REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE SAND SEATROUT, *CYNOSCION ARENARIUS*[1,2]

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ABSTRACT

Cynoscion arenarius females mature at 140-180 mm total length as they approach age I. Spawning occurs from early March through September, but concentrates in a distinct spring period (March-May) and a distinct late summer period (August-September). Spawning occurs in the inshore Gulf of Mexico and coincides with the periodicity of onshore winds and surface currents which probably transport eggs or larvae to estuarine and inshore gulf nurseries. Estuarine nurseries may be most important to late summer spawned groups. The main gulf nursery in the northwestern area is in waters shallower than 18 m. Both spawned groups leave estuarine nurseries in fall to overwinter in the gulf. Late summer spawned groups return to estuaries in midspring but reenter the gulf in August to spawn. Fish average 210-280 mm total length at age I but some were 300 mm. Predicted sizes of late summer fish were 425 mm total length at age II and 574 mm at age III. The largest trawled specimen was 342 mm total length and 99.5% were less than 280 mm. No more than three spawned groups or two year classes occurred at any one time. The typical maximum life span is 1-2 years based on trawl data and possibly as much as 2-3 years for other gear. Total annual mortality rate was 99.79% based on trawling data and appears no lower than 80-90% if maximum lifespan typically is as great as 3 years. *Cynoscion arenarius* can be aged using scales. Total weight-total length, girth-total length, and standard length-total length regressions are presented. Temporal isolation of the two spawned groups produced each year suggests they may be separate populations or species. The life history and population dynamics of *C. arenarius* appear similar to *C. regalis* along the Atlantic coast south of Cape Hatteras, North Carolina. The latter taxon shows zoogeographic change at Cape Hatteras, which needs management consideration.

The sand seatrout, *Cynoscion arenarius* (Ginsburg), is endemic to the Gulf of Mexico (gulf) and ranges from southwest Florida (Roessler 1970) to the Bay of Campeche (Hildebrand 1955). It is one of the most abundant fishes in estuaries and the shallow gulf (Gunter 1945; Christmas and Waller 1973) and is a major component of the industrial fishery landings and shrimp bycatch (Roithmayr 1965; Gutherz et al. 1975).

The life history of *C. arenarius* is essentially undescribed despite its abundance. Food habits have been studied (Darnell 1958; Diener et al. 1974; Moffett et al. 1979), and general material appears in many faunal studies including Franks et al. (1972), Gallaway and Strawn (1974), and Chittenden and McEachran (1976). Much of this information is misleading, however, because the complex life history of this species has not been recognized. Literature on the possibly conspecific

C. regalis might apply to *C. arenarius*, but their taxonomic status is still in doubt (Mohsin 1973; Weinstein and Yerger 1976). We have referred to *C. arenarius* herein as a species separate from *C. regalis* following Bailey et al. (1970).

This paper describes spawning seasonality, periodicity, and areas, seasonal distribution and movements, age determination, growth, mortality, and total weight-total length, girth-total length, and standard length-total length relations.

METHODS

Sand seatrout were collected monthly along a transect in the gulf off Freeport, Tex. (Figure 1), from October 1977 through September 1979 aboard a chartered shrimp trawler using twin 10.4 m (34-ft) trawls with a 4.4 cm stretched mesh cod end. Collections were made during the day through September 1978; thereafter, a day and a night cruise usually were made each month. Stations were occupied at depths of 4.5, 7, 9, 14-15, 18, 22, 27, 37, and 46 m. One or two tows were made at each depth (two tows after October 1978), except
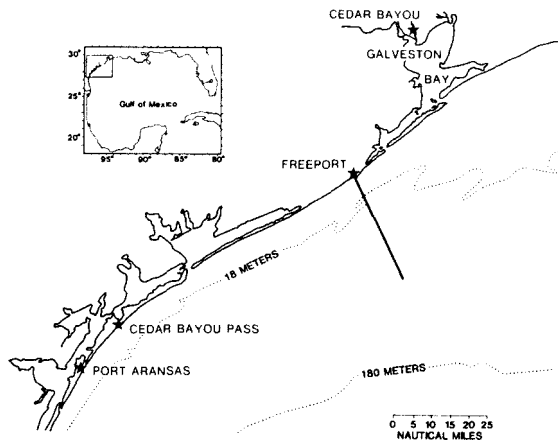
FIGURE 1.—Location of sampling area. Cedar Bayou Pass near Port Aransas is the study location of Simmons and Hoese (1959).

TABLE 1.—Description of gonad maturity stages assigned to *Cynoscion arenarius.*

Stage and name	Description
1 Immature	Gonads barely visible or not visible, sexes indistinguishable.
2 Maturing virgin	Gonads very small, sexes distinguished only with magnification.
3 Early developing	Sexes visually distinguished, ovaries occupy <25% of body cavity, individual eggs not visible to the naked eye.
4 Late developing	Ovaries occupy 25-50% of body cavity, eggs clearly visible to naked eye, no translucent eggs.
5 Gravid	Ovaries occupy at least 50% of body cavity, up to 50% of the eggs translucent.
6 Ripe	Ovaries occupy at least 50% of body cavity, >50% of the eggs translucent.
7 Spawning/spent	Ovaries flaccid and at least partly empty, no opaque eggs.
8 Resting	Ovaries fit same description as those in Stage 3, but fish are large enough and were collected at a time when they could already have spawned.

that 8-12 tows were made at 14-15 m and about 24 tows usually were made at 22 m. The 22 m depth primarily was occupied after October 1978.

Cynoscion spp. were culled from the catch, fixed in 10% Formalin,[4] and stored in 70% ethanol before analysis. *Cynoscion arenarius* was separated from *C. nothus* primarily by comparing the anal fin base to the eye width following DeVries (1979). Total length (TL) was measured on all fish. All specimens captured from October 1977 through December 1978, except as noted, were processed and scales were taken to determine age, standard length (SL), girth (G) at the anterior origin of the dorsal fin, total weight (TW), sex, ovary weight (GW) to the nearest 0.1 g, and gonad maturity stage. In June and early December 1978, 300 specimens were randomly selected except that all fish >120 mm TL were processed in June 1978. Scales were taken above the lateral line below the second dorsal fin following procedures for *C. regalis* (Perlmutter et al. 1956), and cellulose acetate impressions were examined using a scale projector. Females and immature fish were assigned gonad maturity stages (Table 1) slightly modified from Kesteven's system (Bagenal and Baum 1971).

Findings based on collections off Freeport were verified by the following materials. Fish were captured from February through December 1977 and in March, June, and July 1978 off Port Aransas, Tex., aboard the Texas Parks and Wildlife Department (TPWD) RV *Western Gulf* using a 13.7 m

otter trawl with a 5.1 cm stretched mesh cod end. Stations usually were occupied at 11 m at night, at 7, 15, and 18-24 m during the day; and also at night at 20-22, 29-31, and 38 m from May through October 1977. Additional monthly day collections were made in Galveston Bay, Tex., aboard the TPWD RV *Drum II* from December 1977 through July 1979 using a 6 m otter trawl with a 3.8 cm stretched mesh cod end or a 3 m otter trawl with a 2.5 cm stretched mesh cod end. Finally, collections from July 1978 through July 1979 in Cedar Bayou, Tex., using a 3 m otter trawl with a 2.5 cm stretched mesh cod end were made available by Pridgeon.[5]

Spawned groups and their year class identities were indicated by specifying the season and year when they hatched, e.g., spring 1978. Spawning periodicities and group identities assume that a total length of 30 mm at 1 mo of age for *C. regalis* (Welsh and Breder 1923) applies to *C. arenarius.* Hatching dates of 1 April and 1 September were assigned to spring and late summer spawned groups to estimate growth and ages.

MATURATION AND SPAWNING PERIODICITY

Results

Cynoscion arenarius matures at 140-180 mm TL as they approach age I and spawn. Gonad devel-

opment was distinct at 140-200 mm TL as most specimens entered the early developing stage (Figure 2). Fish began to enter the late developing, gravid, or ripe stages at 180 mm TL. These data are supported by regressions of ovary weight on total length (Table 2, Figure 3) in which extrapolated x-intercepts were 120-170 mm TL in the March-September spawning period. Age compositions and sizes presented later indicate that *C. arenarius* matures to first spawn at 12 mo.

Sand seatrout spawn from early March through September. The collections off Freeport of fish 45-55 mm TL in mid-May 1978, 25-80 mm TL in mid-May 1979, and 60-120 mm TL in June and July of 1978 and 1979 (Figure 4) indicate that spawning began in early March and continued through May. This is supported by the collections of: 1) fish 50-75 mm TL off Port Aransas in late May and late June of 1977 and 1978 (Figure 5), 2)

FIGURE 3.—Monthly ovary weight-total length regressions for *Cynoscion arenarius*. The length of each line shows the observed size range. X-intercepts indicate total length at which gonad development begins in what would be a curvilinear regression if smaller lengths were available.

fish 50-80 mm TL in Galveston Bay in May 1978 and 1979 (Figure 6), and 3) fish 20-70 mm TL at Cedar Bayou in the period 1 May-2 July 1979 (Figure 7). Spawning also occurred in August and September; because a distinct group of fish 25-60 mm TL were collected off Freeport in late September 1979 (Figure 4), and fish 65-130 mm TL collected in early December of 1977 and 1978 were too small to represent spring spawning. This is supported by the collections of: 1) fish 25-50 mm TL at Cedar Bayou in September 1978 (Figure 7), 2) fish 70-120 mm TL in Galveston Bay in December 1977 and 50-80 mm TL in September-December 1978 (Figure 6), and 3) fish 70-150 mm TL off Port Aransas in February and December 1977 (Figure 5). Spawning did not occur from October through February, because no fish 25-60 mm TL were collected from November through April in the gulf (Figures 4, 5), in Galveston Bay (Figure 6), or at Cedar Bayou (Figure 7).

Gonad maturity and weight data suggest that females spawned from February or March through September in agreement with length frequencies. Two gravid females were collected in mid-February 1978 and late developing, gravid, or ripe stage fish from March through July 1978 and in September 1978 (Figure 8). No spawning occurred from October through December, because all fish then were in resting, maturing virgin, or early developing stages. Gonad size increased during February (Figure 3), reached a peak in April and May, and rapidly declined through July. Increased
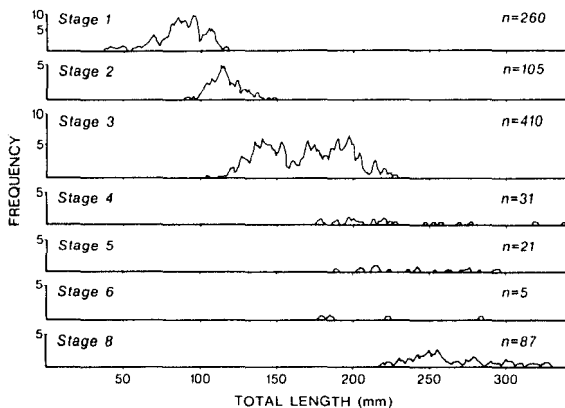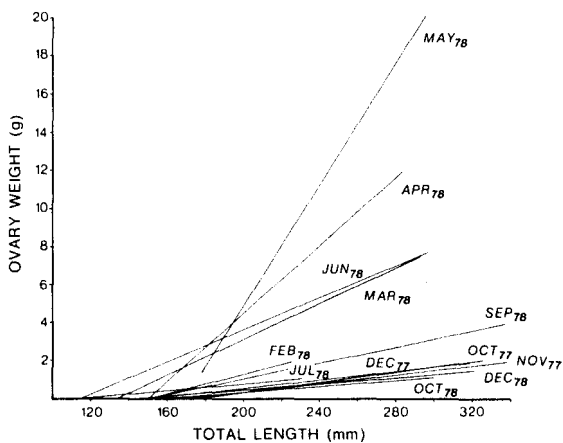

FIGURE 2.—Length frequencies (moving averages of three) of immature and female *Cynoscion arenarius* in maturity stages 1 through 8. Maturity stages are described in Table 1. No stage 7 fish were caught.

TABLE 2.—Analysis for regressions of gonad weight (grams) on total length (millimeters) for female *Cynoscion arenarius* each month, October 1977-December 1978. All regressions are significant at $\alpha = 0.05$.

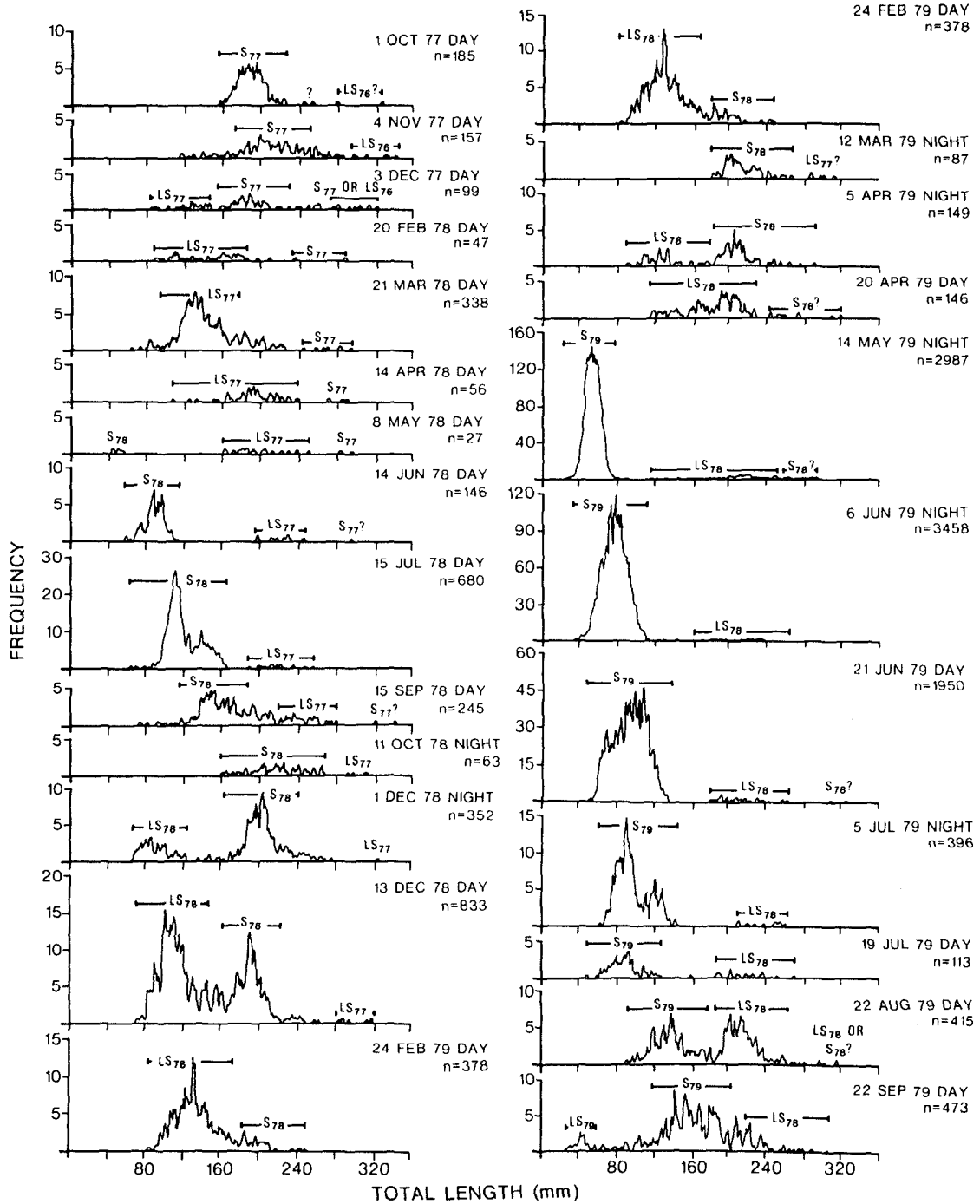| Date	n	r^2	Equation
October 1977	75	0.759	$GW = -2.4537 + 0.0139\,TL$
November 1977	66	.801	$GW = -1.9946 + .0117\,TL$
December 1977	56	.828	$GW = -1.7127 + .0113\,TL$
February 1978	12	.353	$GW = -4.9977 + .0330\,TL$
March 1978	152	.503	$GW = -6.4522 + .0479\,TL$
April 1978	16	.702	$GW = -13.4576 + .0896\,TL$
May 1978	14	.579	$GW = -27.0498 + .1592\,TL$
June 1978	8	.696	$GW = -4.8433 + .0423\,TL$
July 1978	84	.436	$GW = -1.2198 + .0106\,TL$
September 1978	100	.498	$GW = -3.7836 + .0252\,TL$
October 1978	21	.250	$GW = -1.8382 + .0110\,TL$
December 1978	45	.673	$GW = -1.1223 + .0079\,TL$

FIGURE 4.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured off Freeport, Tex. Spawned group identity (S = spring; LS = late summer) is often not clear where spawned groups meet.
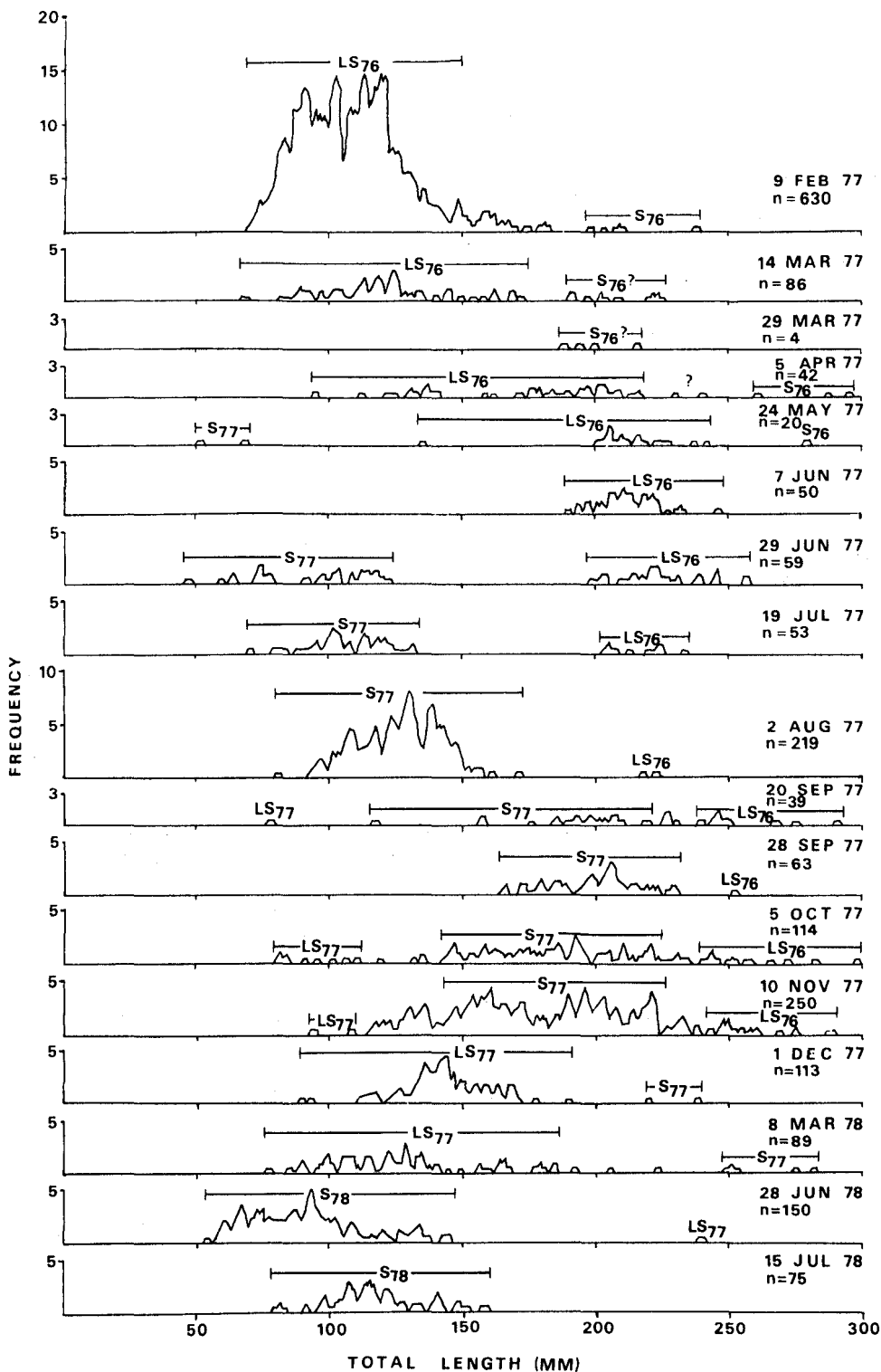
FIGURE 5.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured off Port Aransas, Tex. Spawned group identity (S = spring; LS = late summer) is often not clear where spawned groups meet.
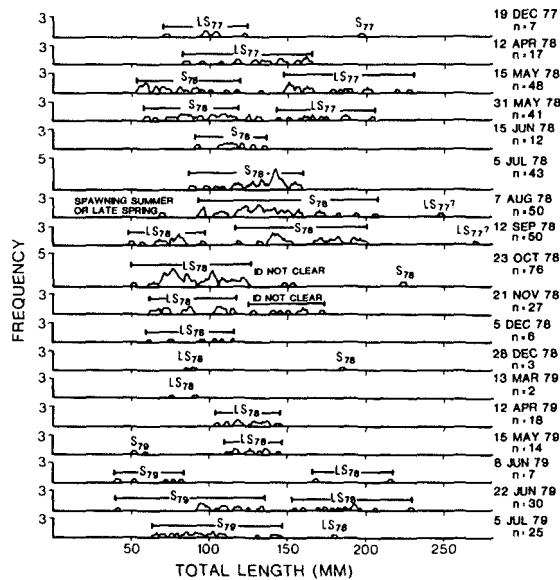
FIGURE 6.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured in Galveston Bay, Tex. Spawned group identity (S = spring; LS = late summer; ID = identity) is often not clear where spawned groups meet. No fish were captured in February and March 1978 and February 1979.
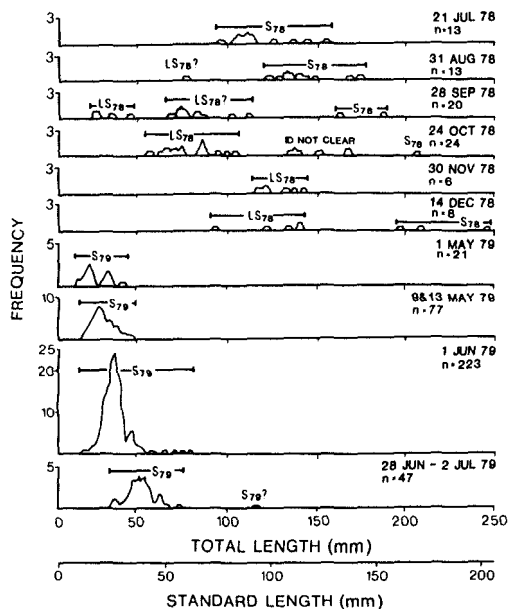

FIGURE 7.—Monthly length frequencies (moving averages of three) of *Cynoscion arenarius* captured in Cedar Bayou, Tex. Spawned group identity (S = spring; LS = late summer; ID = identity) is often not clear where spawned groups meet. No fish were captured from January through April 1979.
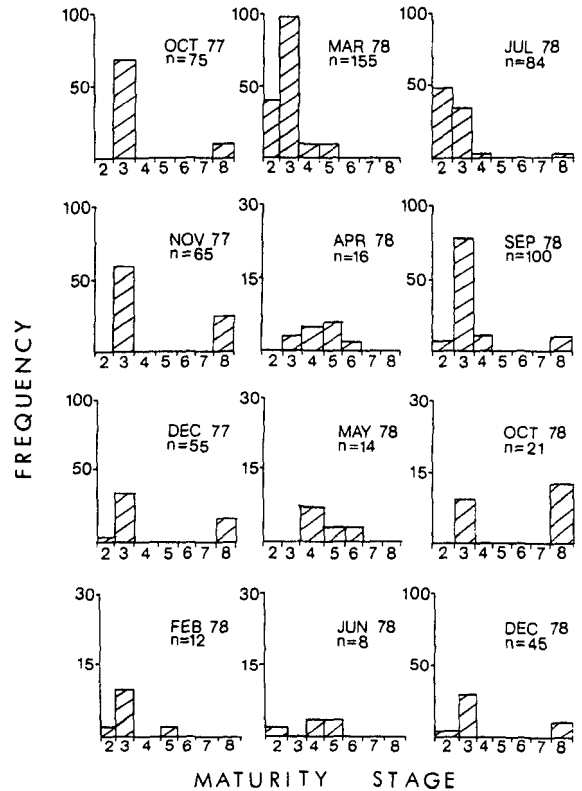

FIGURE 8.—Monthly maturity stages of female *Cynoscion arenarius*. Maturity stages are described in Table 1.

gonad size in mid-September might reflect August-early September spawning.

Although *C. arenarius* spawns over a broad time period, spawning primarily occurs during two discrete periods, a spring spawn from early March through May and a late summer spawn in August and September. Spring spawned fish formed length-frequency modes readily followed in the periods: 1) May-December 1978 and May-September 1979 off Freeport (Figure 4), 2) May-September 1977 and June-July 1978 off Port Aransas (Figure 5), 3) May-September 1978 and May-July 1979 in Galveston Bay (Figure 6), and 4) July-December 1978 and May-July 1979 at Cedar Bayou (Figure 7). Late summer spawned fish formed less distinct modes readily followed in the periods: 1) December 1977-July 1978 and December 1978-August 1979 off Freeport (Figure 4), 2) February-July 1977 off Port Aransas (Figure 5), 3) December 1977-May 1978 and November 1978-May 1979 in Galveston Bay (Figure 6) and 4) September-December 1978 at Cedar Bayou (Figure 7). Little spawning occurred in June and July,

because few fish 25-60 mm TL were captured from late June through August in the gulf (Figures 4, 5), in Galveston Bay (Figure 6), or at Cedar Bayou (Figure 7).

Discussion

Our findings on *C. arenarius* spawning agree with the limited literature. The small size at maturity agrees with Gunter's (1945) capture of a ripe male only 157 mm TL. The broad March-September spawning period found agrees with many studies, including Franks et al. (1972), Gallaway and Strawn (1974), and Moffett et al. (1979). The fact that spawning occurs in distinct spring and late summer peaks has not been recognized clearly but is supported by: 1) the midsummer lull in spawning that Margraf (1978) noted; 2) the late winter-early spring and early fall spawnings that Juneau (1975) observed; and 3) the distinct modes, one formed in spring and one formed in late summer, in size data of Gunter (1945:76), Christmas and Waller (1973, fig. 8), Gallaway and Strawn (1974, table 24), Swingle and Bland (1974:41), Moffett (1975, fig. 19), and Landry (1977, fig. 23, 24). Multiple spawning peaks also have been reported for other *Cynoscion* spp. such as *C. nothus* (DeVries and Chittenden[6]) and *C. regalis* (Daiber 1957 and Harmic 1958 cited in Thomas 1971; Massmann et al. 1958; Merriner 1976).

SPAWNING AREAS, EARLY NURSERIES, AND MOVEMENTS

Results

Sand seatrout of both spring and late summer groups spawn in the inshore gulf. Spawning and nursery areas of spring spawned groups are indicated by distinct size gradients in length frequencies for May-August 1979 (Figure 9B): 1) an estuarine gradient in which the smallest fish were in the upper estuary at Cedar Bayou while larger ones were in Galveston Bay and at 4.5 m in the gulf, 2) a gradient in the gulf in which the smallest fish were at 7-15 m and sizes increased in deeper water, and 3) another gradient in the gulf in which the smallest fish were at 7-15 m but sizes increased in shallower water. Length frequencies from Cedar Bayou, Galveston Bay, and the gulf off

[6]DeVries, D. A., and M. E. Chittenden, Jr. In prep. Spawning, age determination, and population dynamics of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico.

Freeport indicate growth continued in May-August 1979 (Figures 4, 6, 7). Therefore, the first size gradient indicates dispersion of larger juveniles down the estuary. The latter two size gradients indicate outward dispersion of larger young and/or eggs and larvae from spawning grounds near 7-15 m in the gulf to deeper and shallower water. Late summer spawned groups also use inshore gulf spawning grounds as indicated by locations of mature fish at spawning time.

Capture locations of mature and ripe adults at spawning time also suggest an inshore gulf spawning area. Many fish of the late summer 1978 group reached age I and entered the gulf in August 1979 (Figure 4), presumably to spawn near the 7-22 m depths where they were captured; none were captured at 4.5 or 55-100 m (Chittenden unpubl. data), but the 27-46 m depth range was not occupied in that cruise. Five ripe stage fish were captured in April and May 1978 at 14-46 m in the gulf. However, it is not clear how far these fish traveled before spawning.

Discussion

The estuarine size gradient that we found could reflect spawning grounds in the upper estuary, or most probably, spawning grounds that encompass the inshore gulf and/or lower estuary. This gradient probably does not reflect an upper estuarine spawning ground, because the early life history of *C. arenarius* is much like that of the Atlantic croaker, *Micropogonias undulatus*. The Atlantic croaker exhibits egg and/or larval transport to the upper estuary from spawning grounds in the sea (Wallace 1940; Haven 1957) and well-documented estuarine size gradients (Gunter 1945; Haven 1957; Reid and Hoese 1958). Moreover, a similar early life history has been suggested for other Sciaenidae, especially *C. regalis* (many references in Wilk 1979).

Our explanation for the estuarine size gradient conflicts with the size pattern in the gulf. The latter pattern suggests outward dispersal of young and/or transport of eggs and larvae from spawning grounds near 7-15 m. The direction of movement suggested by the estuarine gradient, however, is opposed to the direction of movement suggested by the gulf gradient in which sizes increase inshore. We offer no simple explanation for the apparent dichotomy except that it might reflect: possibly separate estuarine and gulf spawning grounds which might involve temporal
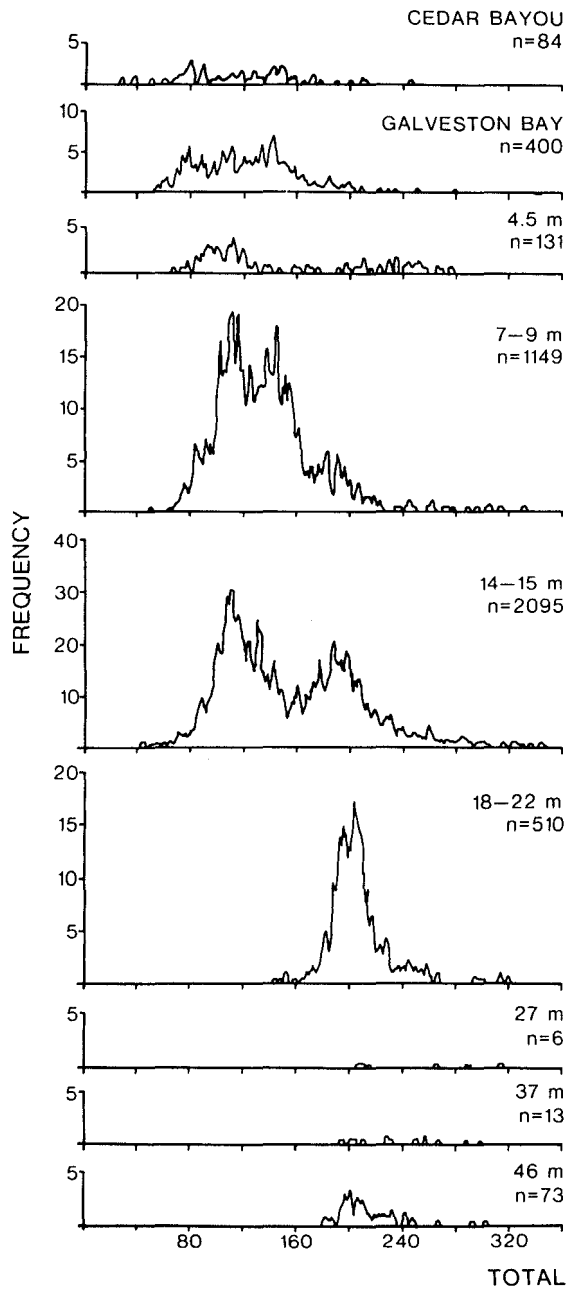
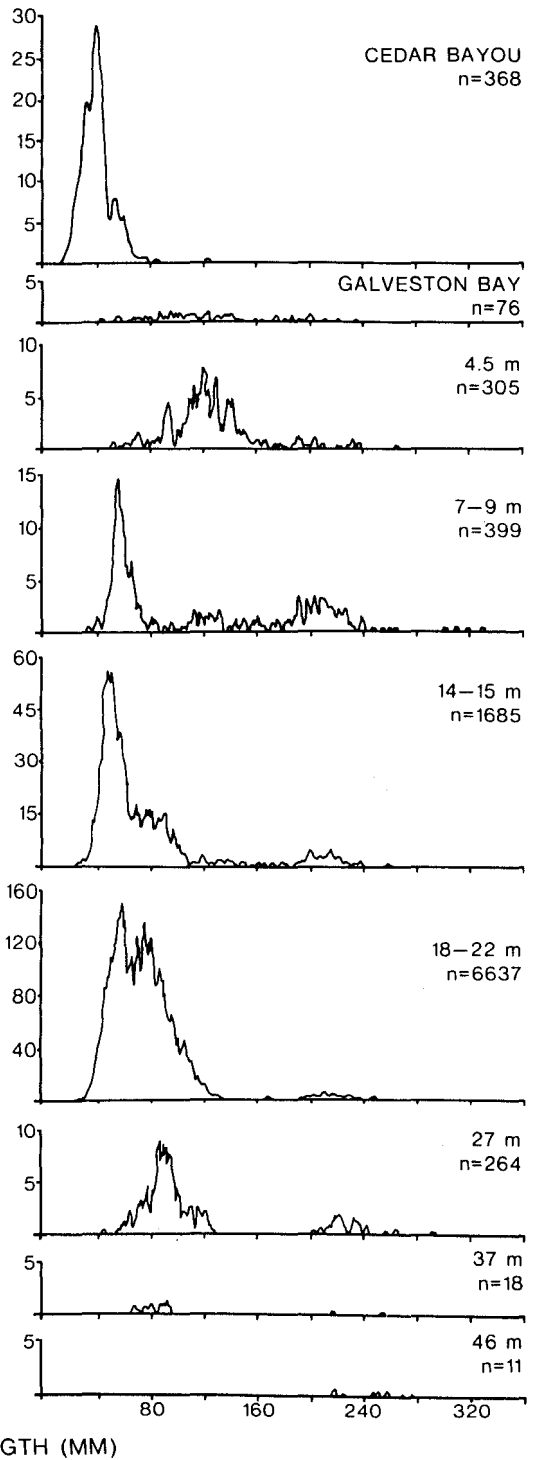A. OCTOBER 1977 — APRIL 1979   B. MAY — AUGUST 1979

FIGURE 9.— Length frequencies (moving averages of three) of *Cynoscion arenarius* collected at each depth off Freeport and in Galveston Bay and Cedar Bayou, Tex.   A. October 1977-April 1979.   B. May-August 1979.

differences in spawning, and as noted shortly, the unusual flooding near Galveston Bay during spring 1979 and current transport phenomena which are strongly wind-driven in the gulf and its estuaries. Under nonflood conditions a single gradient of increasing size extended from the upper estuary out to at least 22 m in the gulf (Figure 9A), which suggests that the dichotomous condition in May-August 1979 (Figure 9B) was an exception caused by flooding.

Our data suggest that *C. arenarius* spawns in the shallow inshore gulf, but the extent of its spawning grounds is not yet clear and could vary seasonally. Other workers also have reported evidence of gulf spawning (Gunter 1945; Moffett et al. 1979). Perry (1970) and Franks et al. (1972) captured running ripe *C. arenarius* in the gulf during February and March at 73-91 m (about 105 km offshore) which could indicate spawning offshore in deep water; but the distance these fish traveled before spawning is not clear. Reid (1955), Hoese (1965), and Copeland and Bechtel (1974) reported spawning in estuaries, but they presented little evidence. However, Harmic (1958) found that the closely related *C. regalis* spawned within Delaware Bay.

Clear delineation of the spawning grounds requires understanding how this species passes from spawning grounds to nurseries. The spring and late summer spawning periods of *C. arenarius* coincide with periods of rising sea level in the northern gulf in response to prevailing onshore winds and surface currents (Collier and Hedgpeth 1950; Marmer 1954). Spawning probably is timed to take advantage of this seasonal phenomenon to transport eggs and/or larvae from inshore gulf spawning grounds to estuarine and gulf nurseries as our size composition data indicate. The bayward movement of postlarvae that Simmons and Hoese (1959) reported on incoming tides could be enhanced by rising sea levels and prevailing onshore winds and currents. However, spawning also coincides with seasonal rainfall peaks (Collier and Hedgpeth 1950) which could modify estuarine transport phenomena. Currents and tides in the nearshore northern gulf and its shallow estuaries are influenced greatly by wind and flooding (Collier and Hedgpeth 1950; Smith 1975). Therefore, spawned group strength of *C. arenarius* and its spatial distribution may be influenced greatly by short-term wind and rainfall patterns that affect current transport and, thereby, survival of the eggs and/or larvae as Nel-son et al. (1977) reported for Atlantic menhaden, *Brevoortia tyrannus*.

NURSERIES AND LATER MOVEMENTS

Results

Spring and late summer spawned groups use both estuarine and inshore gulf nurseries in their early life, although estuaries may be most important for late summer fish. Recently hatched spring fish were abundant in 1977-79 from May through July in the inshore gulf, in Galveston Bay, and Cedar Bayou (Figures 4-7). Few recently hatched late summer fish were in the inshore gulf in September-November of 1977-78 (Figures 4, 5), but they were common then in Galveston Bay and Cedar Bayou (Figures 6, 7) and were abundant in the gulf in December (Figures 4, 5).

The main nursery of *C. arenarius* in the northwestern gulf lies in water <18 m. Fish >160 mm TL occurred throughout the 4.5-46 m depth range (Figure 9A). However, fish <160 mm TL only occurred in <18 m except in May-August 1979 when recently hatched spring 1979 fish were abundant to 27 m and present to 37 m (Figure 9B). The Gulf nursery probably expands or contracts depending on spawned group strength and factors that determine dispersal of the young. For example, the great abundance of small fish in the gulf during May-August 1979 might be due to increased spawned group strength and/or heavy flooding in the Galveston Bay area in that spring (Barris 1979).

Fish that use estuarine nurseries in their early life enter the gulf during mid and late fall to overwinter. Spring fish grew in the gulf from May through September-October 1977 and 1978 (Figures 4, 5), but thereafter showed no growth or decreased sizes through December. This pattern indicates movement from estuaries to the gulf with the larger fish preceding smaller ones, assuming continued growth in that period. Many recently hatched late summer fish entered the gulf during December 1977 and 1978 (Figures 4, 5), because few were in the gulf before then. Few were in Galveston Bay or Cedar Bayou from December through March (Figures 6, 7), although they were abundant in the gulf.

Late summer spawned groups return to estuaries during midspring after overwintering in the gulf. Although abundant in the gulf in the February-April periods of 1977-79 (Figures 4, 5),

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few late summer fish were in the gulf in the following May-July period except in 1977 off Port Aransas. Most must have returned to estuaries in midspring and remained there until they returned to the gulf to spawn in August (Figure 4). Late summer fish were captured in Galveston Bay in May-July (Figure 6), but not in large numbers which may reflect a habitat change by these larger fish or avoidance of the small trawls used there. Sizes of the late summer fish in the gulf remained stable or decreased in July-August 1978 and 1979 (Figure 4). This is similar to the pattern noted in the fall for spring spawned fish and suggests a similar gradual dispersal of the late summer groups to the gulf.

Movements of spring spawned groups as they reach age I are not clear. We captured few age I fish in the spring or following summer except in March and April 1979 in the gulf (Figure 4). Most apparently die after spawning, but our data do not clarify movements of the survivors.

Cynoscion arenarius exhibits little diel variation in size composition. The two spawned groups off Freeport during December 1978 and in April, June, and July 1979 showed little day-night size variation (Figure 4). Some differences—e.g., December 1978—probably reflect growth or movements in the 2-wk period between collections.

Discussion

Our findings on the nurseries and later movements of *C. arenarius* agree with the limited literature, although the complex life history of this species has not been recognized. The fact that the young occur in both estuaries and the inshore gulf has been reported (Gunter 1945; Miller 1965; Christmas and Waller 1973), but these workers did not recognize separate spring and late summer spawned groups nor possible differences in their nurseries. Our finding that *C. arenarius* move in fall from estuaries to overwinter in the gulf has been reported by many workers including Gunter (1938, 1945), Chambers and Sparks (1959), Perret and Caillouet (1974), and Ogren and Brusher (1977) who based their findings only on apparent change in abundance without recognizing size composition changes, or the differences between spring and late summer spawned groups. Movement of "mature" *C. arenarius* in the period April-May from the gulf to estuaries has been reported (Simmons 1950-51 cited in Guest and Gunter 1958; Simmons and Hoese 1959). These

might have been late summer fish in agreement with our findings, but these workers did not recognize different spawned groups. Data of Perret and Caillouet (1974, fig. 6), however, show return of late summer fish to Vermillion Bay, La., in April and May. The absence of diel size variation in *C. arenarius* contrasts with its presence in *C. nothus* (DeVries and Chittenden footnote 6).

GROWTH AND AGE DETERMINATION BY LENGTH FREQUENCY

Results

No more than two year classes of *C. arenarius* occurred in any 1 mo in the gulf, in Galveston Bay, or in Cedar Bayou (Figures 4-7). Only one year class was captured from February through April, except possibly in March 1979 off Freeport. Two year classes usually were present in the gulf and in Galveston Bay from May through December—but no more than three spawned groups.

Cynoscion arenarius averages 210-280 mm TL at age I depending on spawned group. Spring fish averaged 160-190 mm TL at 6 mo and 220-280 mm at age I (Figure 10), although many were 200 mm or more at 6 mo and some were 300 mm at age I (Shlossman 1980, tables 1, 2). Late summer fish were slightly smaller, averaging 120-150 mm TL at 6 mo and 210-250 mm at age I (Figure 10), although many were 175 mm or more at 6 mo and some were 300 mm at age I (Shlossman 1980, tables 1, 2). Mean sizes predicted by regression (Figure 10) were 250 mm TL at age I, 425 mm at age II, and 574 mm at age III for late summer fish. Predictions for spring fish were 260 mm TL at age I, 301 mm at age II, and 160 mm at age III. Predictions for spring fish are unrealistic at age III and probably too low at age II, because the simple polynomial regression used describes growth as a parabola.

Growth generally was greatest in warmer months and least in colder months. Both spring and late summer spawned fish grew slowest (5-10 mm TL/30 d) in winter (Figure 11). Spring fish grew fastest (35 mm TL/30 d) from May through October; much variation occurred, however, and zero increments in summer and mid to late fall reflect movement of larger fish from estuaries to the gulf, not lack of growth. Late summer fish grew rapidly in spring; decreased increments in late spring and early summer may reflect movement of larger fish from estuaries to the gulf.
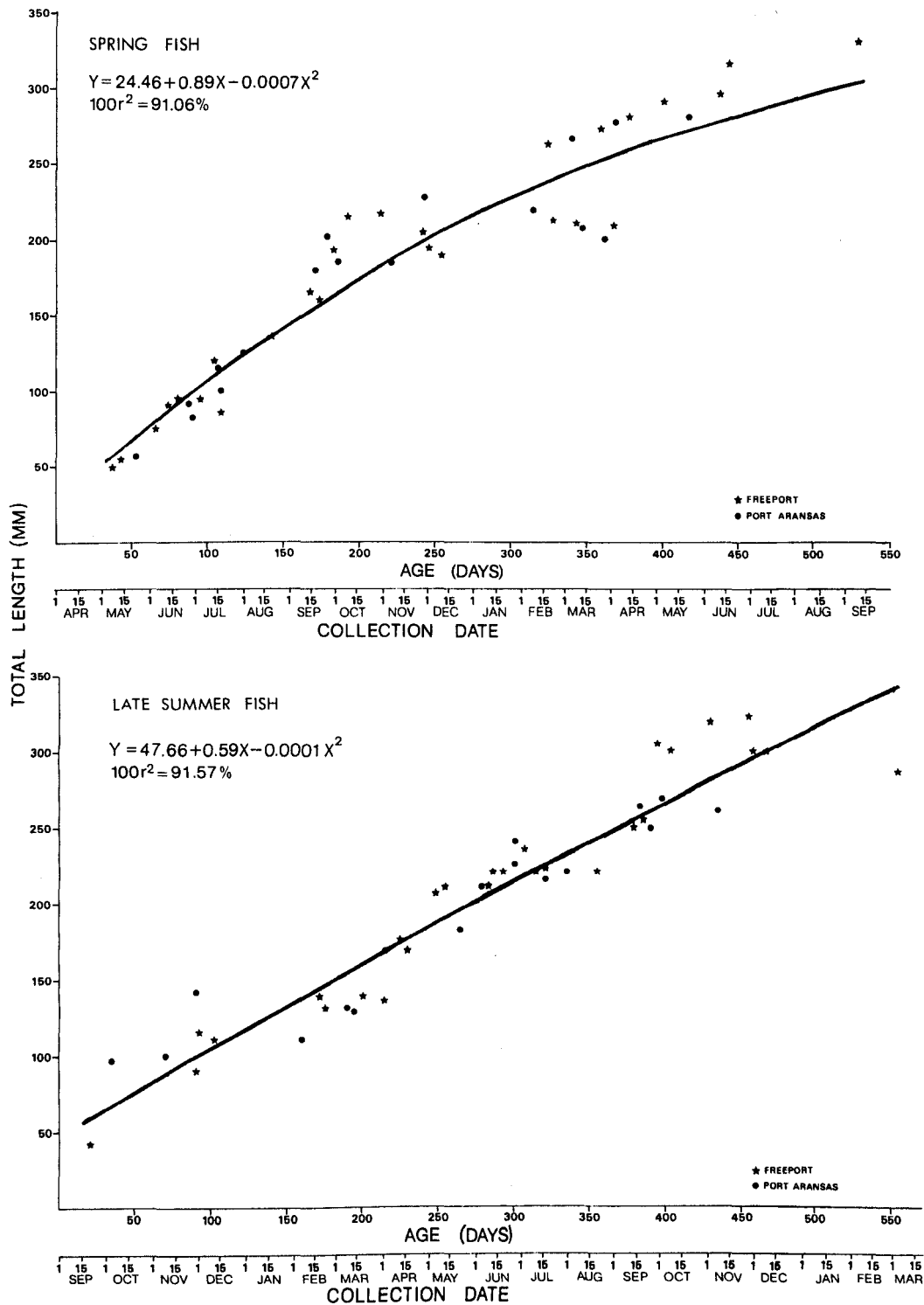
FIGURE 10.—Observed and predicted sizes at age of *Cynoscion arenarius* from the gulf off Freeport and Port Aransas, Tex., for spring spawned fish and late summer spawned fish. Modal sizes (Shlossman 1980, tables 1, 2) were regressed on ages after assigned hatching dates. Regression was significant at $\alpha = 0.01$.
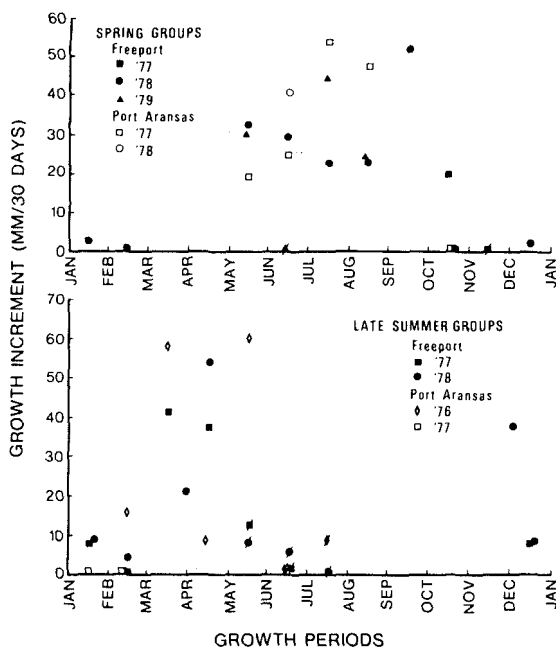
FIGURE 11.—Monthly growth increments of *Cynoscion arenarius* for spring and late summer groups from the Gulf of Mexico. Unadjusted well-defined increment data of Shlossman (1980, tables 1, 2) were converted to growth per 30 d. Increments with a diagonal (/) reflect movement, not necessarily low growth. Negative increments were rounded to zero.

Female *C. arenarius* reach larger sizes than males. All fish >300 mm TL (n = 13) and 88% examined >250 mm (n = 80) were female.

Discussion

Our findings on *C. arenarius* growth agree with the limited literature. Our average growth estimates—210-280 mm TL at age I depending upon the spawned group—agree with data of Perret and Caillouet (1974, fig. 6), but slightly exceed data of Swingle and Bland (1974:41) and estimates of Hoese et al. (1968), McEachron et al. (1977), and Chittenden (1977). Decreased growth in winter agrees with observations of Gunter (1945) and Hoese et al. (1968). Seasonal growth is similar to that of *C. nothus* (DeVries and Chittenden footnote 6), *C. nebulosus* (Pearson 1929; Tabb 1961), and *C. regalis* (Welsh and Breder 1923; Hildebrand and Cable 1934; Merriner 1973). However, *C. arenarius* is larger at age I than its three congeners in the western North Atlantic: 1) *C. nothus*, 130-190 mm SL = 158-229 mm TL (DeVries and Chittenden footnote 6); 2) *C. regalis*, 143-180 mm

SL = 173-218 TL (Taylor 1916 in Merriner 1973; Perlmutter et al. 1956; Merriner 1973); and 3) *C. nebulosus*, 116-165 mm SL = 144-201 mm TL (Pearson 1929; Moody 1950; Klima and Tabb 1959; Moffett 1961; Tabb 1961). Our findings that females grow larger than males has been reported (Franks et al. 1972), and similar differences occur in *C. nebulosus* (Pearson 1929; Klima and Tabb 1959; Tabb 1961).

AGE DETERMINATION USING SCALES

General Basis

Cynoscion arenarius can be aged using scales. Annuli were identified using standard criteria (Tesch 1971) and procedures for *C. nebulosus*, *C. nothus*, and *C. regalis* (Klima and Tabb 1959; Tabb 1961; Merriner 1973; DeVries and Chittenden footnote 6). Characters used to identify annuli included: 1) a clear zone between bands of circuli in the anterior field (Figures 12, 13), 2) a band of crowded circuli adjacent to a band of more widely spaced circuli (Figure 12), 3) secondary radii radiating from a clear zone or changed spacing between circuli (Figures 12, 13), 4) cutting over of circuli (Figures 12, 13), and 5) appearance of these characters on all or most scales. Marks identified as false annuli: 1) appeared on only a few scales from a fish, 2) had secondary radii not accompanied by a clear zone or changed spacing of circuli, 3) had a clear zone or changed spacing between circuli not accompanied by other characters, and 4) lacked distinct cutting over. False annuli were common, as Merriner (1973) found for age 0 and age I *C. regalis*.

Results

Few fish had scales with an annulus. Only 159 of 1,602 fish (10%) examined had one annulus and only 6 fish (0.4%) had two annuli. This finding that 10% had one annulus is not consistent with the 99% annual mortality rate reported later. However, the sample aged was biased by arbitrary selection of large fish. Moreover, the annulus primarily forms at 0.5-0.75 yr which is before annual mortality is complete.

The first annulus forms from April through November, although spring and late summer spawned fish may form annuli at different times. Marginal increments in late summer fish were smallest in spring and early summer (Figure 14),

FIGURE 12.—Scale from a spring spawned 338 mm TL *Cynoscion arenarius* captured in September showing two annuli (A). The first annulus shows cutting over in the lateral field and changed spacing of circuli associated with secondary radii in the anterior field. The second annulus shows cutting over in the lateral field and a clear zone between circuli in the anterior field. A false annulus (F) had a few secondary radii but lacked changed spacing between circuli or a clear zone and distinct cutting over and was absent on most scales.
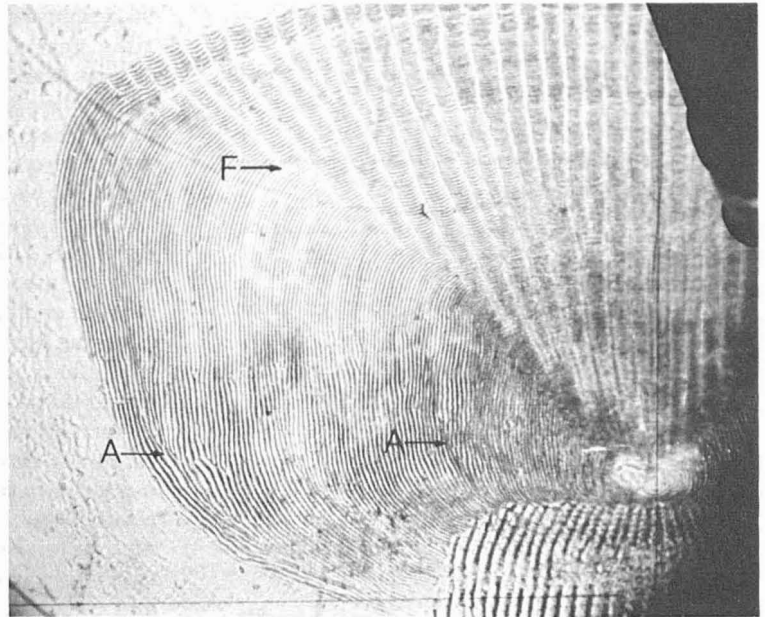

FIGURE 13.—Scale from a late summer spawned 300 mm TL *Cynoscion arenarius* captured in December showing one annulus (A). Note the cutting over in the lateral field and secondary radii in conjunction with a clear zone between circuli in the anterior field.

so that their first annulus primarily formed from April through July. Marginal increments in spring

fish were smallest in late summer and fall, so that their first annulus formed primarily from September (possibly August) through November. Therefore, both spring and late summer fish primarily formed their first annulus at about 0.5-0.75 yr of age.

Fish with one annulus were 136-329 mm TL. The percentage having a first annulus increased with size: 1) 8% at 150-199 mm TL ($n = 518$), 2) 24% at 200-249 mm ($n = 268$), 3) 52% at 250-299 mm ($n = 77$), and 4) 71% at 300 mm and greater ($n = 14$). Fish with two annuli were 265-338 mm TL.

Back-calculated lengths were smaller than lengths at age determined from length frequencies. Lengths at annulus formation for spring fish using Jones' (1958, equation 2) formula were 81-257 mm TL, and the mean was 162 mm with 95% confidence limits of 154-171 mm. Back-calculated lengths at annulus formation for late summer fish were 96-255 mm TL, and the mean was 178 mm with 95% confidence limits of 169-186 mm. These data support analyses of marginal increments that indicate the first annulus primarily forms at 0.5-0.75 yr, because lengths at age I determined from length frequencies were 220-280 mm TL for spring fish and 210-250 mm for late summer fish. The back-calculated size range of 81-257 mm TL for spring fish agrees with their sizes at age 0 during summer and early fall (Figures 4, 5). Similarly, the back-calculated size range of 96-255 mm TL for late summer fish agrees
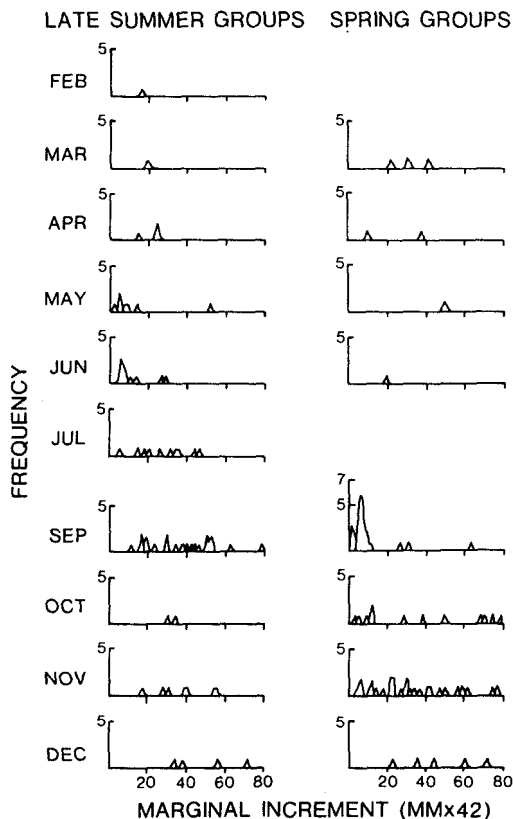
LATE SUMMER GROUPS   SPRING GROUPS

FIGURE 14.—Monthly marginal increments for *Cynoscion arenarius* with one mark.

with their sizes at age 0 in spring and early summer (Figures 4, 5).

Repeated examination suggests that age determination was consistent. We found 86% agreement in a second reading of scales from 361 fish 120-338 mm TL, including all fish initially determined to have an annulus. Disagreement occurred primarily when the scales had a mark close to the margin or had one annulus and one false annulus.

Discussion

Scales can be used to age *C. arenarius*, but length-frequency analysis is simpler and at least as accurate except possibly with fish much older than those we caught. Separate spring and late summer spawning periods complicate age determination. Age, growth, and mortality estimates should be based on individual spawned groups to avoid misinterpretation. Valid estimates require assignment of individuals to correct spawned groups; and that requires length-frequency analy-

sis, because annulus formation occurs over a broad time period in both spring and late summer groups. Exact age determination may be impossible for the apparently few fish older than say, age II or III. Their ages probably would not be distinct in length frequencies and a spawned group probably could not be assigned.

Causes of annulus formation in *C. arenarius* are not clear, although temporary growth cessation may be associated with movements between estuaries and the gulf and/or gonad development. Annulus formation in late summer fish coincides with their spring movement to estuaries and gonad development. Similarly, annulus formation in spring fish coincides with fall movements from estuaries. However, many spring fish use only gulf nurseries in their early life which might minimize mark formation in those fish. False annulus formation might be associated with movements between estuaries and the gulf. *Cynoscion arenarius* and *C. regalis* are similar in that both migrate between the sea and estuaries (Welsh and Breder 1923; present studies) and their scales exhibit many false annuli (Merriner 1973; present studies). In contrast, *C. nothus*, a gulf resident, exhibits few false annuli (DeVries and Chittenden footnote 6).

MAXIMUM SIZE, LIFESPAN, AND MORTALITY

Cynoscion arenarius is small and short lived. The largest of the 13,780 fish we captured was 342 mm TL, although few exceeded 300 mm. Our findings agree with Gunter (1945), Hildebrand (1954), Perry (1970), and Chittenden and McEachran (1976) who captured fish to 377 mm TL but few >300 mm. Many other studies have reported even smaller maxima including Miller (1965), Christmas and Waller (1973), and Perret and Caillouet (1974). The only published records much >300-375 mm TL include a few trawl-caught fish 425-497 mm TL from the north-central gulf (Franks et al. 1972; Adkins and Bowman 1976) and off Texas (Mohsin 1973), 590 and 540 mm TL gill net caught fish from northwestern Florida (Vick 1964; Trent and Pristas 1977), and fish as large as 483 and 503 mm TL captured in Galveston Bay, Tex., by commercial and recreational fishermen, respectively (Heffernan et al.[7]). The latter study gave size data

[7]Heffernan, T. L., A. W. Green, L. W. McEachron, M. G. Weixelman, P. C. Hammerschmidt, and R. A. Harrington. 1976. Survey of finfish harvest in selected Texas

from fisheries whose gear was biased seriously to capture large fish about 12 mo and older. However, even these fish averaged only 280 mm TL in recreational catches and 343 mm in commercial catches; and few were >330 mm and 406 mm TL, respectively.

The maximum lifespan of *C. arenarius* typically is 1-2 yr at most for trawl-caught fish and possibly as much as 2-3 yr for other gear. In the period October 1977-April 1979, 90% of the 3,988 fish that we captured off Freeport were <215 mm TL (Figure 15), 99% were <280 mm, and 99.5% were <300 mm. Similarly, of the 2,073 fish collected off Port Aransas during February 1977-July 1978 (Figure 15), 90% were <210 mm TL, 99% were <260 mm, and 99.5% were <275 mm. A t_L value of 1-2 yr at most is reasonable for the Beverton-Holt model parameter (Gulland 1969) for trawl-caught *C. arenarius* because fish >260-300 mm TL made up <0.5-1.0% of our catch. This is about the average size at age I (210-280 mm TL), which many individuals exceed, and approaches the maximum sizes usually reported. Our trawling, moreover, shows the scarcity of fish with more than one annulus, a disappearance of all fish by 14-18½ mo of age (Table 3), and agrees with Chittenden and McEachran's (1976) suggestion that the typical lifespan is no more than 1-2 yr. Even recreational and commercial gear seriously selective for larger sizes (references cited above) catch fish whose typical maximum age appears to be only 2-3 yr, at most, because mean sizes at these ages predicted by polynomial regression were 431 mm TL at age II and 574 mm at age III for late summer fish and a

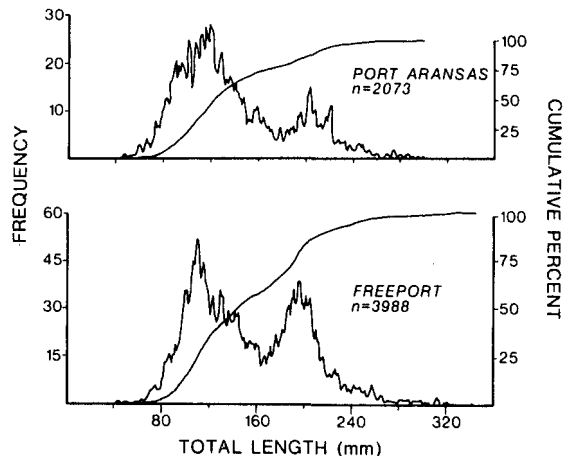bays. Tex. Parks Wildl. Dep., Coastal Fish Branch, Proj. Rep. 2-231-R-1, 116 p.

FIGURE 15.—Length frequency (moving average of three) and cumulative percentage of all *Cynoscion arenarius* collected in the Gulf of Mexico off Freeport, Tex., October 1977-April 1979 and off Port Aransas, Tex., February 1977-July 1978.

probably unrealistically low 301 mm at age II for spring fish.

Sand seatrout has a total annual mortality rate that approaches 100% and has a best estimate of 99.79% based on trawling data. Time-specific values of total annual mortality $(1 - S)$ were calculated for each individual month from the expression $S = N_t/N_o$ where S = rate of survival and N_o and N_t are the number of fish collected from consecutive spring or late summer groups. Of the 20 mo when collections were made off Freeport, only one spring group was present in 14 mo and only one late summer group was present in 17 mo (Figure 4). Of the 14 mo when collections were made off Port Aransas, only one spring group was present in 13 mo and only one late summer group was

TABLE 3.—Periods of time, sizes, and ages when spawned groups of *Cynoscion arenarius* were last captured off Freeport and Port Aransas, Tex.

Spawned group and location	Disappeared in the period	TL (mm)	Age (mo)	Comments
Spring 1976:				
Port Aransas	5 Apr.-28 May 1977	260-295	12-14	Few specimens ever captured
Late summer 1976:				
Freeport	4 Nov.-3 Dec. 1977	275-340	14-15	Few specimens ever captured
Port Aransas	10 Nov. 1977	240-285	14-15	
Spring 1976:				
Freeport	14 June-15 Sept. 1978	295-340	14½-17½	Few captured after December 1977
Port Aransas	8 Mar. 1978	250-280	11-12	Few captured after November 1977
Late summer 1977:				
Freeport	13 Dec. 1978-12 Mar. 1979	280-320	15½-18½	Few captured after September 1978
Port Aransas	28 June 1978	240	11	
Spring 1978:				
Freeport	21 June 1978	305-325	14½	Few captured after April 1979
Port Aransas	15 July 1978	80-150	4½	Still being recruited when last collection was made
Last summer 1978:				
Freeport	22 Sept. 1979	205-305	13	Still abundant when last collection was made; sizes not distinct

present in 11 mo (Figure 5). The apparent values of $1 - S$ were 100% within each month when N_t was zero. In six other months the youngest group in the ratio N_t/N_o was incompletely recruited off Freeport, so that the following mortality rates would be underestimates: 1) June 1978, 99.2%, spring fish; September 1978, 98.9%, spring fish; 2) May 1979, 99.5%, spring fish; June 1979, 99.9%, spring fish; August 1979, 99.0%, spring fish; and 3) December 1978, 98.8%, late summer fish. Because the youngest spawned group in the ratio strongly showed incomplete recruitment, realistic mortality estimates were not possible for the following months: 1) spring groups, May 1977, Port Aransas; 2) late summer groups, September, October, and November 1977, Port Aransas; 3) spring groups, May 1978, Freeport; and 4) late summer groups, December 1977, September 1979, Freeport. Following the first procedure of Robson and Chapman (1961), we calculated an average value of $1 - S =$ 99.79% by pooling identifiable N_o and N_t values from each month except the seven in which the youngest spawned group strongly showed incomplete recruitment.

Our observed estimates agree with the theory (Royce 1972:238) that the total annual mortality rate is about 90% if the lifespan is about 2 yr and approaches 100% if 1 yr. Our high mortality estimates are consistent with maximum sizes and length frequencies in many published faunal studies based on trawling in estuarine and gulf waters. Theoretical values that $1 - S = 80\text{-}90\%$ based on lifespans of 2-3 yr appear to be lowest tenable values even if the data include recreational or trammel/gill net caught fish.

TOTAL WEIGHT-, GIRTH-, AND STANDARD LENGTH-TOTAL LENGTH RELATIONS

Total weight-total length, girth-total length, and standard length-total length relationships are presented in Table 4. Regressions of total weight on total length were significantly different in elevation between sexes ($F = 5.38$; 1, 1,501 df; $\alpha = 0.05$) but not in slope ($F = 2.41$; 1, 1,500 df; $\alpha = 0.05$). Calculated slopes significantly exceeded $\beta = 3.0$ at $\alpha = 0.5$ (data pooled, $t = 18.85$; males, $t = 15.10$; females, $t = 14.85$).

GENERAL DISCUSSION

The fact that C. arenarius produces two distinct, major spawned groups each year may be important to its systematic status, management, and to understanding its population fluctuations.

The temporal separation of the spawned groups implies reproductive isolation, the extent of which remains to be determined. The existence of the two spawned groups—and their systematic status—must be considered in resolving the status of C. arenarius. Ginsburg (1929), Mohsin (1973), and Weinstein and Yerger (1976) did not indicate the spawned groups studied. The two spawned groups may be separate populations or, possibly, separate species. That should be determined and considered in management because fishing could affect them differently.

The production of two major spawned groups each year would minimize year to year population fluctuations even though C. arenarius is short lived and little more than an annual crop. As DeVries and Chittenden (footnote 6) noted for C. nothus, each spawned group buffers population stability as a multiple year class structure buffers longer lived species. Ricker reproduction curves (Ricker 1954, 1975) might be useful to simulate fluctuations of multiple spawned-group stocks.

Many aspects of the life history and population dynamics of C. arenarius differ from C. regalis in the Middle Atlantic Bight north of Cape Hatteras, but C. arenarius appears similar to C. regalis south of Cape Hatteras. In general, it appears that for C. arenarius: 1) spawning lasts from March through September but mainly occurs in two peaks, a spring period (March-May) and a late summer period (August-September); 2) maturity is reached at 140-180 mm TL as they approach age I and spawn; 3) maximum size typically is 350-375 mm TL, but most fish are much smaller so that C. arenarius is not a major commercial food fish; 4) maximum age typically is 1-2 yr, or 3 yr at most; 5) total annual mortality rate is 80-90% or more, our best estimate being 99%, and 6) fish reach 210-280 mm TL at age I.

The life history of C. regalis in the Middle Atlantic Bight is more difficult to enumerate, because it makes north-south and onshore-offshore migrations (Pearson 1932; Nesbit 1954; Wilk 1979). Moreover, at least two intermixing populations may occur there (Nesbit 1954; Perlmutter et al. 1956; Seguin 1960), although stocks remain undefined (Joseph 1972; Merriner 1973; Wilk 1979). However, it appears that C. regalis north of Cape Hatteras 1) spawn from May to August with one peak period about April-June (statements of sev-

TABLE 4.—Total weight-total length, total length-girth, and standard length-total length regressions for *C. arenarius* with supporting statistics. All regressions were significant at $\alpha = 0.05$. Measurements are grams and millimeters.

Equation	n	TL range	100r^2	Residual MS	Corrected total SSx	Corrected total SSy	$\overline{X}$	$\overline{Y}$
$\log_{10} TW = -5.6609 + 3.2572 \log_{10} TL$ (males)	851	—	97.7	0.0027	9.52	103.35	2.2096	1.5359
$\log_{10} TW = -5.6325 + 3.2420 \log_{10} TL$ (females)	653	—	98.4	0.0025	9.48	101.32	2.2346	1.1612
$\log_{10} TW = -5.4698 + 3.1715 \log_{10} TL$ (males, females, immatures)	1,776	40-338	98.5	0.0032	38.67	394.07	2.1780	1.4379
$G = 1.197 + 0.512 TL$	1,776	40-338	97.0	20.20	1,220,591 (G)		159.2	82.7
$TL = 2.269 + 1.897 G$	1,776	40-338	97.0	74.80	4,519,719 (TL)		82.7	159.2
$SL = -6.49 + 0.85 TL$	1,776	40-338	99.7	4.56	3,369,130 (SL)		159.2	128.8
$TL = 8.01 + 1.17 SL$	1,776	40-338	99.7	6.30	4,641,233 (TL)		128.8	159.2

eral workers including Welsh and Breder 1923; Hildebrand and Schroeder 1928; Nesbit 1954) or with two peak periods about June and July (Daiber 1957 and Harmic 1958 cited in Thomas 1971); 2) mature at 160-230 mm TL (130-190 mm SL) and spawn at age I throughout their range (Merriner 1976), the validity of which might be reexamined for the New York Bight, because females in Delaware Bay first spawn at age III-IV when fish average 280-330 mm TL (Welsh and Breder 1923); 3) more or less commonly reached maximum weights of 4.54-7.72 kg (10-17 lb) or more (Welsh and Breder 1923; Wilk 1979), maximum lengths of about 400-600 mm TL or more (Welsh and Breder 1923; Hildebrand and Schroeder 1928; Nesbit 1954; Perlmutter et al. 1956), and average long enough to support important commercial food fisheries (Nesbit 1954; Perlmutter et al. 1956; Joseph 1972; Merriner 1973); 4) commonly reach or once reached ages of 3-7 yr (Welsh and Breder 1923; Nesbit 1954; Perlmutter et al. 1956; Massmann 1963; Wilk 1979), although Massmann (1963) described a long-term reduction in size and presumably age composition in Chesapeake Bay; 5) have total annual mortality rates of 48-73% (Nesbit 1954; Massmann 1963; Merriner 1973) which agree with theoretical estimates of 48-68% for lifespans of 4-7 yr assuming negative exponential survivorship; and 6) reach 170-220 mm TL (143-180 mm SL) at age I (Thomas 1971, table 13; Merriner 1973, table 2.23), although reported growth varies and ages may be questionable (Merriner 1973; Wilk 1979).

Although less has been published from south of Cape Hatteras, it appears that those *C. regalis* generally 1) spawn from March through August with a peak about March-June (Hildebrand and Cable 1934; Mahood 1974; Merriner 1976), although a second smaller peak may occur in July-August (Merriner 1976); 2) mature at 160-230 mm TL and spawn at age I throughout their range

(Merriner 1976); 3) are much smaller than more northern fish, because few have been reported much >350-375 mm TL (unpubl. data of Anderson from 1930 to 1932 in Mahood 1974, fig. 11; Wolff 1972; Hoese 1973; Mahood 1974; Wenner[8]); 4) commonly reach ages of only 2-3 yr (Wolff 1972; Merriner 1973: data from Morehead City, N.C., fig. 2.7) although age IV fish were common in Pamlico Sound at Hatteras, N.C. (Merriner 1973, fig. 2.7); 5) have total annual mortality rates of 48-73% (Merriner 1973), which might be too low if maximum age typically is 2-3 yr; and 6) average 180-195 mm TL (150-160 mm SL) at age I (Merriner 1973, table 2.11).

The preceding comparisons indicate typical maximum sizes and ages of *C. regalis* differ north and south of Cape Hatteras, and this suggests different total annual mortality rates. New York Bight fish might be older at maturity than fish south of Cape Hatteras, although Merriner (1976) felt they matured at age I throughout their range. Although *C. regalis* migrates north-south and stocks need study, tagging (Nesbit 1954) indicated that North Carolina does not contribute much to New York Bight catches at least. Therefore, movements should not affect the basic conclusion of zoogeographic change in population dynamics at Cape Hatteras. Large *C. regalis* do appear near Cape Hatteras at times as Pearson (1932) and Merriner (1973, fig. 2.7, data from Hatteras) observed, but these may be from northern stocks that had moved south (Pearson 1932).

Zoogeographic changes in the life history and population dynamics of *C. regalis* support the suggestion (White and Chittenden 1977) that species widely distributed along the east coast of the United States may show marked change in life

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[8]E. Wenner, Assistant Marine Scientist, South Carolina Department of Wildlife and Marine Resources, P.O. Box 12559, Charleston, SC 29400, pers. commun. August 1980.

history and population dynamics at Cape Hatteras. This phenomenon needs to be considered in management; because given rates of fishing, for example, would more strongly affect stocks north of Cape Hatteras.

In contrast to the zoogeographic differences within *C. regalis*, the life history and population dynamics of *C. arenarius* appear similar to *C. regalis* south of Cape Hatteras. Reproduction is similar in age at maturation, age at first spawning, and the spawning period. The bimodal spawning periodicity in *C. arenarius* differs, at first glance, from that of *C. regalis* south of Cape Hatteras, but this has been recognized only recently for *C. arenarius* and may exist in southern *C. regalis* (Merriner 1976). Differences in typical maximum sizes and ages are small, if real, and this suggests mortality rates more similar than present data indicate. The similarity of the life history and population dynamics of *C. arenarius* to that of *C. regalis* south of Cape Hatteras is consistent with Weinstein and Yerger's (1976) suggestion that they may be one species.

Finally, the population dynamics of *C. arenarius*, including its short lifespan, high mortality rate, and rapid turnover of biomass, are similar to those of *C. nothus* (DeVries and Chittenden footnote 6) and Atlantic croaker of the Carolinean Province (White and Chittenden 1977; Chittenden 1977). This supports the suggestion (Chittenden and McEachran 1976; Chittenden 1977) that the abundant species of the white and brown shrimp communities in the gulf have evolved towards a common pattern of population dynamics. Moreover, Chittenden's (1977) simulations on Atlantic croaker could serve as a first approximation of the effects of harvesting *C. arenarius*, and *C. regalis*, south of Cape Hatteras.

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