REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE LONGSPINE PORGY, *STENOTOMUS CAPRINUS*[1,2]

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ABSTRACT

Stenotomus caprinus mature at 90-125 mm TL as they approach age I. Spawning occurs once a year in a discrete period of 50-80 days duration from January through April with peak activity in February or March. The male-female sex ratio was 1:1.21 in the spawning period. Spawning occurs in waters deeper than 27 m, and its timing coincides with the periodicity of onshore surface currents in the northern Gulf of Mexico. These currents probably transport eggs and larvae inshore to nursery areas <27 m deep where recruitment occurs. Young-of-the-year gradually disperse as they mature to waters 36-55 m deep where age I and II fish are most abundant. *Stenotomus caprinus* are most vulnerable to trawling at night. Growth in length is fastest in their first 8 months but slows greatly as they mature and divert energy towards reproduction. *Stenotomus caprinus* averaged 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. Maximum size is about 200 mm TL and maximum lifespan typically is 2.5-3 years. Total annual mortality rate is 83-99%, but postspawning survival, mortality rates, and lifespan vary greatly between year classes. Total weight-total length, length-length, and girth-total length relationships are presented. The population dynamics of *S. caprinus* appear quite different from those of *S. chrysops*, and the genus *Stenotomus* may show zoogeographic change at Cape Hatteras, N.C.

Stenotomus caprinus, the longspine porgy, ranges in the Gulf of Mexico (Gulf) from Campeche Bank, Mexico, to Apalachee Bay, Fla., (Caldwell 1955) and occurs rarely in the Atlantic to North Carolina (Dawson[5]). It is very abundant at depths of 40-110 m and is the dominant fish in the brown shrimp community (Hildebrand 1954; Chittenden and McEachran 1976; Chittenden and Moore 1977). *Stenotomus caprinus* makes up a significant portion of the catch in the industrial fishery of the north central Gulf (Roithmayr 1965; Gutherz et al. 1975).

Despite its abundance, little is known about this species. Its life history is known from general faunal studies such as Miller (1965), Moore et al. (1970), and Franks et al. (1972), although Henwood et al. (1978) described its food habits. Only Caldwell (1955), Henwood (1975), Henwood et al. (1978), and Dawson (footnote 5) have made studies specifically directed at *S. caprinus*.

This paper describes maturation and spawning seasonality, movements and spawning areas, growth and sizes at age, mortality and lifespan, merits of age determination by scales and length-frequency analysis, length-length, total weight-total length, and girth-total length relationships for *S. caprinus*.

METHODS AND MATERIALS

Stenotomus caprinus were collected monthly along a transect in the Gulf off Freeport, Tex., (Fig. 1) from October 1977 through March 1980 aboard a chartered shrimp trawler using double rigged 10.4 m shrimp trawls with 4.4 cm stretched cod end mesh and a tickler chain. Stations were occupied at depths of 5, 9, 13, 14, 16, 22, 24, 27, 36, 47, 55, 64, 73, 82, 86, and 100 m. Collections were made during the day through September 1978; thereafter, a day and night cruise were usually made each month. The 22 m depth range was primarily occupied after October 1978, and depths >47 m were first occupied in June 1979. Two tows of 10 min bottom time were made at each depth except that 1 tow was made prior to October 1978, 8-12 tows were made at 14 m, and 24 tows usually were made at 22 m.

All *S. caprinus* were separated from the catch, measured for total length, fixed in 10% Forma-

[1]Based on a thesis submitted by the senior author in partial fulfillment for the M.S. degree, Texas A&M University.

[2]Technical Article 17149 from the Texas Agricultural Experiment Station, College Station, TX 77843.

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[5]Dawson, R. A systematic revision of the sparid genus *Stenotomus*. M.S. Thesis in prep., The College of Charleston, Charleston, S.C.

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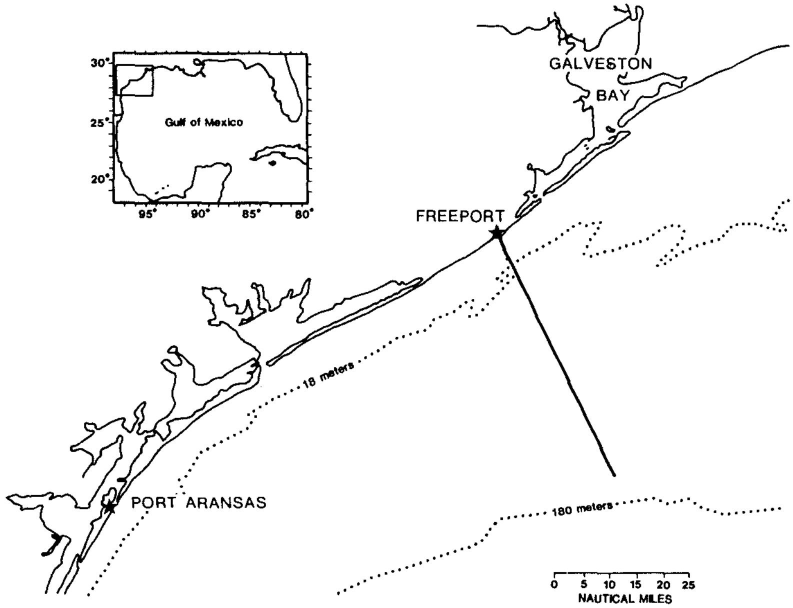


FIGURE 1.—Location of sampling areas with transect indicating stations occupied off Freeport, Tex.

lin,[6] and later preserved in 70% ethanol. For the period October 1978 to March 1980, 300 fish each month were selected by stratified random sampling to determine total length (TL), fork length (FL), standard length (SL), girth (G) at the fourth dorsal spine, total weight (TW), and ovary maturity stage and to take scale samples, except that only total weight, total length, sex, gonad weight, and ovary maturity stage were determined from October 1979 to March 1980. Female and immature fish were assigned gonad maturity stages (Table 1) similar to Kesteven's system (Bagenal and Braum 1971). Scales were taken below the lateral line near the tip of the pectoral fin following procedures for *S. chrysops* (Dery and Rearden[7]), and cellulose acetate impressions were examined using a scale projector.

Supplemental collections were made aboard the FRS *Oregon II* (NMFS) from 10 April to 1 May 1980 in the north central Gulf at depths of 9-91 m between long. 91°31′ and 92°00′W (Rohr et al.[8]). *Stenotomus caprinus* were selected from the catch without randomization procedures and measured in fork length.

TABLE 1.—Description of gonad maturity stages assigned to *Stenotomus caprinus*.

Stage	Description
1 Immature	Gonads barely or not visible.
2 Maturing virgin	Gonads very small, sexes not distinguishable.
3 Early developing	Sexes distinguishable but individual eggs are not visible.
4 Late developing	Eggs opaque, ovaries extending along <90% of gut cavity.
5 Gravid	Ovaries extend along 90% or more of lateral wall of gut cavity, < 50% of eggs translucent.
6 Ripe	Ovaries extend 90% or more of lateral wall of gut cavity, >50% of eggs translucent.
7 Spent/resting	Ovaries barely extend along lateral wall of gut cavity, flaccid with few small eggs. Similar in appearance to Stage 3, but occurs in fish large enough to have already spawned.

Year class identities were indicated by specifying the years in which the fish hatched. Age was determined by analysis of length frequencies, e.g., the Petersen method (Lagler 1956; Tesch 1971). The superior merits of this procedure for *S. caprinus* are noted in the section on Age Determination Using Scales. Size descriptions for each year class and each cruise (Table 2, Fig. 2) were based on major portions of frequency distributions cited. Boundaries between groups are indicated in Table 2 and Figure 2; mortality and growth calculations were based on groups defined by these boundaries. Arithmetic means were used to describe central tendencies for each year class and each cruise because length frequencies within year classes were

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[7]Dery, L., and C. Reardon. 1979. Report of the State-Federal scup (*Stenotomus chrysops*) age and growth workshop. Woods Hole Lab. Ref. 79-57, 10 p. Northeast Fisheries Center Woods Hole Laboratory, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543.

[8]Rohr, B. A., A J. Kemmerer, and W. H. Fox, Jr. 1980. FRS *Oregon II* Cruise 106 4/10-5/1/80. Cruise Report, 12 p. Southeast Fisheries Center Pascagoula Laboratory, National Marine Fisheries Service, NOAA, P.O. Drawer 1207, Pascagoula, MS 39567.

approximately normally distributed. Hatching dates of 15 February and 15 March were assigned to the 1978 and 1979 year classes, respectively, to estimate their growth and ages. Descriptions of spawning periodicity and growth assume that *S. caprinus* reach 20-30 mm TL 1-2 mo after hatching. This assumption and assigned hatching dates seem reasonable because: 1) *Stenotomus caprinus* average 13-14 mm TL/30 d growth during their first 8 mo of life (Fig. 3); 2) the slope and elevation of the regression of ovary weight on total length for the 1979 year class was greatest in mid-March (Fig. 4, Table 3) and back calculated length of this year class was −5.26 mm TL at 0 d of age (Fig. 5). A hatching date of 15 February was assigned to the 1978 year class because this year class recruited about 1 mo earlier in 1978, although gonad data are lacking for this period. There appears to be no published data on size at early age other than our findings.

Our interpretations of the life history of *S. caprinus* obviously apply best to the area off Freeport, Tex., but they probably apply to much broader areas in the Gulf, judging from the agreement of our findings with the general published data on this species.

MATURATION AND SPAWNING SEASONALITY

Results

Stenotomus caprinus mature at 90-125 mm TL as they approach age I. Sex could be determined by eye at 90 mm TL as many fish entered the Early Developing stage (Fig. 6). Fish entered the Late Developing, Ripe, and Gravid stages at 100-125 mm TL. These data are supported by the extrapolated x-intercepts of ovary weight on total length which were 80-100 mm TL during the January-April spawning period (Fig. 4, Table 3). Our estimates of size at maturity agree with the mean sizes at age I given later.

Little somatic growth occurs after *S. caprinus* enters the later stages of gonad maturation (Fig. 6). Mean sizes of fish approaching age I were 110 mm TL in the Early Developing, 113 mm in the Late Developing, 115 mm in the Gravid and Ripe, and 118 mm in the Spent/Resting stages.

Stenotomus caprinus spawn once a year in a discrete period from January through April. This period is indicated by collections off Texas of fish that were 30-40 mm TL in April 1978, 20-50 mm in May 1979, and 20-40 mm in February-March 1980 (Fig. 2), and by the capture of fish 20-80 mm TL in late April 1980 in the north central Gulf (Fig. 7). No spawning occurs from May through December, because the smallest fish collected in that period belong to year classes hatched before May. Peak spawning occurred in March and early April in 1979 and from January through March 1980 as indicated by the increased slopes and elevated ovary weight-total length regression lines in those periods (Fig. 4, Table 3). The sharply defined and readily followed length-frequency modes for each year class indicate that spawning occurs in one discrete period each year.

Gonad maturity data support a January-April spawning period and indicate that virtually all *S. caprinus* spawn at 12 mo of age. Fish in Gravid or Ripe stages occurred only in the period January-April, and Spent/Resting stage fish appeared immediately thereafter (Fig. 8). Virtually all spawning occurs in the period January-April and few fish delay spawning until age II because extremely few fish were in the Immature, Maturing Virgin, or Early Developing stages in that period.

The spawning period probably spans about 50-80 d within the January-April interval, assuming larger fish were spawned before smaller ones, and all fish grew at the same rate as noted later. The spawning period duration was approximated from growth increments and size ranges (expressed as 99% confidence limits for observations) of the 1978 and 1979 year classes in June and July (Table 2), their first months of full recruitment. The mean 99% confidence limit for observations in the June-July period was 22.19 mm in 1978 and 40.27 mm in 1979, and respective mean daily growth was 0.45 mm/d and 0.50 mm/d. Calculated lengths of spawning periods were 49 d in 1978 (22.19 mm ÷ 0.45 mm/d) and 82 d in 1979 (40.85 mm ÷ 0.50 mm/d). These estimates suggest that the successful spawning period is much shorter than the January-April interval indicated by length compositions and gonad data.

Stenotomus caprinus exhibited a sex ratio of 1.00 male to 1.21 females. This ratio was observed in 1,506 fish examined during the spawning period and differs significantly from 1:1 ($\chi^2 = 13.01$, $\alpha = 0.05$, df = 1).

Discussion

Our findings agree with the limited literature on *Stenotomus* reproduction. Previous workers

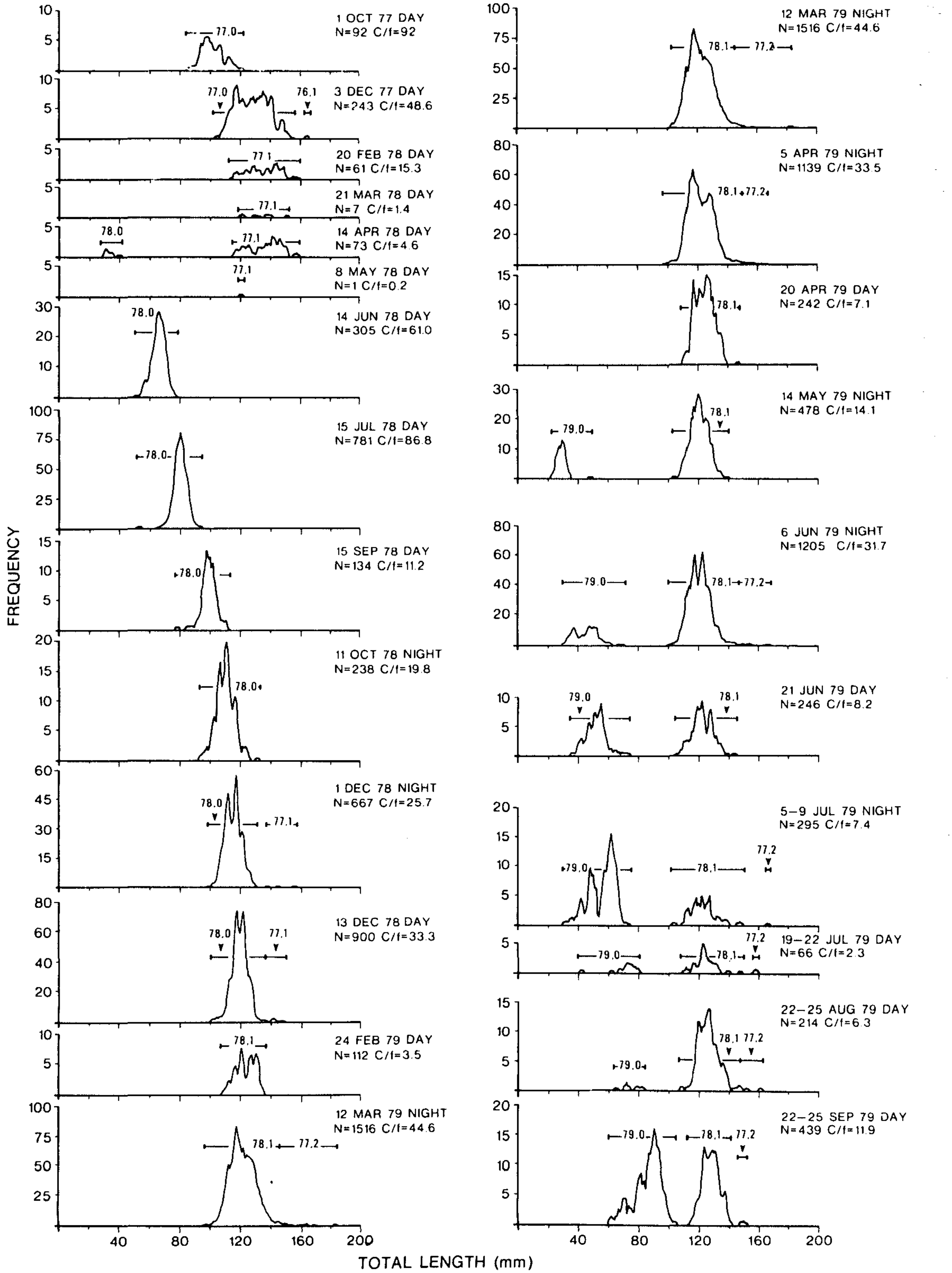
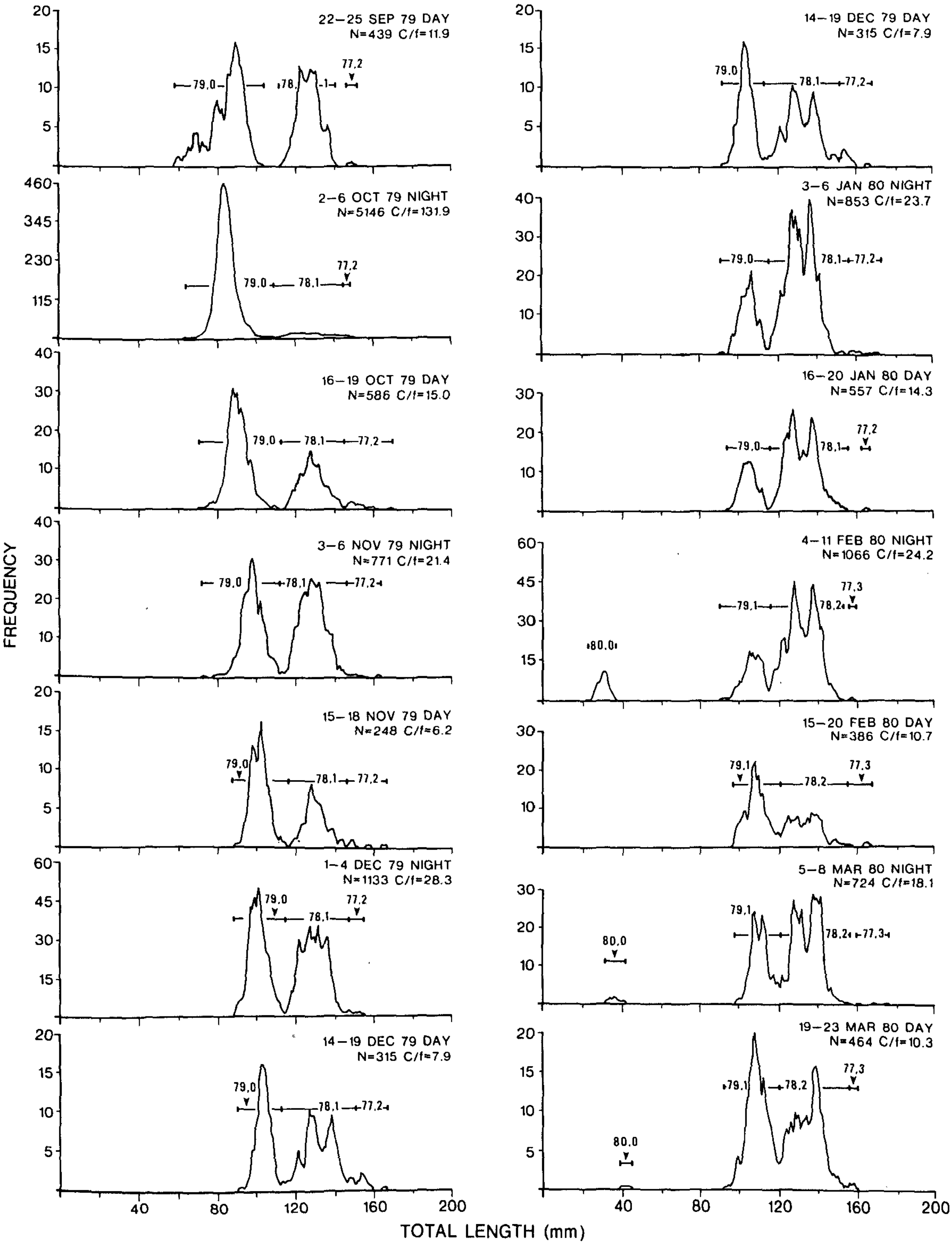


FIGURE 2.— Monthly length frequencies (moving averages of three) of *Stenotomus caprinus* off Freeport, Tex. Bars in each panel



indicate the size range of a year class. The first two digits within a bar indicate the year class; the last digit is age in years; e.g., 78.I represents the 1978 year class when age I. C/f indicates number of individuals per 10-min tow.

TABLE 2.—Growth data (mm TL) for *Stenotomus caprinus* from the Gulf off Freeport, Tex. Increments with an asterisk (*) were adjusted to growth per 30 d and plotted in Figure 3. Night and day cruises are indicated by N and D. Observed size ranges delineate year class boundaries used in growth and mortality calculations.

Collection date	n	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
			1977 Year Class				
1 Oct. 1977, D	92	85-120	100.5	54.1	99.0-102.0	81.3-119.4	
5 Nov. 1977, D	0	—	—	—	—	—	—
3 Dec. 1977, D	242	103-157	127.6	123.3	126.2-129.0	99.0-156.2	+27.1
20 Feb. 1978, D	61	113-157	134.4	125.0	131.6-137.2	105.6-163.2	+6.8
21 Mar. 1978, D	7	119-150	132.0	116.0	122.4-141.6	94.3-169.7	−2.4
14 Apr. 1978, D	66	95-157	135.9	115.2	133.3-138.5	108.3-163.5	+3.9
8 May 1978, D	1	120	120.0	0	120.0	120.0	−15.9
14 June 1978, D	0	—	—	—	—	—	
15 July 1978, D	0	—	—	—	—	—	
15 Sept. 1978, D	0	—	—	—	—	—	
11 Oct. 1978, N	0	—	—	—	—	—	
1 Dec. 1978, N	3	136-155	145.3	82.3	128.6-162.0	92.3-198.3	+25.3
13 Dec. 1978, D	12	136-147	141.2	11.1	139.1-143.3	131.0-151.4	−4.1
24 Feb. 1979, D	0	—	—	—	—	—	
12 Mar. 1979, N	15	146-182	155.8	99.2	150.3-161.3	126.4-185.2	+14.6
5 Apr. 1979, N	7	151-165	156.4	22.3	152.2-160.6	139.9-172.9	+0.6
20 Apr. 1979, D	0	—	—	—	—	—	
14 May 1979, N	0	—	—	—	—	—	
6 June 1979, N	10	145-166	154.6	40.9	150.1-159.1	134.3-174.9	−1.8
21 June 1979, D	0	—	—	—	—	—	
5 July 1979, N	1	165	165.0	0	165.0	165.0	+11.4
19 July 1979, D	3	145-157	153.0	37.0	141.8-164.2	117.5-188.5	−12.0
22 Aug. 1979, D	3	146-159	151.7	44.3	139.5-163.9	112.8-190.6	−1.3
22 Sept. 1979, D	2	146-148	147.0	2.0	110.1-183.9	133.1-160.9	−4.7
2 Oct. 1979, N	4	145-160	153.0	38.7	144.4-161.6	124.4-181.6	+6.0
16 Oct. 1979, D	19	145-167	151.7	34.3	148.9-154.5	134.9-168.5	−1.3
3 Nov. 1979, N	6	144-161	149.8	38.2	143.6-150.0	126.9-172.7	−1.9
15 Nov. 1979, D	5	144-164	152.4	56.3	143.8-161.0	122.1-182.7	+2.6
1 Dec. 1979, N	12	144-153	148.7	7.9	146.9-150.5	140.1-157.3	−3.7
14 Dec. 1979, D	4	150-164	157.6	19.7	151.3-163.7	137.1-177.9	+8.8
3 Jan. 1980, N	8	154-170	161.5	20.3	156.8-165.2	146.4-176.6	−4.0
16 Jan. 1980, D	1	164	164.0	0	164.0	164.0	+2.5
4 Feb. 1980, N	2	155-157	156.5	0.5	154.3-158.7	149.5-163.5	−7.5
15 Feb. 1980, D	4	156-165	162.2	17.6	155.4-168.0	142.9-181.5	+5.7
5 Mar. 1980, N	4	154-175	164.5	77.7	152.3-176.7	116.1-205.1	+2.3
19 Mar. 1980, D	3	155-158	156.7	1.3	154.6-158.8	150.0-163.4	−7.8
			1978 Year Class				
14 Apr. 1978, D	7	29- 40	32.3	11.9	29.2- 35.4	20.2- 44.4	
8 May 1978, D	0	—	—	—	—	—	
14 June 1978, D	305	50- 76	64.9	19.5	64.4- 65.4	53.5- 76.3	+32.6*
15 July 1978, D	781	51- 93	79.0	17.6	78.7- 79.3	68.2- 89.8	+14.1*
15 Sept. 1978, D	134	78-111	98.7	25.4	97.8- 99.6	85.7-111.7	+19.7*
11 Oct. 1978, N	238	93-131	109.2	35.8	108.4-110.0	93.8-124.6	+10.5*
1 Dec. 1978, N	664	98-135	114.3	28.2	113.9-114.7	100.6-128.0	+5.1*
13 Dec. 1978, D	888	100-135	117.8	26.9	117.5-118.1	104.4-131.2	+3.5*
24 Feb. 1979, D	112	107-133	121.8	40.9	120.6-123.0	105.3-138.3	+4.0*
12 Mar. 1979, N	1,501	96-145	120.7	65.1	120.3-121.1	99.9-141.5	−1.1*
5 Apr. 1979, N	1,132	98-150	121.4	64.9	120.9-121.9	100.6-142.2	+7.0*
20 Apr. 1979, D	241	110-146	123.5	39.7	122.7-124.3	107.3-139.7	+2.1*
14 May 1979, N	389	100-138	119.8	33.7	118.9-120.7	104.8-134.8	−3.7*
6 June 1979, N	988	100-144	119.5	48.9	119.4-119.6	101.5-137.5	−0.3*
21 June 1979, D	135	100-143	121.7	47.3	120.5-122.9	104.0-139.4	+2.2*
5 July 1979, N	73	101-145	121.4	59.2	120.9-121.9	101.6-141.2	−0.3*
19 July 1979, D	46	110-144	122.2	34.2	120.5-123.9	106.4-138.0	+0.8*
22 Aug. 1979, D	202	105-145	124.4	42.3	123.5-125.3	107.6-141.2	+2.2*
22 Sept. 1979, D	190	110-145	125.6	30.4	124.8-126.4	111.4-139.8	+1.2*
2 Oct. 1979, N	209	110-144	124.7	50.5	123.7-125.7	106.4-143.0	−0.9*
16 Oct. 1979, D	212	113-144	127.6	38.7	126.8-128.4	111.6-143.6	+3.6*
3 Nov. 1979, N	410	116-143	127.3	35.9	126.7-127.9	111.9-142.7	−0.3*
15 Nov. 1979, D	88	116-143	128.6	37.9	127.3-129.9	112.7-144.5	+1.3*
1 Dec. 1979, N	608	116-143	129.0	45.1	128.5-129.5	111.7-146.3	+0.4*
14 Dec. 1979, D	175	116-149	131.9	71.9	130.6-133.2	110.1-153.7	+2.9*
3 Jan. 1980, N	647	116-153	131.6	48.3	131.1-132.1	113.7-149.5	−0.3*
16 Jan. 1980, D	418	116-155	131.4	54.8	130.7-132.1	112.3-150.5	−0.2*
4 Feb. 1980, N	769	116-154	131.3	54.0	130.8-131.6	112.4-150.2	−0.1*
15 Feb. 1980, D	153	120-155	132.2	44.1	131.2-133.4	115.2-149.4	+1.0*
5 Mar. 1980, N	464	120-153	133.9	44.0	133.3-134.5	116.8-151.0	+1.6*
19 Mar. 1980, D	234	120-154	133.7	53.6	132.8-134.6	114.8-152.6	−0.2*

TABLE 2.—*Continued.*

Collection date	n	Observed size range (mm)	Mean length (mm)	s^2	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
			1979 Year Class				
14 May 1979, N	89	22- 49	27.6	10.5	26.9- 28.3	19.3- 35.9	
6 June 1979, N	207	29- 69	43.7	59.0	42.7- 44.7	23.9- 63.5	+16.1*
21 June 1979, D	111	35- 74	50.8	44.3	50.2- 51.4	33.7- 67.9	+7.1*
5 July 1979, N	220	30- 76	55.0	74.1	73.0- 75.2	32.8- 77.2	+4.2*
19 July 1979, D	17	40- 80	69.2	76.9	64.7- 73.7	46.6- 91.8	+14.2*
22 Aug. 1979, D	9	63- 81	72.9	33.1	68.8- 77.2	58.1- 87.7	+3.7*
22 Sept. 1979, D	247	58-102	83.3	78.8	77.7- 79.9	60.4-106.2	+10.4*
2 Oct. 1979, N	4,933	58-109	83.7	24.3	83.6- 83.8	71.0- 96.4	+0.4*
16 Oct. 1979, D	363	70-112	89.4	50.9	88.7- 90.1	71.0-107.8	+5.7*
3 Nov. 1979, N	355	72-115	96.8	36.5	96.2- 97.4	81.2-112.4	+7.4*
15 Nov. 1979, D	155	87-115	100.4	18.0	99.7-101.1	89.5-111.3	+3.6*
1 Dec. 1979, N	525	88-115	100.5	21.3	100.1-100.9	88.6-112.4	+0.1*
14 Dec. 1979, D	136	91-115	102.6	15.9	101.9-103.3	92.3-112.9	+2.1*
3 Jan. 1980, N	198	91-115	104.6	17.8	104.0-105.2	93.7-115.5	+2.0*
16 Jan. 1980, D	138	94-115	104.1	16.4	103.4-104.8	93.7-114.5	+0.5*
4 Feb. 1980, N	223	91-115	105.7	23.3	105.1-106.3	93.3-118.1	+1.6*
15 Feb. 1980, D	223	96-119	107.3	25.3	106.6-108.0	94.3-120.3	+1.6*
5 Mar. 1980, N	243	98-119	109.4	17.7	108.9-110.0	98.6-120.2	+2.1*
19 Mar. 1980, D	225	96-119	107.7	27.4	107.0-108.4	94.2-121.2	−1.7*

proposed a spring or late winter-early spring spawning period (Hildebrand 1954; Miller 1965; Chittenden and McEachran 1976) based on the captures of fish 106-159 mm TL with well-developed gonads in February (Hildebrand 1954) and fish 31-89 mm TL in early May and June (Caldwell 1955; Miller 1965). Henwood's (1975) histological studies indicated spawning from November through April, but our data indicate little or no spawning before January. Our finding that

TABLE 3.—Analyses of the monthly regressions of ovary weight (Y) in grams on total length (X) in millimeters for female *Stenotomus caprinus*, December 1978-March 1980. Regressions were significant (at $\alpha = 0.05$) except on 11 October 1978, 6 June 1979, 19 July 1979, 22 August 1979, and 22 September 1979.

Cruise	n	$100\ r^2$	Equation
1 Dec. 1978	144	23.70	$Y = -0.963 + 0.010\ X$
24 Feb. 1979	41	17.89	$Y = -0.913 + 0.016\ X$
12 Mar. 1979	168	37.35	$Y = -3.096 + 0.038\ X$
5 Apr. 1979	109	48.18	$Y = -3.295 + 0.036\ X$
20 Apr. 1979	84	7.00	$Y = -0.496 + 0.008\ X$
14 May 1979	110	23.26	$Y = -0.166 + 0.002\ X$
5 July 1979	24	36.97	$Y = -0.333 + 0.004\ X$
2 Oct. 1979	79	41.52	$Y = -0.352 + 0.004\ X$
16 Oct. 1979	53	10.58	$Y = -0.109 + 0.002\ X$
3 Nov. 1979	89	47.78	$Y = -0.232 + 0.003\ X$
15 Nov. 1979	65	58.86	$Y = -0.564 + 0.007\ X$
1 Dec. 1979	68	71.36	$Y = -1.486 + 0.016\ X$
14 Dec. 1979	83	62.26	$Y = -1.450 + 0.016\ X$
3 Jan. 1980	97	51.04	$Y = -1.613 + 0.020\ X$
16 Jan. 1980	85	82.36	$Y = -2.329 + 0.026\ X$
4 Feb. 1980	93	73.57	$Y = -3.132 + 0.036\ X$
15 Feb. 1980	79	59.02	$Y = -1.962 + 0.024\ X$
5 Mar. 1980	81	48.07	$Y = -2.203 + 0.028\ X$
19 Mar. 1980	64	69.22	$Y = -2.148 + 0.026\ X$

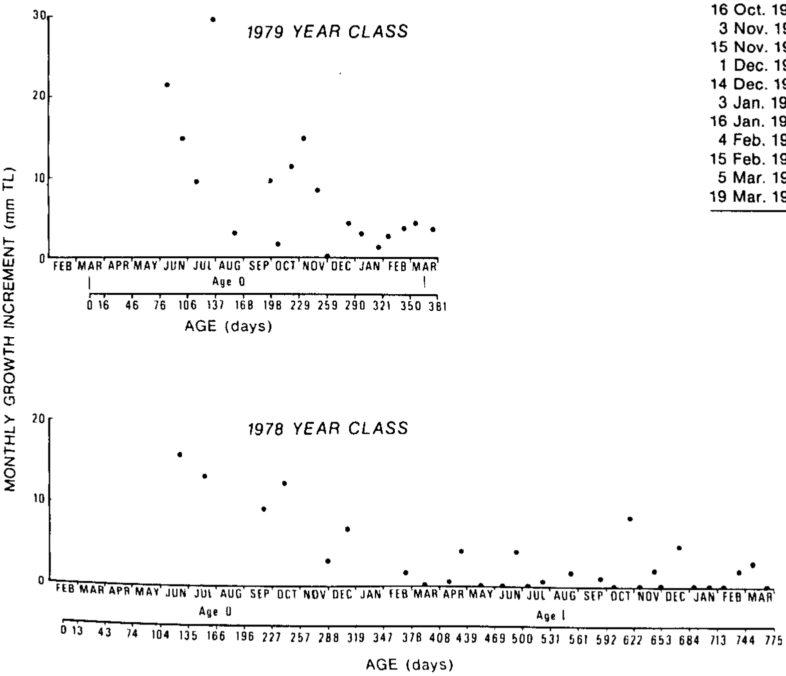


FIGURE 3.—Monthly growth increments for the 1978 and 1979 year classes of *Stenotomus caprinus*. Unadjusted growth increments (Table 2) were converted to growth per 30 d. Negative growth was rounded to 0.

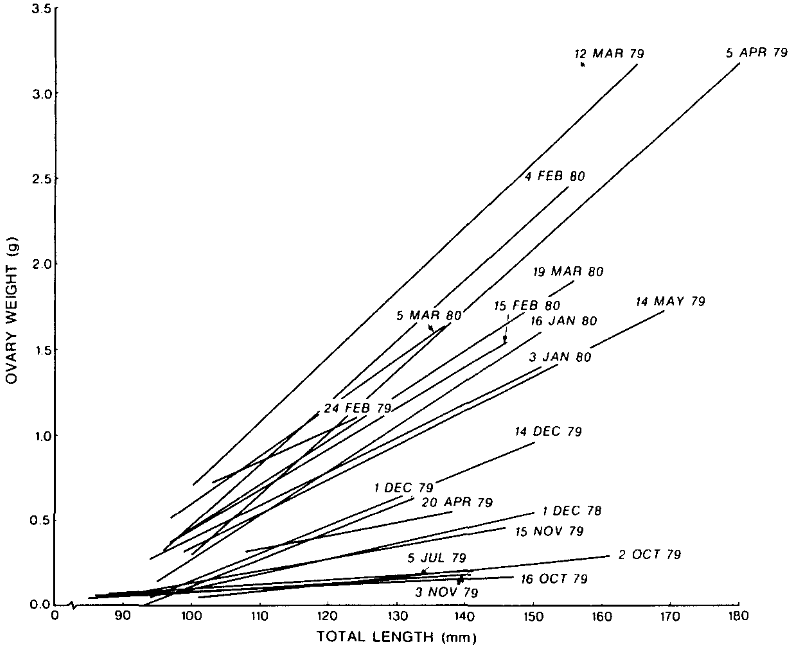


FIGURE 4.—Monthly ovary weight-total length regressions for *Stenotomus caprinus*. The length of each line shows the observed size range.

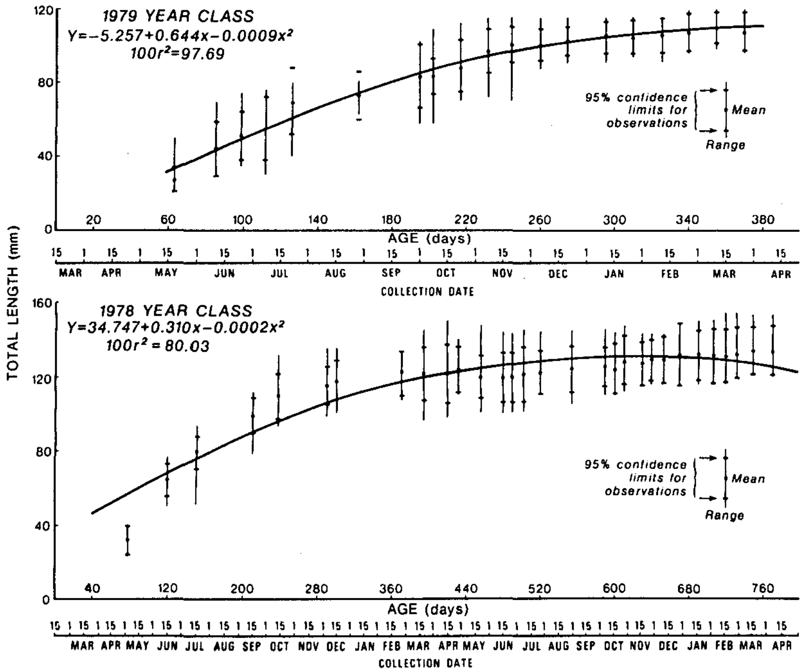


FIGURE 5.—Mean observed and predicted sizes at age for the 1978 and 1979 year classes of *Stenotomus caprinus*. Mean sizes at age (Table 2) were regressed on age after assigned hatching dates of 15 February and 15 March for these respective year classes. Regressions were significant at $\alpha = 0.05$.

virtually all *S. caprinus* spawn at 12 mo of age has not been reported, nor has the discrete and short duration of spawning been recognized. Sex ratios have not been reported for *S. caprinus*, although 1:1 and 1:1.26 male to female ratios have been reported for its congener *S. chrysops* (Smith and Norcross 1968; Morse 1978). The pattern of spawning in *S. caprinus* is several months earlier in timing but similar to *S. chrysops* which spawns once a year from May through August with greatest spawning in June (Bigelow and Schroeder 1953; Finkelstein 1969a).

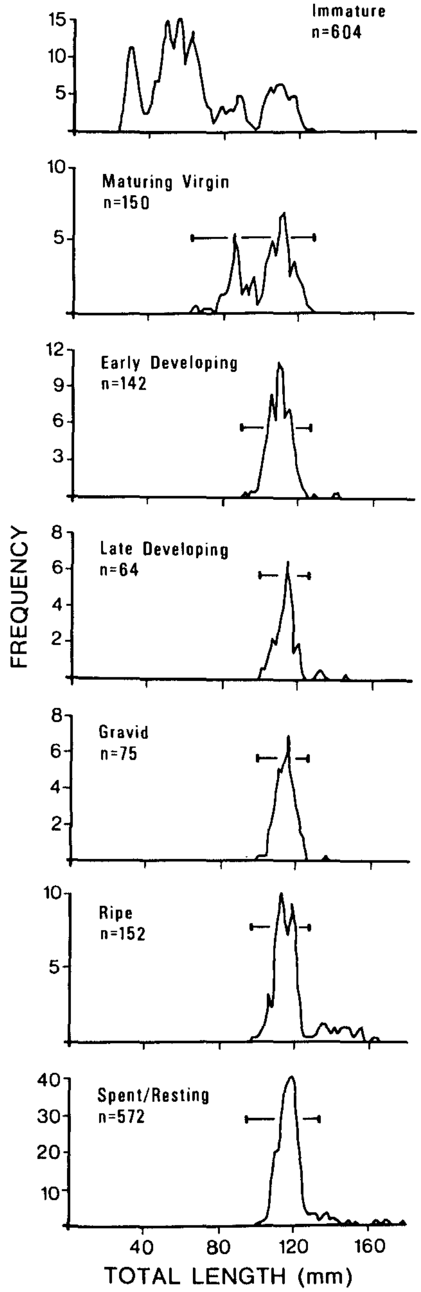


FIGURE 6.—Length frequencies (moving averages of three) of immature and female *Stenotomus caprinus* by maturity stages. See Table 1 for definitions of maturity stages. Brackets indicate size ranges used to calculate the mean length of fish approaching age I for each maturity stage.

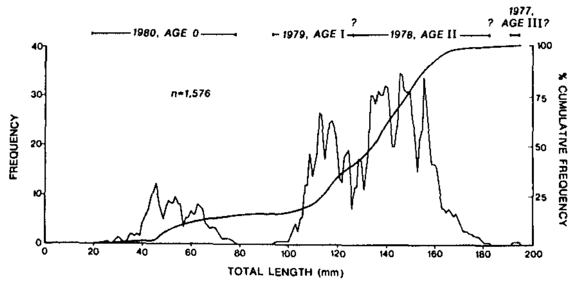


FIGURE 7.—Length frequency (moving averages of three) of *Stenotomus caprinus* captured in the north central Gulf aboard the *Oregon II*, 10 April-1 May 1980. Probable ages and year class identities are indicated.

MOVEMENTS, SPAWNING AREAS, AND DIEL VARIATION IN CATCH

Results

Stenotomus caprinus exhibit size and age gradients with depth related to their movements, spawning areas, and recruitment. Although captured from 18 m to 100 m (Fig. 9), they were most common between 36 m and 55 m.

Young-of-the-year recruited in inshore waters during the spring and moved towards deeper water as they grew. Recently hatched fish 20-50 mm TL appeared only in 18-27 m depths in the period February-May (Fig. 9), but became distributed as deep as 36-47 m by June to September. The larger young-of-the-year continued to disperse gradually to deeper water as indicated by their size gradients with depth in June-September 1979 and in October 1979-January 1980.

Adult *S. caprinus* reside and spawn in waters deeper than 27 m. No adults were found in waters shallower than 27 m during the January-April spawning period (Fig. 9). Fish of ages I and II occurred in waters deeper than 27 m throughout the year but showed no size gradient with depth. This indicates that they were uniformly mixed throughout the 27-100 m depth range.

Stenotomus caprinus appear most vulnerable to trawling at night. Mean catch per tow at night in the 18-100 m depth range that *S. caprinus* occupies averaged three times that of day catches on 10 of 11 occasions in the period December 1978-March 1980 when day and night cruises were made each month or close together in time (Fig. 2).

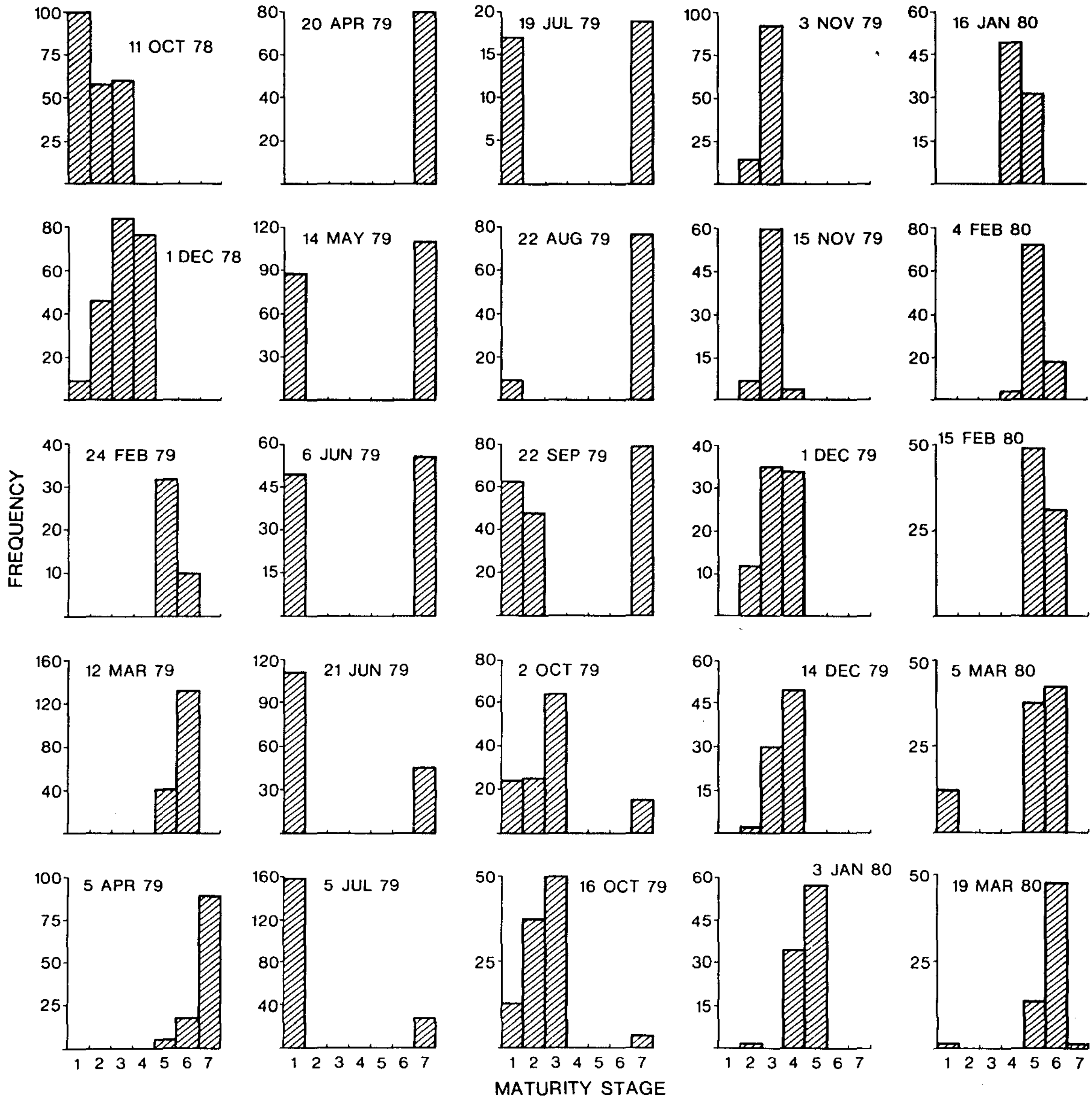


FIGURE 8.—Monthly maturity stages of female *Stenotomus caprinus*. Maturity stages are described in Table 1.

Discussion

The spawning periodicity of *S. caprinus* appears timed to coincide with the late winter-early spring periodicity of onshore surface currents on the continental shelf of the northwestern Gulf. Rising sea levels in the period January-April (Marmer 1954) coincide with onshore surface currents (Kimsey and Temple 1963; Smith 1975). This current system could transport eggs and larvae from offshore spawning areas to inshore nurseries where the young recruit, assuming that *S. caprinus* have pelagic eggs and larvae like *S. chrysops* (Johnson 1978).

Our findings on the movements and distribution of *S. caprinus* agree with the literature. The size-depth relationship in which younger individuals occur inshore in the spring has been reported (Hildebrand 1954; Caldwell 1955; Miller 1965). Our findings on size-depth gradients during the summer support Henwood's (1975) suggestion that young-of-the-year gradually dis-

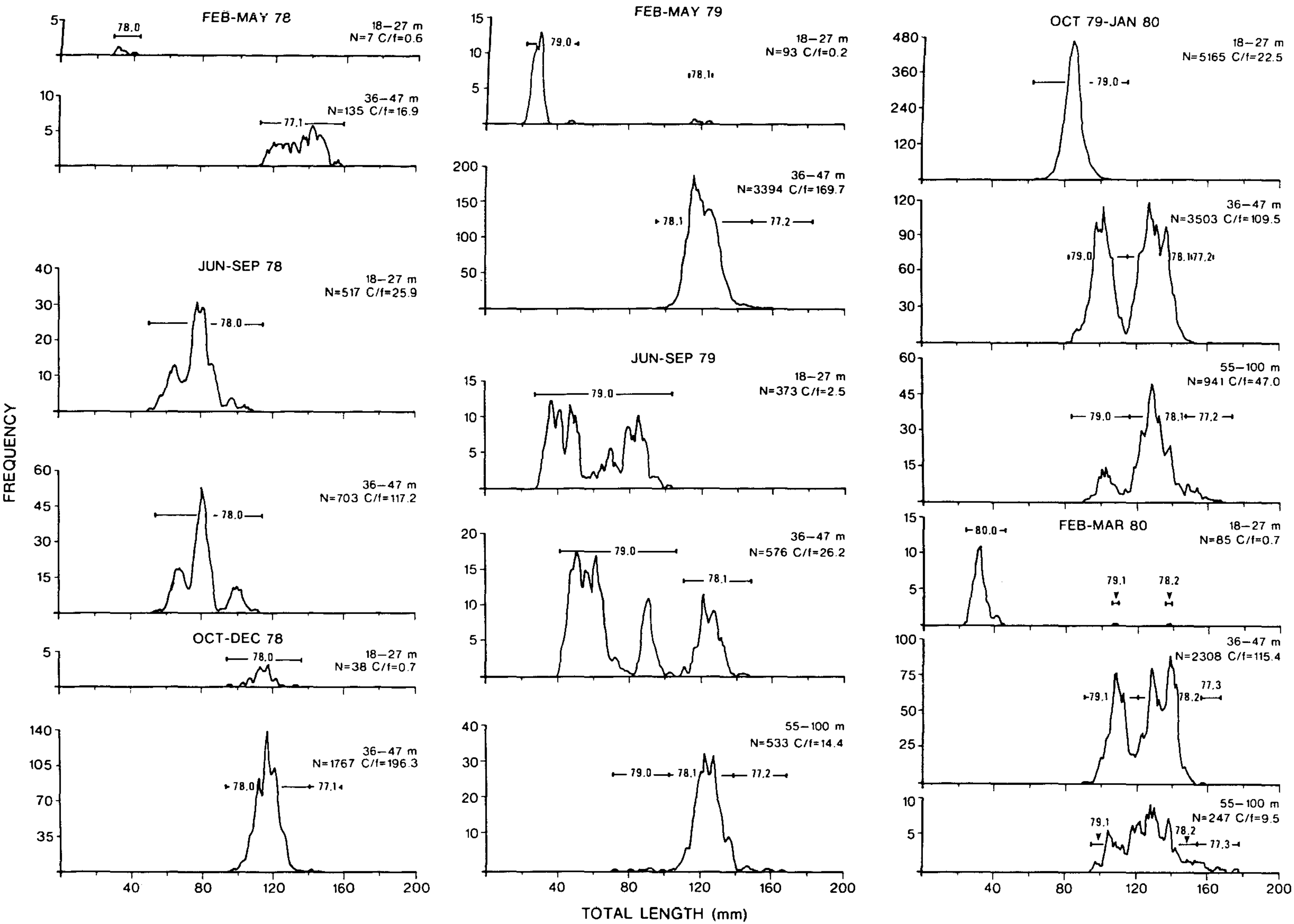


FIGURE 9.—Length frequencies (moving averages of three) by depth for *Stenotomus caprinus* off Freeport, Tex. Multiple peaks within size ranges designated as age 0 reflect growth. C/f indicates number of individuals per 10-min tow.

perse to deeper water. Our finding that age-I and age-II fish show no size-depth gradient and are mixed throughout 27-100 m depths has not been reported but agrees with Moore's (1964) finding that average weight did not increase in waters deeper than 64 m.

Our findings that *S. caprinus* is most vulnerable to trawling at night has not been reported, although similar behavior has been recorded for *S. aculeatus* (Powles and Barans 1980). Fritz (1965) found that *S. chrysops* made up a greater percentage of the catch at night, although Smith and Norcross (1968) reported crepuscular catches were greatest. Henwood et al. (1978) suggested that *S. caprinus* actively feeds during the day. These fish might be inactive and near the bottom at night, and thus more vulnerable to trawling.

AGE DETERMINATION USING SCALES

Results

Stenotomus caprinus cannot be aged readily using scales. Scales from 2,342 fish were examined for annuli using criteria of Dery and Rearden (footnote 7) which include cutting over, irregular spacing, and breaking of circuli. Marks similar to annuli were occasionally observed, but these marks varied greatly between scales from the same fish and between fish of the same size, age by length-frequency analysis, and date of capture. Annuli frequently were not apparent on fish that must have been age II or III according to length-frequency analysis, although one important criterion for valid use of the scale method (Lagler 1956; Tesch 1971) is that this procedure should agree with ages determined from length frequencies.

Discussion

Our finding that it is difficult to age *S. caprinus* using scales agrees with Henwood (1975). In contrast, several authors have used scales successfully to age *S. chrysops* (Finkelstein 1969a; Hamer 1979[9]); although this becomes difficult beyond age III (Smith and Norcross 1968).

Stenotomus caprinus are best aged using length frequencies, particularly if, as in the present study, there is a long-term set of data from cruises made close together in time. Under these conditions age determination by length-frequency analysis may be obvious, as we found. Length-frequency analysis would be less reliable if cruises were several months apart in time, because year class frequencies could merge after age I as our data indicate. The superior merits of age determination by length-frequency analysis are not surprising for *S. caprinus* because 1) this species spawns once a year in a discrete period, 2) within year class frequencies appear normally distributed, and 3) growth of large and small fish within a year class is uniform as evidenced by the observed constant variance. In addition, length-frequency analysis generally is most clear for younger ages (Lagler 1956; Tesch 1971), and *S. caprinus* only lives a few years (see section on Mortality and Postspawning Survival).

AGE DETERMINATION AND GROWTH USING LENGTH-FREQUENCY ANALYSIS

Results

No more than four year classes of *S. caprinus* were present at any time off Texas and only one or two predominated. These year classes represented young-of-the-year and ages I, II, and III (Fig. 2). Only one year class predominated in any month from October 1977 through April 1979, although two year classes often were captured. The 1977 year class predominated initially in this period but virtually disappeared at age I after the 1978 year class recruited. Three year classes usually were captured after the 1979 year class recruited in May. In contrast to the virtual disappearance of the 1977 year class, the 1978 year class remained abundant at age I after the new year class recruited. As a result, two year classes (1978 and 1979) were equally predominant from May 1979 through March 1980. Four year classes were present after the 1980 year class recruited in February, but only the 1978 and 1979 year classes predominated.

Minor qualifications should be noted to the designation of the 1977 year class. The group identified as the 1977 year class in the period December 1977-April 1978 may contain members of the 1976 year class. This is suggested because 1) the size range of fish in that period may be too broad for one year class; 2) apparent

[9]Hamer, P. 1979. Studies of the scup, *Stenotomus chrysops*, in the Mid-Atlantic Bight. N.J. Div. Fish, Game, Shellfish., Necote Creek Res. Stn., Misc. Rep. 18m, 66 p.

growth between October and December 1977 is high when compared with the same period in other years; and 3) size at age I is comparatively large for the 1977 year class. The 1977 and 1978 year classes were difficult to distinguish after December 1978, so that the 1977 year class thereafter may include fast growing members of the 1978 year class.

Stenotomus caprinus growth varied between year classes, but sizes averaged 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. Observed mean sizes at age I, based on pooled data from February and March (Table 2), were 134.2 mm TL for the 1977 year class (range 113-157 mm), 120.8 mm for the 1978 year class (range 96-145 mm), and 107.5 mm for the 1979 year class (range 91-119 mm). These sizes at age I agree with regression predictions (Fig. 5) of 114.8 mm TL for the 1978 year class and 110.0 mm for the 1979 year class. Observed mean size at age II was 132.5 mm TL for the 1978 year class (range 116-155) (Table 2), which closely agrees with a regression prediction of 128.6 mm (Fig. 5). The few survivors of the 1977 year class averaged 155.8 mm TL (range 146-182) at age II and 160.8 mm at age III (range 154-175 mm) (Table 2). Many fish approached the maxima in the size ranges at age cited for each year class, and the ranges at age appeared constant between collections indicating uniform growth (Table 2).

Possible error in assigned hatching dates would have little effect on our estimates for mean sizes at age because 99% confidence intervals of observations were constant within the following periods (Table 2): December 1977-April 1978 for the 1977 year class; December 1978-June 1979 for the 1978 year class; and December 1979-March 1980 for the 1979 year class.

Stenotomus caprinus grow rapidly in their first 8 mo, but growth slows greatly as they mature and appears negligible after maturity. The 1978 and 1979 year classes showed a rapid, almost linear decline in monthly growth increments during their first 8 mo (Fig. 3). Growth of the 1978 year class averaged 13.62 mm TL/30 d from 15 February through early October 1978, and the 1979 year class averaged 12.66 mm/30 d from 15 March to early November 1979, ignoring the regression effect. In contrast, the 1978 year class grew only 13 mm TL in its second year; and the 1977 year class grew only 23 mm in its second year and 4 mm in its third year. This growth pattern may result in gradual merging of year class size compositions after age I as indicated by the 1978 and 1979 year classes (Fig. 2). The small amount of growth after maturity seems to occur primarily during the late spring-early fall interim between reproductive activities (Fig. 3). Very little growth occurred in the January-April spawning period when the 1978 year class averaged 0.83 mm TL/30 d in that period in 1979 and 0.80 mm/30 d in 1980.

Size at age I varies between *S. caprinus* year classes, but growth is not obviously density dependent. No simple relationship was apparent for the 1977-79 year classes (Fig. 10) between mean size at age I and their index of year class strength, calculated as $\Sigma c_i / \Sigma f_i$ where Σf_i is the total number of tows and Σc_i is the total catch at age I for each year class at depths of 27-47 m. Fish of the weak 1979 year class averaged smaller at age I (107.5 mm TL) than the strong 1978 year class (120.8 mm), a pattern not consistent with density dependent growth. Growth of the 1979 year class might have been depressed by interaction with the strong 1978 year class, but no density dependent relationship was apparent even when a pooled index of population strength was substituted for the 1979 year class strength index.

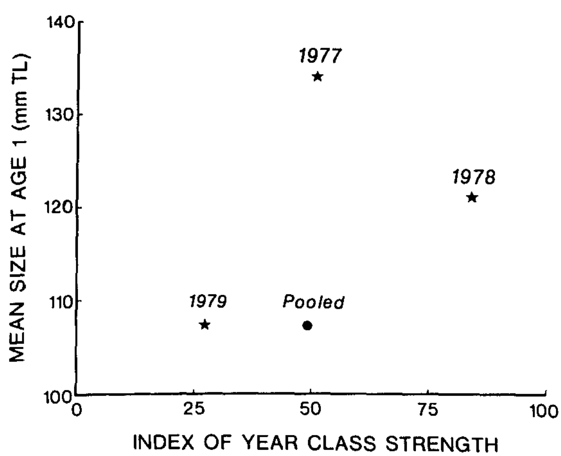


FIGURE 10.—Relationship between mean sizes at age I and year class strength for *Stenotomus caprinus* off Freeport, Tex. Indices of individual year class strength are indicated by stars and the pooled index by solid circle.

Discussion

Our findings on growth are largely new because the growth of *S. caprinus* has not been described previously. Sizes at age I agree with Chittenden and McEachran's (1976) suggestion that *S. caprinus* reaches 90-123 mm TL at age I. Back-calculated lengths of *S. chrysops* are 120-155 mm TL at age I and 182-213 mm at age II (Finkelstein 1969a; Hamer footnote 9). Sizes at age I appear to be similar in these species, but *S. chrysops* is much larger at age II. Our growth data and the constant size noted in later gonad maturity stages (Fig. 6) indicate that *S. caprinus* markedly diverts energy from somatic growth to gonadal development as it matures. The different sizes of these congeners at age II probably reflect this drastic diversion of energy in *S. caprinus*.

MAXIMUM SIZE AND LIFESPAN

Results

The maximum size typically reached by *S. caprinus* is about 200 mm TL. The largest fish collected off Texas ($n = 22{,}924$) was 182 mm TL, and the largest specimen collected in the north central Gulf ($n = 1{,}576$) aboard the *Oregon II* was 193 mm TL.

The maximum lifespan of *S. caprinus* typically appears to be 2.5-3 yr. In the period October 1977-March 1980, 99% of the specimens captured off Texas were <146 mm TL, and 99.5% were <149 mm (Fig. 11). Many age II fish captured off Texas were as large as 155 mm TL. The largest fish collected was age II when captured in March 1979, or age III if it was a member of the poorly defined 1976 year class (Fig. 2). These data indicate that a value of $t_L = 2.5$-3 yr is reasonable for this Beverton-Holt model parameter (Gulland 1969). This estimate is supported by data from the north central Gulf (Fig. 7) in which 99% of the fish were <172 mm TL and 99.5% were <176 mm. Fish of these sizes were age II or III in the north central Gulf (Fig. 7).

Discussion

The maximum sizes reported herein are slightly larger than the maximum size reported by Hildebrand (1954), Caldwell (1955), and Chittenden and McEachran (1976). The only published record of *S. caprinus* much larger than 200 mm TL is that of Franks et al. (1972) who captured a specimen 256 mm TL in the north central Gulf. The apparent larger size of individuals at given percentages of the catch in the north central Gulf might reflect growth differences between areas, or the nonrandom subsampling from the *Oregon II* catch which would probably select larger fish. Values of t_L would vary from year to year due to variation in postspawning survival noted later.

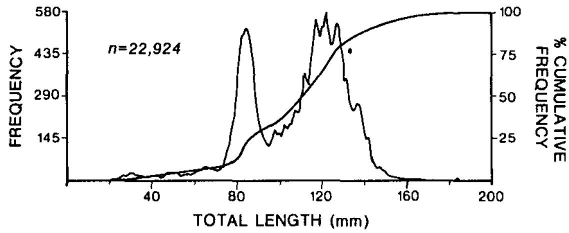


FIGURE 11.—Length frequency (moving averages of three) and cumulative percent frequency of all *Stenotomus caprinus* collected off Freeport, Tex., October 1977-March 1980.

MORTALITY AND POSTSPAWNING SURVIVAL

Results

Stenotomus caprinus has a total annual mortality rate of about 83-99% on a time-specific basis. Time-specific total annual mortality rates $(1 - S)$ were calculated from the expression $S = N_t/N_0$ where S = rate of survival, and N_t and N_0 are the numbers of fish collected at age each cruise in depths of 18-100 m. The pooled estimate, using Heincke's procedure (Ricker 1975) was 98.95% comparing the 1977 and 1978 year classes and individual rates generally exceeded 98%. These values probably overestimate $1 - S$, because the 1978 year class was stronger than the 1977 year class (Fig. 10). The pooled estimate comparing the apparent 1976 and 1977 year classes was 99.79%. The pooled estimate comparing the 1978 and 1979 year classes was 84.94% which may be fortuitous because it included one data set (October 1979) for which an exceptionally large number of fish from the 1979 year class were captured. A minimum pooled mortality estimate for the 1978 and 1979 year classes is 40.73%, if the exceptional October 1979 data set is excluded. This is probably a large underestimate because the 1979 year class was so much weaker than the 1978 year class. Realistic estimates could not be calculated in most instances comparing the 1978 and 1979 year classes because N_t exceeded N_0, which largely reflects the much greater strength of the 1978 year class (Fig. 10). Time-specific mortality estimates made from Chittenden and McEachran's (1976) raw data were 99% for late September 1973 ($S = 5/435$) and 83% for January 1974 ($S = 395/2{,}468$). Pooled cohort-specific estimates of $1 - S$ were 99.23% for the 1977 year class and 83.36% for the 1978 year class using Heincke's procedure. The different mortality rates for these year classes are consistent with theoretical mortality rates given later, and the greater postspawning survival of the 1978 year class.

Postspawning survival of *S. caprinus*, total annual mortality rates, and maximum lifespan varies greatly between years and year classes. The 1977 and apparently 1976 year classes rarely appeared after they spawned at age I (Fig. 2). In contrast, many members of the 1978 year class survived after spawning at age I and spawned again at age II. White and Chittenden (1977) suggested somatic weight variation as a factor in the survival of the Atlantic croaker, *Micropogonias undulatus*. Somatic weight of female *S. caprinus* did not change in a regular monthly pattern, and regression elevations differed widely in consecutive months (Fig. 12, Table 4).

Discussion

Both time-specific and cohort-specific estimates indicate that the total annual mortality rate of *S. caprinus* is about 83-99%, depending on postspawning survival. Lower values in this range agree with theory (Royce 1972:238) that total annual mortality is 78-84% if the maximum age is 2.5-3 yr as observed. Higher values are consistent with theoretical annual rates of 90-100% given the 1-2 yr lifespan observed for some year classes.

Variation in postspawning survival might not be due to somatic weight changes because of the lack of a regular monthly pattern and the wide variation in regression elevations between adjacent months, although our somatic weight regressions are based primarily on the 1978 and 1979 year classes which did not disappear after spawning.

TOTAL WEIGHT-TOTAL LENGTH, GIRTH-TOTAL LENGTH, AND LENGTH-LENGTH RELATIONSHIPS

Regression and related analyses for total weight-total length, girth-total length, and length-length relationships are presented in Table 5.

TABLE 4.—Analyses for the monthly regressions of somatic weight (Y) in grams on total length (X) in millimeters for female *Stenotomus caprinus*, October 1978-March 1980. All regressions were significant at $\alpha = 0.05$.

Collection date	n	100 r^2	Equation
11 Oct. 1978	53	86.01	$Y = -50.789 + 0.699\,X$
1 Dec. 1978	144	87.44	$Y = 71.240 - 1.323\,X + 0.008\,X^2$
24 Feb. 1979	41	78.88	$Y = -32.009 + 0.506\,X$
12 Mar. 1979	168	94.57	$Y = 73.409 - 1.361\,X + 0.008\,X^2$
5 Apr. 1979	109	97.15	$Y = 59.722 - 1.234\,X + 0.008\,X^2$
20 Apr. 1979	84	80.36	$Y = 234.333 - 4.095\,X - 0.020\,X^2$
14 May 1979	110	84.32	$Y = 68.022 - 1.327\,X + 0.008\,X^2$
6 June 1979	56	92.71	$Y = -69.449 + 0.843\,X$
21 June 1979	49	70.44	$Y = -34.932 + 0.539\,X$
5 July 1979	24	91.41	$Y = 137.564 - 2.44\,X + 0.013\,X^2$
19 July 1979	20	60.11	$Y = -48.541 + 0.663\,X$
22 Aug. 1979	70	80.01	$Y = 186.455 - 3.150\,X + 0.015\,X^2$
22 Sept. 1979	82	68.32	$Y = -38.548 + 0.584\,X$
2 Oct. 1979	79	95.62	$Y = 71.630 + 1.233\,X + 0.007\,X^2$
16 Oct. 1979	53	88.69	$Y = -44.643 + 0.631\,X$
3 Nov. 1979	89	93.90	$Y = -37.481 + 0.578\,X$
15 Nov. 1979	65	95.70	$Y = 4.819 - 0.237\,X + 0.004\,X^2$
1 Dec. 1979	37	68.44	$Y = -30.428 + 0.508\,X$
14 Dec. 1979	82	96.32	$Y = -43.178 + 0.609\,X$
3 Jan. 1980	96	95.34	$Y = 35.286 - 0.762\,X + 0.006\,X^2$
16 Jan. 1980	86	97.36	$Y = 35.576 - 0.795\,X + 0.006\,X^2$
4 Feb. 1980	93	97.57	$Y = 20.722 - 0.526\,X + 0.005\,X^2$
15 Feb. 1980	79	96.23	$Y = 20.382 - 0.506\,X + 0.005\,X^2$
5 Mar. 1980	80	83.65	$Y = -38.256 + 0.565\,X$
19 Mar. 1980	64	79.38	$Y = -49.710 + 0.662\,X$

Total length-total weight regressions for adult males and females were not significantly different in slope ($F = 0.029$, df $= 1{,}657$, $\alpha = 0.05$) or in adjusted means ($F = 1.63$, df $= 1{,}658$, $\alpha = 0.05$) so that one pooled regression equation was presented for them. Calculated slopes varied significantly from $\beta = 3.0$ ($t = 13.2$, df $= 1{,}682$, $\alpha = 0.05$) except when data for immatures, males, and females were pooled ($t = 0.197$, df $= 2{,}792$, $\alpha = 0.05$).

GENERAL DISCUSSION

Stenotomus caprinus, which inhabits the warm temperate Gulf, exhibits markedly different population dynamics from *Stenotomus chrysops*, which primarily inhabits the cold temperate Atlantic north of Cape Hatteras, N.C. Our data and the literature agree that for *S. caprinus*: 1) spawning occurs in one discrete period a year with peak spawning in February or March; 2) all individuals reach maturity and spawn at 90-125 mm TL as they approach age I; 3) maximum size typically is about 200 mm TL, but most fish are much smaller; 4) maximum lifespan is 2.5-3 yr; 5) total annual mortality rate is 83-99%, but postspawning survival, total annual mortality rates, and lifespan vary between year classes; and 6) average sizes are 110-135 mm TL at age I, 130-155 mm at age II, and 160 mm at age III. In contrast, *S. chrysops* north of Cape Hatteras 1)

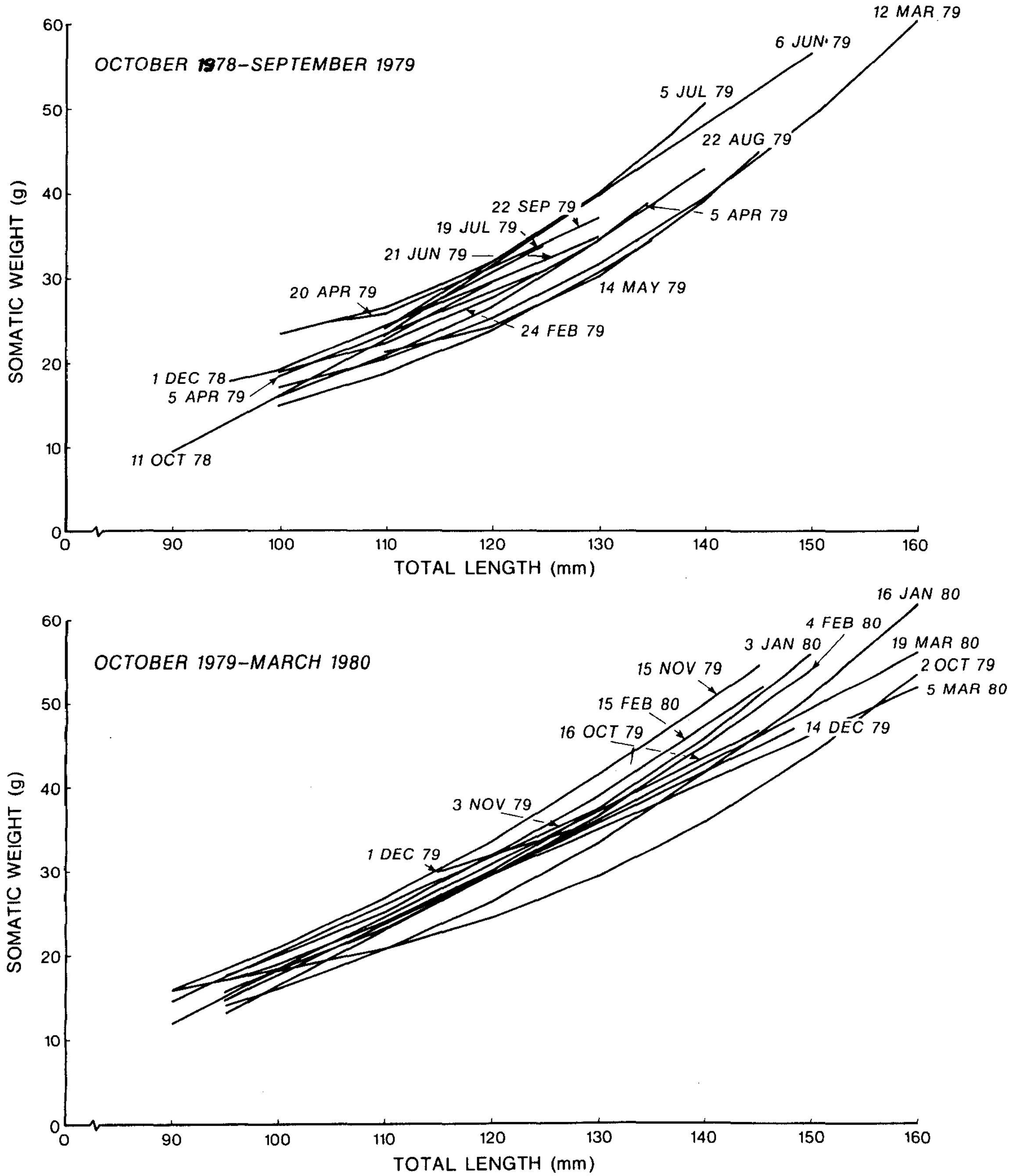


FIGURE 12.—Monthly somatic weight-total length regressions for *Stenotomus caprinus*. The length of each line shows the observed size range.

spawns in the period May-August with peak spawning in June (Bigelow and Schroeder 1953; Finkelstein 1969a); 2) reaches maturity at age II at 182-213 mm TL (Finkelstein 1969a, b; Hamer footnote 9); 3) reaches a maximum size of approximately 480 mm TL (Hamer footnote 9); 4) has a maximum lifespan of 15 yr (Finkelstein 1969a); 5) apparently has a much lower total an-

TABLE 5.—Analyses of total length-total weight (A), length-length (B), and total length-girth (B) relationships for *Stenotomus caprinus*. Lengths and girths are in millimeters and weights are in grams. All regressions were significant at $\alpha = 0.05$. See Methods and Materials for symbols.

Relation	Equation	n	$100\ r^2$	Residual mean square	Corrected total SS for both variables	Means of variables	Observed TL range (not transformed)
A. All fish	$\text{Log}_{10}\text{TW} = -4.85 + 3.05\ \text{Log}_{10}\text{TL}$	2,793	99.32	0.0017	Log TW = 705.12 Log TL = 75.17	Log TW = 1.28 Log TL = 2.01	21-182
Adult fish	$\text{Log}_{10}\text{TW} = -4.13 + 2.71\ \text{Log}_{10}\text{TL}$	1,683	90.51	0.0010	Log TW = 18.27 Log TL = 2.25	Log TW = 1.50 Log TL = 2.08	91-182

Relation	Equation	n	$100\ r^2$	Residual mean square	Corrected total SS for dependent variable	Mean of dependent variable	Observed range for dependent variable (not transformed)
B. SL-TL	SL = 0.41 + 0.76 TL	2,776	99.26	3.55	1,326,361.42	81.88	21-182
TL-SL	TL = 0.26 + 1.31 SL	2,776	99.26	6.10	2,280,443.91	116.86	21-182
SL-FL	SL = 0.85 + 0.11 FL	2,421	97.12	4.01	337,068.73	81.88	26-182
FL-SL	FL = 2.90 + 1.14 SL	2,421	97.12	5.40	453,813.15	104.88	26-182
FL-TL	FL = 1.99 + 0.88 TL	2,402	97.36	4.98	452,549.20	104.88	26-182
TL-FL	TL = 0.93 + 1.11 FL	2,402	97.36	6.24	567,821.45	116.86	26-182
TL-G	TL = 8.27 + 0.94 G	2,792	98.00	16.32	2,286,249.29	107.26	21-182
G-TL	G = −6.54 + 1.04 TL	2,792	98.00	18.17	2,545,019.98	105.50	21-182

nual mortality rate, theoretically 26% based on a 15-yr lifespan (Royce 1972:238); and 6) averages 120-155 mm TL at age I, 183-213 mm at age II, and 232-257 mm at age III (Finkelstein 1969a; Hamer footnote 9).

The basic pattern of population dynamics characteristics enumerated for *S. caprinus* is similar to that reported from the Gulf for *Micropogonias undulatus* (White and Chittenden 1977), *Cynoscion nothus* (DeVries and Chittenden 1982), *C. arenarius* (Shlossman and Chittenden 1981), and *Peprilus burti* (Murphy 1981). These findings give additional support to the suggestions (Chittenden and McEachran 1976; Chittenden 1977) that the abundant species of the white and brown shrimp communities in the Gulf have evolved a common pattern of population dynamics that stresses small size, short lifespan, high mortality rates, and rapid turnover of biomass, especially when compared with congeners or conspecifics north of Cape Hatteras.

The intrageneric variation in *Stenotomus* supports the suggestion of White and Chittenden (1977) that zoogeographic variation in life histories and population dynamics occurs at Cape Hatteras. Unfortunately, the meager information published from the Atlantic coast south of Cape Hatteras does not permit enumeration of population dynamics of *Stenotomus* from that area. However, our findings on *Stenotomus* are consistent with the intrageneric variation in population dynamics within the genus *Cynoscion* at Cape Hatteras (Shlossman and Chittenden 1981), and are similar to the zoogeographic variation reported for *M. undulatus* (White and Chittenden 1977). This zoogeographic variation in population dynamics characteristics has important management implications, because Carolinean Province fish should be less sensitive to growth overfishing than their congeners or conspecifics north of Cape Hatteras.

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