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Life History of Silver Perch *Bairdiella chrysoura* (Lacepède, 1803) in North-Central Gulf of Mexico Estuaries

GRETCHEN L. GRAMMER, NANCY J. BROWN-PETERSON, MARK S. PETERSON, AND BRUCE H. COMYNS

Silver perch, *Bairdiella chrysoura* (Lacepède) [$n = 485$, 70.0–171.0 mm standard length (SL)] were collected from April 2002 through June 2003 in estuaries along the coast of Mississippi to quantify their life history. Ages estimated from sagittal otoliths ranged from 0 to 4 yr. Adult females were significantly longer and heavier than males at a given age. Silver perch became sexually mature at the end of their first year of life (0 yr), with 50% sexual maturity of the population occurring in the 91–95 mm SL size class. Gonadosomatic index (GSI) values for females began to increase in January and peaked in April (mean GSI = 11.99 ± 0.77), whereas mean male GSI values peaked in March at $1.70 (\pm 0.11)$. Female silver perch were reproductively active for 6 mo, but peak spawning occurred from mid-March to June. Both oocyte maturation (OM) and postovulatory follicles (POF) were used to estimate spawning frequency. The OM method appeared to be the best estimate, paralleling most closely what was observed histologically, with spawning occurring every 1.25 d at the height of the season. Additionally, histological evidence suggested that 24% of the females sampled were capable of daily spawning. This life history information fills in data gaps to further the development of community-based models of estuarine systems, in turn facilitating best ecosystem management practices.

The family Sciaenidae includes numerous species of commercial and recreational importance worldwide. Most of these species are estuarine dependent at some stage of their life history, and the juveniles of many sciaenids rely on the marsh edge and submerged aquatic vegetation as nursery habitat (Rooker et al., 1998; Peterson et al., 2000; Geary et al., 2001). In the southeastern United States important commercial and recreational species of sciaenids such as the sea trouts *Cynoscion* spp., red drum *Sciaenops ocellatus* (Linnaeus), spot *Leiostomus xanthurus* Lacepède, black drum *Pogonias cromis* (Linnaeus), and Atlantic croaker *Micropogonias undulatus* (Linnaeus) have been well studied. However, many of the small, noncommercial, but trophically important sciaenid species such as silver perch *Bairdiella chrysoura* (Lacepède), banded drum *Larimus fasciatus* Holbrook, and star drum *Stellifer lanceolatus* (Holbrook) have been neglected (Waggy et al., 2006). In particular, silver perch are an essential component of estuarine systems in terms of abundance, residence, and trophic interactions. Common snook (*Centropomus undecimalis* (Bloch); Blewett et al., 2006), juvenile blacktip sharks (*Carcharhinus limbatus* Müller and Henle; Heupel and Hueter, 2002), and bottlenose dolphins (*Tursiops truncatus* (Montagu); Luczkovich et al., 2000) are examples of large estuarine predators that prey upon silver perch. Indeed, silver perch are one of the five most abundant species of sciaenid in

estuaries along the Gulf of Mexico (GOM) and the Atlantic coast of the United States (Chao and Musick, 1977; Rooker et al., 1998; Gelwick et al., 2001) and support a small commercial fishery in the southern GOM (Ocaña-Luna and Sánchez-Ramírez, 1998; Ayala-Perez et al., 2006).

Despite the ecological importance of silver perch, their life history has not been well documented. There have been neither histological examinations of the gonads nor estimates of spawning frequency for this species. Age-morphometric relationships of silver perch have only been estimated from scale annuli (Welsh and Breder, 1924); the largest fish examined was 230 mm total length (TL) and 6 yr old. However, ages of fishes are often underestimated with the scale method, and the use of otoliths often provides more accurate estimates of age (Lowerre-Barbieri et al., 1994; Paperno et al., 1997). Hales and Hurley (1991) validated daily increment formation in the sagittal otoliths of juvenile silver perch [39–66 mm standard length (SL)], but adult fish (using annuli) have not been aged with otoliths. It is known that spawning occurs at dusk in estuaries (Holt et al., 1985) between March and June in the southeastern United States (Hildebrand and Schroeder, 1928; Hildebrand and Cable, 1930; Mok and Gilmore, 1983). Fish from the Everglades, FL, have a mean relative fecundity of $1,249 \pm 130$ eggs/g (Schmidt, 1993). Age and size at maturity varies from 2 yr and 150–210 mm TL in Beaufort, NC

Fig. 1. Map of collection sites (black circles) for silver perch in the northern Gulf of Mexico.

(Welsh and Breder, 1924) to 5 mo and 100 mm TL in Terminos Lagoon, Mexico (Chavance et al., 1984).

Fish communities are vital components of estuarine systems, and species such as silver perch maintain and process great amounts of biomass in estuaries as a predator on benthic resources and as prey for a host of higher level piscivores, many of which are of considerable economic value. We currently have almost no life history data on some of the dominant estuarine species throughout their range, and therefore their importance in estuaries is often overlooked. Clarifying the ecological role of silver perch within the estuarine landscape first requires a detailed understanding of its life history characteristics. Information of this nature is extremely important to coastal managers to ensure accurate data are included in predictive ecosystem models. The objective of this study was to investigate life history characteristics of silver perch in Mississippi Sound, MS. Specifically, age–weight–length relationships, reproductive seasonality, and spawning frequency were examined.

MATERIALS AND METHODS

Fish collections and procedures.—Silver perch were collected monthly from April 2002 through June 2003 by trawling (dawn to noon), gill netting (dawn to noon), and hook and line (dusk to dawn) within the Mississippi Sound and waters just to the south of the Mississippi barrier islands and to the east of Chandeleur Islands, LA (Fig. 1). The collections were fishery independent and made opportunistically, taking advantage of bycatch from other scientific activities and the live bait industry. These fish were used for histological analysis of female gonads, the determination of spawning frequency, gonadosomatic indices (GSI), and age–size relationships. The silver perch were immediately placed in an ice slurry for euthanization (ASIH/AFS/AIFRB, 1988; Huntingford et al., 2006) and to maintain the quality of the gonads. Total length (mm), SL (mm), sex, macroscopic maturation, gonad weight (GW, 0.001 g), and eviscerated wet somatic weight (EWW, 0.001 g) were measured for each fish. Male silver perch were examined macroscopically to determine whether they were

in the actively spawning reproductive phase, characterized by creamy white testes with milt flowing freely under light pressure on the abdomen. Gross maturation of the ovarian tissue is based on descriptions by Brown-Peterson (2003) for spotted sea trout *Cynoscion nebulosus* (Cuvier). Gonads were removed and weighed, and a 1 cm³ tissue section was removed from the midsection of the left or right ovary of each female. The tissue was placed in a cassette and preserved in 10% neutral buffered formalin for histological determination of female reproductive status. For select females in the oocyte maturation (OM) stage, a portion of ovarian tissue was removed and preserved from the posterior, anterior, and middle sections of both the right and left ovary to ensure that oocyte distribution was homogenous throughout. Sagittal otoliths were removed through the upper neurocranium, rinsed in water, and stored dry in envelopes for annular age estimation.

Age determination.—Otolith preparation and analysis followed Panella (1971) and Secor et al. (1991). The otoliths were embedded in epoxy resin, sectioned in the transverse plane with a Buehler Isomet saw, and mounted on microscope slides. Annuli (refers to opaque ring, each presumed to mark 1 yr of growth) were counted with transmitted light using a dissecting microscope at $\times 2.5$ magnification. Two independent reads of the annuli were performed on each otolith by counting the annuli or daily increments and the two were compared. Otoliths for which counts disagreed were reread, and if there was still a deviation, a second reader counted and compared the increments. If agreement could not be reached, the otolith was removed from further analysis. Fewer than 1% of the otoliths were removed from analysis.

Marginal increment analysis was used to confirm annulus formation. The distance from the outer edge of the last presumed annulus to the edge of the otolith was measured under transmitted light with an ocular micrometer (0.01 mm) on a dissecting microscope at $\times 2.5$. These measurements were plotted by size class and month to determine the time of annulus formation. Because the majority of silver perch spawn between March and May, and ring formation occurred between March and May, each fish was assigned a biologically realistic median hatching date of 1 April. The adult and juvenile fish were split into age classes: year class 0, year class 1, year class 2, etc. The age of each fish was used in conjunction with its TL, SL, and EWW to develop a length–age key, to examine

age–weight characteristics, and to determine age at sexual maturity.

Reproductive biology.—The presence of cortical alveoli oocytes was used as an indication that a fish was sexually mature and would spawn during that reproductive season (Brown-Peterson, 2003). At the end of the season, atretic oocytes indicated sexual maturity. The GSI was calculated for all adult specimens with $GSI = [GW/EWW] \times 100$ (Crim and Glebe, 1990). Females with hydrated oocytes were included in these calculations. Preserved ovarian tissue was dehydrated, embedded in paraffin, sectioned at 4 μ m, and stained with hematoxylin 2 and eosin Y (Richard Allen Scientific) following standard histological procedures. Ovarian maturity phases were assigned microscopically following Brown-Peterson et al. (2007) and include immature, developing, spawning capable, actively spawning, regressing, and regenerating. Oocyte terminology and staging follows Grier et al. (2009). However, oocyte maturation stages follow Brown-Peterson (2003), and postovulatory follicles (POF) were classified following Hunter et al. (1986). For each fish examined, three haphazardly chosen views were examined under a compound microscope at $\times 100$, all stages of oocytes and POF were counted, and the percentages of each were estimated.

Spawning frequency was estimated with the OM and POF methods (Hunter and Macewicz, 1985; Brown-Peterson and Warren, 2001) and is expressed as the mean number of days between successive spawning events. These estimates are based on the monthly percentage of spawning-capable and actively spawning females with ovaries containing either OM or POF ≤ 24 hr old. Spawning frequency was estimated for months when there were ≥ 25 females within the spawning-capable and actively spawning phases. However, the late season estimate (June–August) was based on only 16 individuals.

Statistical analysis.—Linear regression between GSI and EWW was performed to check for a lack of correlation between the two and, thus, for the usefulness of the index as a measure of spawning preparedness (Jons and Miranda, 1997). Female silver perch determined to be immature by histological examination and male silver perch with GSI values < 0.1 were excluded from GSI data analysis. Standard length–TL correlations were also estimated with linear regression to facilitate comparison with published literature. Eviscerated wet somatic weight–SL, age–EWW, and age–SL relationships were compared by sex with analysis of covariance

Fig. 2. Transverse section of a year class 3 silver perch sagittal otolith viewed using transmitted light. The arrows indicate annular rings.

(ANCOVA). The covariates were age for the age relationships and SL for EWW–SL. Linear regression was also used to determine predictive equations for the aforementioned relationships. Potential differences in monthly spawning frequency were tested with chi-square (Brown–Peterson et al., 2002). Kruskal–Wallis analysis of variance (KW) was used to examine oocyte stage homogeneity within an ovary lobe, and a Mann–Whitney U-test (MW U) was used to compare oocyte stage homogeneity between the lobes of the ovaries. Data sets were tested for homogeneity of variance (Levene’s test) and normality (Kolmogorov–Smirnov one-sample test), and if these conditions were not met, the data were log-transformed to stabilize the variance. All GSI values and percent oocyte stages were arcsine-square root transformed prior to analysis (Sokal and Rohlf, 1995). SPSS 15.0 (SPSS, Inc., Chicago, IL) was used to conduct all statistical tests, and results were considered significant if $P < 0.05$.

RESULTS

All silver perch for this research were captured within estuarine areas closely associated with a landmass in Mississippi and Louisiana. Collections in offshore waters (not represented in Fig. 1) did not produce any silver perch. Thus, silver perch are considered estuarine residents, i.e., they feed, reproduce, and grow to maturity within an estuarine ecosystem.

Age structure and morphometrics.—Distinct annuli were evident in cross-sections of silver perch otoliths (Fig. 2). Five age classes were found in the mature population of silver perch, year class 0, year class 1, year class 2, year class 3, and year class 4. Marginal increments of year class 1 ($n = 132$) and 2 ($n = 63$) silver perch were plotted by month (± 1 SE), and only one trough appeared, suggesting one opaque increment is formed per year, with the opaque portion being formed between March and May (Fig. 3). Marginal increments of year class 1 fish were greatest in the late fall and winter months (October–February; Fig. 3A). Few year class 2 fish (Fig. 3B) were captured during these months.

The majority of the sample population was composed of year class 0 and year class 1 silver perch. Year class 0 fish comprised 44.2% of the sample population, and 38.8% were in year class 1. Year classes 2, 3, and 4 made up the remainder of the population and had values of 13.1%, 3.1%, and 0.8%, respectively. Silver perch attained a maximum age of 4 yr in the Mississippi Sound.

Female silver perch ranged from 79.7 mm to 171.0 mm SL, and males ranged from 70.0 mm to 136.0 mm SL (total $n = 485$). Equations to predict SL from TL for males and females are given in Table 1. Eviscerated wet weight of both sexes increased with increasing SL (Table 1). Male and female slopes were parallel (ANCOVA: $F_{1,481} = 0.369$, $P = 0.544$) with no significant difference in SL ($F_{1,481} = 0.433$, $P = 0.511$)

Fig. 3. Marginal increment analysis (± 1 SE) of silver perch otoliths. (A) Year class 1 ($n = 185$); (B) Year class 2 ($n = 63$).

between the sexes when adjusted for weight (i.e., no difference in weight between male and female silver perch at a given length; Table 1). Because there was no difference in EWW

between sexes, a pooled SL–EWW regression was calculated (Table 1) to allow a comparison of the data with relationships presented in the literature.

Both male and female silver perch >70 mm SL had a significant positive relationship between SL and age (Table 1); the slopes of males and females were not parallel (ANCOVA: $F_{1,476} = 4.951$, $P = 0.027$) when adjusted for SL. Females displayed a steeper slope (3.086) than the males (2.689), suggesting females increase in SL at a significantly faster rate than males when adjusted for age. There was also a significant positive relationship between EWW and age for both sexes (Table 1). Slopes of males and females were not parallel in relation to age when adjusted for EWW (ANCOVA: $F_{1,476} = 0.023$, $P = 0.022$). Females had a steeper slope (0.958) than the males (0.852), suggesting the females increase in weight at a significantly faster rate than males when adjusted for age.

Reproductive biology.—There was no significant relationship between GSI and EWW in either silver perch females ($r^2 < 0.001$, $P = 0.891$, $n = 279$) or males ($r^2 = 0.009$, $P = 0.323$, $n = 113$), confirming that GSI could be used as an indicator of reproductive preparedness. Mean female GSI values (Fig. 4) peaked in April at 11.99 ± 0.77 SE, while males peaked a month earlier in March with a mean GSI value of 1.70 ± 0.11 SE. Female silver perch appeared to be reproductively active (as indicated by elevated GSI values) for 7 mo (mid-January–mid-August) with peak reproduction occurring from March to June based on GSI values (Fig. 4). Elevated GSI values in males corresponded with the presence of actively spawning males, which did not appear in the population until March and were observed until July, although there were no actively spawning males collected in June. During April and May, all males captured were actively spawning.

TABLE 1. Summary of morphometric equations and statistics. SL, standard length (mm); TL, total length (mm); and EWW, eviscerated wet weight (g).

Comparison	Equation	Sample size	r^2	P
SL–TL (σ)	$\log SL = 0.960 (\log TL) - 0.000$	145	0.927	0.001
SL–TL (φ)	$\log SL = 0.976 (\log TL) - 0.033$	340	0.970	0.001
SL–EWW (σ)	$\log SL = 0.288 (\log EWW) + 1.629$	145	0.919	0.001
SL–EWW (φ)	$\log SL = 0.291 (\log EWW) + 1.630$	340	0.946	0.001
SL–EWW ($\varphi\sigma$)	$\log SL = 0.282 (\log EWW) + 1.641$	419	0.910	0.001
Age–SL (σ)	$\log age = 3.086 (\log SL) - 6.368$	336	0.569	0.001
Age–SL (φ)	$\log age = 2.689 (\log SL) - 5.522$	144	0.393	0.001
Age–EWW (σ)	$\log age = 0.852 (\log EWW) - 1.248$	144	0.437	0.001
Age–EWW (φ)	$\log age = 0.958 (\log EWW) - 1.428$	336	0.612	0.001

Fig. 4. Plot of mean GSI (%; ± 1 SE) by month for both sexes of silver perch for fish collected between April 2002 and June 2003. No mature males were collected in November. In September (males) and November (females), only one fish represents the sample. $\circ$ females, $n = 279$; $\blacksquare$ males, $n = 113$.

Histological analysis verified the 7 mo female reproductive period indicated by GSI values. The reproductive period is defined as the period of time in which cortical alveoli oocytes are present in the ovaries; this period is different from, but encompasses, the spawning period (presence of late secondary growth and OM oocytes in ovary; high GSI values). Silver perch exhibit asynchronous oocyte development, with multiple oocyte stages present in a mature ovary at any given time (Fig. 5A). The number of all oocyte stages in silver perch ovaries was found to be homogenous within (KW = 3.121, $df = 2$, $P = 0.210$) and between (MW U = 604.5, $n = 72$, $P = 0.577$) each lobe of the ovary. Therefore, only the middle sections of the ovaries were used for histological analysis.

Ovarian recrudescence began in mid-January with the appearance of the early developing subphase, defined as the presence of only primary and cortical alveolar oocytes. By mid-March, 74.4% of females were reproductively

Fig. 5. Histological sections of silver perch ovaries. (A) Spawning-capable phase, showing asynchronous oocyte development. $\times 200$ magnification. (B) Actively spawning phase with 24-hr POF, indicating daily spawning. Note the presence of mature, nonhydrated oocytes. $\times 100$ magnification. Key: PG, primary growth oocyte; CA, cortical alveolar oocyte; SGfg, full grown oocyte; SGe, early secondary growth oocyte; SGI, late secondary growth oocyte; OM, oocyte maturation; POF, 24-hr postovulatory follicle.

TABLE 2. Monthly percentages of female silver perch ovaries in various reproductive phases. n = the number of females collected during each month.

Month	n	Reproductive phases (%)						
		Immature	Early developing	Developing	Spawning capable	Actively spawning	Regressing	Regenerating
January	21	66.7	33.3					
February	11	9.1	81.8	9.1				
March	39		15.4	10.2	71.8	2.6		
April	50				20.0	80.0		
May	35				31.5	45.7	11.4	11.4
June	25				8.0	28.0	28.0	36.0
July	26				7.7	3.8	19.2	69.3
August	47	61.7			4.3	4.3	2.1	27.6
September	23	30.4						69.6
October	17	100.0						
November	5	80.0						20.0
December	9	55.6						44.4

active (spawning-capable and actively spawning phases, Table 2). Some females were in spawning condition through August, although 22.8% had ceased spawning by May (regressing and regenerating phases, Table 2). There were usually multiple phases of maturation in the population at a given time (Table 2). Immature silver perch were not collected during the main portion of the reproductive season (March–July), suggesting all silver perch are reproductively capable in their first year of life.

All stages of OM, from lipid coalescence through hydration, were observed in silver perch collected during this study. Oocyte maturation was synchronous in an individual female with only one stage of OM evident in the ovary (Fig. 5B), although females collected at the same time of day were in different stages of OM. Not all vitellogenic oocytes undergo OM for the same spawning event, as seen by the presence of fully grown oocytes in actively spawning fish (Fig. 5B).

Silver perch in the north-central GOM are capable of spawning multiple batches of eggs during the reproductive season, as indicated by the presence of POF in ovaries in the spawning-capable and actively spawning phases (Fig. 5B). Only 24-hr POF were found in silver perch ovaries. Actively spawning fish with ovaries containing both oocytes undergoing OM and 24-hr POFs were found in 23.8% of the fish examined (Fig. 5B), indicating daily spawning.

Fifty percent sexual maturity of females occurred in the 91–95 mm SL length class, and all females were sexually mature by the 121–125 mm SL length class (Table 3). Mature and immature silver perch were easily discernable later in the season (August–December); the mature fish were >110 mm SL with clearly

visible atretic oocytes. The largest mature female examined was 171.0 mm SL and was in year class 4; the smallest mature female was 84.0 mm SL and was in year class 0. Silver perch appear to mature just before their first birthday as year class 0 fish. At the beginning of the reproductive season in mid-January, female fish <84 mm SL and males <80 mm SL were not present in collections. Because fish below this size were not captured at the beginning of the reproductive season, a predictive equation for 50% maturity could not be determined. Out of 304 female silver

TABLE 3. Fifty percent maturity of silver perch in Mississippi Sound. Fishes were placed in 5 mm length groups and age classes were based on a 1 April birthday.

Length group (mm SL)	n	Age class	% Maturity
81–85	6	0	0.0
86–90	8	0	0.0
91–95	16	0–1	58.3
96–100	23	0–1	86.7
101–105	31	0–1	95.5
106–110	25	0–1	90.0
111–115	40	0–1	90.6
116–120	24	0–1	95.5
121–125	28	0–1	100.0
126–130	22	1	100.0
131–135	22	1–2	100.0
136–140	14	1–3	100.0
141–145	14	1–3	100.0
146–150	13	2–3	100.0
151–155	9	2–3	100.0
156–160	5	3–4	100.0
161–165	2	3	100.0
166–170	1	4	100.0
171–175	1	4	100.0

perch examined for both age and reproductive purposes, 67 were in the actively spawning phase. Of these, 43.3% were year class 0, 32.8% were year class 1, 17.9% were year class 2, and 5.9% were year class 3. Thus, 76.1% of actively spawning silver perch were 1 yr or less in age.

At the peak of the spawning season in April, the spawning frequency was every 1.25 d (OM method; Table 4). During the most active part of the spawning season (April and May), the spawning frequency was every 1.36 d and declined to every 1.60 d later in the season (June–August). When the POF method was used, spawning frequency estimates decreased. The spawning frequency from POF was every 3.57 d at the peak of the spawning season in April (Table 4). There was a significant difference overall (April–August) between OM and POF spawning frequency values ($\chi^2 = 23.276$, $df = 1$, $P < 0.001$). There was also a significant difference between OM and POF values during the most active part of the spawning season (April–May, $\chi^2 = 17.053$, $df = 1$, $P < 0.001$) and again late in the spawning season (June–August, $\chi^2 = 7.364$, $df = 1$, $P = 0.007$). The OM method appears to best estimate the spawning frequency of silver perch when compared to histological specimens showing evidence of daily spawning (i.e., 24-hr POF in actively spawning phase ovaries, Fig. 5B).

DISCUSSION

Population characteristics.—Changes in population characteristics of silver perch become evident when comparing fish from different regions. Within the Mississippi Sound, silver perch attained a maximum age and size of 4 yr and 171 mm SL (208 mm TL), although the majority (83%) of the population was in year class 0 or year class 1. Silver perch reached 50% sexual maturity between 91 and 95 mm SL (about 112–119 mm TL) as year class 0 fish just before their first birthday. Welsh and Breder (1924) found silver perch in Beaufort, NC, and Chesapeake Bay, VA, to reach 6 yr in age and attain a length of 230 mm TL with the size at maturity being 150 to 210 mm TL at 2 yr of age, although this study used scales to estimate ages. Silver perch in Terminos Lagoon, Mexico, reach maturity at 100–104 mm TL and 5 mo of age based on otoliths with a maximum age of 13 mo (Chavance et al., 1984). The change in maximum age, age at maturity, and size at maturity may be a function of latitude. The maximum age and age at maturity has been shown to decrease with decreasing latitude in other species (Leggett and Carscadden, 1978; Brown-Peterson and Thomas,

TABLE 4. Spawning frequency of silver perch within the Mississippi Sound using both the OM and POF calculation methods. Only females in the spawning-capable and actively spawning phases were used for this analysis. During June and August, there were no fish collected with POF ≤ 24 hr (NA).

	Total number of fish in analysis	OM spawning frequency (d)	POF spawning frequency (d)
April	50	1.25	3.57
May	26	1.63	4.33
Peak season (April–May)	76	1.36	3.80
Late season (June–August)	16	1.60	16.00

1988; Snyder and Peterson, 1999). Additionally, silver perch are caught in the northern GOM and on the Atlantic coast of the United States as a bycatch species (trawling, bait, etc.). Although there is not a commercial fishery for them in these areas as there is in the southern GOM, they are being impacted by fishing practices (Warren, 1981; Meyer et al. 1999; Steele et al., 2002). Because of this and well-documented evidence of latitudinal shifts in life history characteristics of many species of fish, we feel that fishing intensity probably does not play a large role in the latitudinal gradient of age at maturity.

Marginal increment formation in otoliths of silver perch occurred between March and May, which corresponds with the main portion of the spawning season. Similarly, annulus formation in *Cynoscion* spp. also occurs in spring, corresponding to the beginning of the spawning season (Lowerre-Barbieri et al., 1994; Murphy and Taylor, 1994; Nieland et al., 2002). Other sciaenids, like Atlantic croaker and red drum, also deposit an annular ring in the spring (February–May), although this does not correspond to their fall–winter spawning season (White and Chittenden, 1977; Murphy and Taylor, 1990; Barbieri et al., 1994). Annuli formation has been attributed to a number of factors, including seasonal temperature, wet and dry seasons, fish feeding, and reproductive cycles (Beckman and Wilson 1995). In general, fish deposit annuli during spring and summer months in the northern and southern hemisphere of nontropical regions, whereas in tropical regions, opaque zone formations appear to be related more to spawning than to environmental seasonality (Beckman and Wilson 1995).

Females of many fish species are more robust and exhibit faster growth rates than do the males. The faster growth rate observed in female silver perch may be advantageous for reproduction. Female fish that are more robust have a

larger body cavity to possess larger gonads, a trait that increases reproductive potential. Female silver perch can have maximum GSI values almost nine times greater than the males. The females of other sciaenids such as red drum, southern kingfish (*Menticirrhus americanus* (Linnaeus)), spotted sea trout, and weakfish (*Cynoscion regalis* (Bloch and Schneider)) are also more robust (longer in length and heavier in weight) than males (Bearden, 1963; Mercer, 1989; Wilson and Nieland, 1994; Nieland et al., 2002).

Reproductive biology.—Silver perch in Mississippi spawn in the estuarine regions of Mississippi Sound. In other nearshore regions of the GOM they have also been found to spawn within estuarine areas. Mok and Gilmore (1983) analyzed sound production of silver perch in the Indian River Lagoon in east-central Florida using hydrophones and found seasonal peaks in “drumming” to occur in the spring, corresponding to the height of the silver perch spawning season. Additionally, Walters (2005) mapped spawning aggregations of silver perch over the entire geographic area of Tampa Bay, FL, during spring and summer using hydrophones. Further evidence that silver perch are estuarine spawners was presented by Chavance et al. (1984) and Ayala-Peréz et al. (2006), who collected actively spawning females throughout Terminos Lagoon, Mexico. Finally, Holt et al. (1985) collected recently spawned (<3 hr old) silver perch eggs near shallow seagrass meadows in Aransas Bay, TX, throughout the spring and summer. This evidence, in conjunction with the results from the current study, supports the premise of silver perch as an estuarine resident. Estuaries provide spawning, nursery, and adult habitats for this species, as they do for other sciaenids such as spotted sea trout (Brown-Peterson et al., 2002).

Silver perch within the Mississippi Sound have the potential to actively spawn for 6 mo from mid-March through mid-August. Furthermore, histological observations of asynchronous oocyte development and the presence of POFs provide definitive proof that silver perch spawn multiple batches of eggs during their extended spawning season. Peak spawning occurs from mid-March through June, which corresponds to the May–July recruitment pulse of juvenile silver perch to marsh-edge habitats in the Mississippi Sound (Waggy, 2004). This spawning season is similar to previous reports of March through June spawning in Chesapeake Bay (Hildebrand and Schroeder, 1928; Hildebrand and Cable, 1930) and Florida (Mok and Gilmore, 1983) but is shorter than the spawning season of silver perch from

Terminos Lagoon, Mexico (February–July; Chavance et al., 1984).

Generally, the GSI values reported here for silver perch are much higher than those reported for other multiple spawning sciaenids with an extended reproductive season. This may be due, in part, to the inclusion of fish with hydrated oocytes in the GSI calculations. However, banded drum has a life history similar to silver perch, in that they are short lived and mature at a young age and small size (Ross, 1984), yet silver perch have a much higher mean GSI for both males (1.70) and females (11.99) than do the banded drum (males ~0.75 and females ~4.50; Ross, 1984). The congener *Bairdiella ronchus* (Cuvier) also exhibits lower GSI values (males 0.32–1.09 and females 2.97–5.09; Torres-Castro et al., 1999) than silver perch. Ross (1984) and Torres-Castro et al. (1999) also included females with hydrated oocytes in their GSI calculations. The higher GSI values found in silver perch are probably related to the high percentage of actively spawning fish containing hydrated oocytes in our samples. Since silver perch are capable of daily spawning, high GSI values are not unexpected due to the large volume of full grown and hydrated oocytes present in the ovary during the reproductive period.

Daily spawning is uncommon in the Sciaenidae, although cubbyu (*Pareques umbrosus* (Jordan and Eigenmann)), a small coral reef species, has been reported to spawn 3–5 times weekly, or every 1.5 to 2.3 d (Holt and Riley, 1999). In contrast, most larger sciaenids have spawning frequencies of 2 to 3 d (weakfish; Lowerre-Barbieri et al., 1996), 2 to 4 d (red drum; Wilson and Nieland, 1994), 3 to 4 d (black drum; Fitzhugh et al., 1993; Macchi et al., 2002; whitemouth croaker *Micropogonias furnieri* (Desmarest); Macchi et al., 2003), and 4 to 5 d (spotted sea trout; Brown-Peterson, 2003). Daily spawning in silver perch may be a strategy to maximize reproductive potential in a small, short-lived species. Other sciaenids such as whitemouth croaker (7 yr; Manickchand-Heileman and Kenny, 1990), spotted sea trout (9 yr; Murphy and Taylor, 1994), red drum (24–33 yr; Murphy and Taylor, 1990), and black drum (43–59 yr; Beckman et al., 1990; Jones and Wells, 1998) have a much longer life span. Therefore, silver perch would need higher spawning frequencies than other sciaenids in order to maximize their reproductive potential.

The method of calculating spawning frequency using OM appeared to give the most accurate spawning frequency estimate for silver perch in association with what was seen histologically. Brown-Peterson (2003) found that while the OM

or POF methods gave reasonable spawning frequency estimates for spotted sea trout, they did differ slightly. Although the lower spawning frequency estimates obtained for silver perch using the POF method could be due to sampling bias, the fact that 24% of females in the actively spawning phase had ovaries with 24 hr POFs strongly supports the high spawning frequency estimates obtained with the OM method. While both methods showed a decrease in spawning frequency estimates in the late portion of the season, these estimates should be viewed with caution since they are based on only 16 fish. This is particularly evident for the 16 d spawning frequency estimate using the POF method.

Immature fish were not present in the population during the main portion of the spawning season; therefore, all fish hatched in the previous year were mature by their first birthday, designated as 1 April. Most other sciaenids mature after they are 1 yr old, such as spotted sea trout (Brown-Peterson, 2003), spot (Hales and Van Den Avyle, 1989), red drum (Murphy and Taylor, 1990; Wilson and Nieland, 1994), black drum (Nieland and Wilson, 1993), banded drum (Ross, 1984), southern kingfish (Bearden, 1963), and whitemouth croaker (Manickchand-Heileman and Kenny, 1990).

Many of the life history characteristics that define silver perch contrast sharply with those of larger sciaenids (Waggy et al., 2006). Highlighting these differences suggests the need for an improved understanding of life history patterns of the small but trophically important sciaenids. The information presented here concerning life history characteristics of silver perch may likely provide insight to the relatively unknown reproductive biology of other small sciaenids such as cubbyu, highhat (*Pareques acuminatus* (Bloch and Schneider)), jack-knife fish (*Equetus lanceolatus* (Linnaeus)), spotted drum (*Equetus punctatus* (Bloch and Schneider)), and star drum.

Silver perch are very abundant and valuable to estuarine systems in terms of reproductive capacity, prey resources, and energy transfer to higher trophic levels. The life history and population structure of this species has only recently been elucidated, and the information provided here will be important in developing community-based models of estuarine systems. Given that ecosystems are complex and hierarchical in nature, it is crucial to obtain the maximum amount of information about each component in order to provide realistic data for ecosystem modeling programs. This allows the best possible strategy to be applied to ecosystem management practices.

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