et al., 1969), with corresponding minimum sizes at maturity of approximately 80–111 mm SL (Mansueti and Pauly, 1956; Wockley, 1968). Castagna (1955) reported a gravid female of 47 mm SL in a Florida population, and the smallest mature female examined in the present study was 75 mm SL. Although female age at maturity found in the Back Bay of Biloxi population is the same as that reported for the Maryland populations, the Gulf specimens are maturing at smaller sizes. From the data presented here and in Castagna's thesis, a smaller size at maturity for females appears to be characteristic of the southern form, indicating another alteration of a life history character between subspecies.

The two subspecies of *T. maculatus* vary in all life history traits examined except for the occurrence of the migration pattern (Peterson, 1996), timing of annulus formation, and SL–TL conversion factors. The results of this study suggest that female size at maturity, adult size and shape, and longevity increase with latitude. Similar patterns of life history variables in relation to latitudinal gradients have been documented many times (*Oncorhynchus* spp.: Leggett and Carscadden, 1978; *Cynoscion regalis*: Sheperd and Grimes, 1983; demersal fishes: Edwards, 1984). Ray (1960) concluded that Bergman's Rule of larger body size with increasing latitude could also be applied to poikilotherms, and Lindsey (1966) proposed that this gradient could be expanded to entire faunas. Numerous factors have been identified as being important in the evolution of the gradients, including temperature, degree of specialization, physiological processes related to the surface–volume ratio, size-selective winter mor-

tality, length of growing season, innate growth capacity, and larval survival strategies (Lindsey, 1966; Leggett and Carscadden, 1978; Roff, 1980; Conover, 1990, 1992; Conover and Present, 1990; Shuter, 1990). For the hogchoker subspecies, which are both relatively small fish having similar diets and habitats, the influences of surface–volume ratios and differential degrees of specialization are unlikely to be factors responsible for the differences between subspecies. However, the interactions of temperature, length of the growing season, and over-winter survival are probably the most important (Roff, 1982).

Southern hogchokers, which have evolved under warmer and less variable environmental conditions, may not require a larger body size to survive the milder winter period. The reduced resource requirements for somatic growth would allow both for a greater portion of resources to be devoted to reproduction and for this allocation to occur earlier, at smaller sizes. In conclusion, there is substantial variation in life history patterns between hogchoker subspecies, which appears to be an example of countergradient variation. For hogchokers, the southern form is more robust, shorter lived, has smaller lengths at age, and matures at smaller sizes.

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