REPRODUCTION, MOVEMENTS, AND POPULATION DYNAMICS OF THE BANDED DRUM, *LARIMUS FASCIATUS*, IN THE GULF OF MEXICO[1, 2]

GARY W. STANDARD[3] AND MARK E. CHITTENDEN, JR.[4]

ABSTRACT

Collections of banded drum, *Larimus fasciatus*, were made from 5 to 100 m in the Gulf of Mexico along a cross-shelf transect off Texas during the period October 1977-August 1981. *Larimus fasciatus* mature at 80-130 mm as they approach age I. Spawning occurs during two discrete periods, a major fall period (September-November) and a very minor spring period (April-June), coincident with downcoast along-shore currents (toward Mexico) and onshore surface Ekman transport. Fish first spawning at 12-14 months old produce the predominant fall-spawned groups. Fall-spawned fish spawning at 19-21 months old produce the minor spring-spawned groups, so that temporal reproductive isolation does not exist between spring and fall cohorts. *Larimus fasciatus* in the northwestern Gulf range from <5 to 55 m but are most abundant at 5-16 m. Adults occupy the 13-24 m bathymetric range, while the young recruit in waters of <5-16 m when 2-4 months old. Larger, older, spawning or postspawning individuals may undergo more or less permanent emigration from the northwestern Gulf to the north central area as they approach age I. Apparent mean sizes of fall-spawned fish were 130-150 mm at age I and 155-180 mm at or approaching age II. Von Bertalanffy parameters for fall-spawned fish were 201 and 176 mm for L_∞ and 1.15 and 1.34 for K (annual), respectively. Maximum size is about 180 mm in the northwestern Gulf, but more typically only 160-165 mm. Typical maximum life span (t_L) in the northwestern Gulf is only 1-2 years but may be 2-3 years if the the stock ranges in both the northwestern and north central Gulf. Apparent mean time-specific and cohort-specific total annual mortality rates are 92-100% in the northwestern Gulf but true values probably are 80-90% for a stock that ranges in both the northwestern and north central Gulf. Fecundity, weight, girth, and length relationships are presented.

The banded drum, *Larimus fasciatus*, is a common demersal fish that ranges along the Altantic coast of the United States from Chesapeake Bay to southern Florida and in the Gulf of Mexico (Gulf) from the west coast of Florida to Campeche Bay (Hildebrand and Schroeder 1928; Hildebrand 1954; Briggs 1958). It primarily occurs in near-shore marine waters (Hildebrand and Cable 1934; Powles 1980) and only occasionally enters the lower reaches of estuaries (Gunter 1938; Swingle 1971; Dahlberg 1972). In the northern Gulf this species is most abundant off Louisiana (Gunter 1945; Behre 1950; Hildebrand 1954).

The life history of *L. fasciatus* is poorly known despite its common occurrence. No detailed study describes its life history in the Gulf, although Ross

(1978) did so for North Carolina. Life history notes appear in Hildebrand and Cable (1934), Miller and Jorgenson (1969), Christmas and Waller (1973), Chao and Musick (1977), Johnson (1978), and Powles (1980).

This paper describes maturation, spawning periodicity, bathymetric distribution, recruitment, movements, age determination and growth using length frequencies, maximum size, life span, mortality, sex ratios, fecundity, and length-weight, length-girth, and standard-total length relationships of *L. fasciatus* in the northwestern Gulf.

METHODS

Larimus fasciatus were collected in 71 monthly or twice monthly cruises from October 1977 through August 1981 along a transect in the Gulf off Freeport, Tex., (Fig. 1) aboard a chartered shrimp trawler using twin 10.4 m (34-ft) trawls with a 4.4 cm stretched mesh cod end and a tickler chain. Initial stations usually were located at depths of 9, 13, 16, 18, 22, 27, 36, and 47 m. Sampling was expanded to include stations at 5 and 24
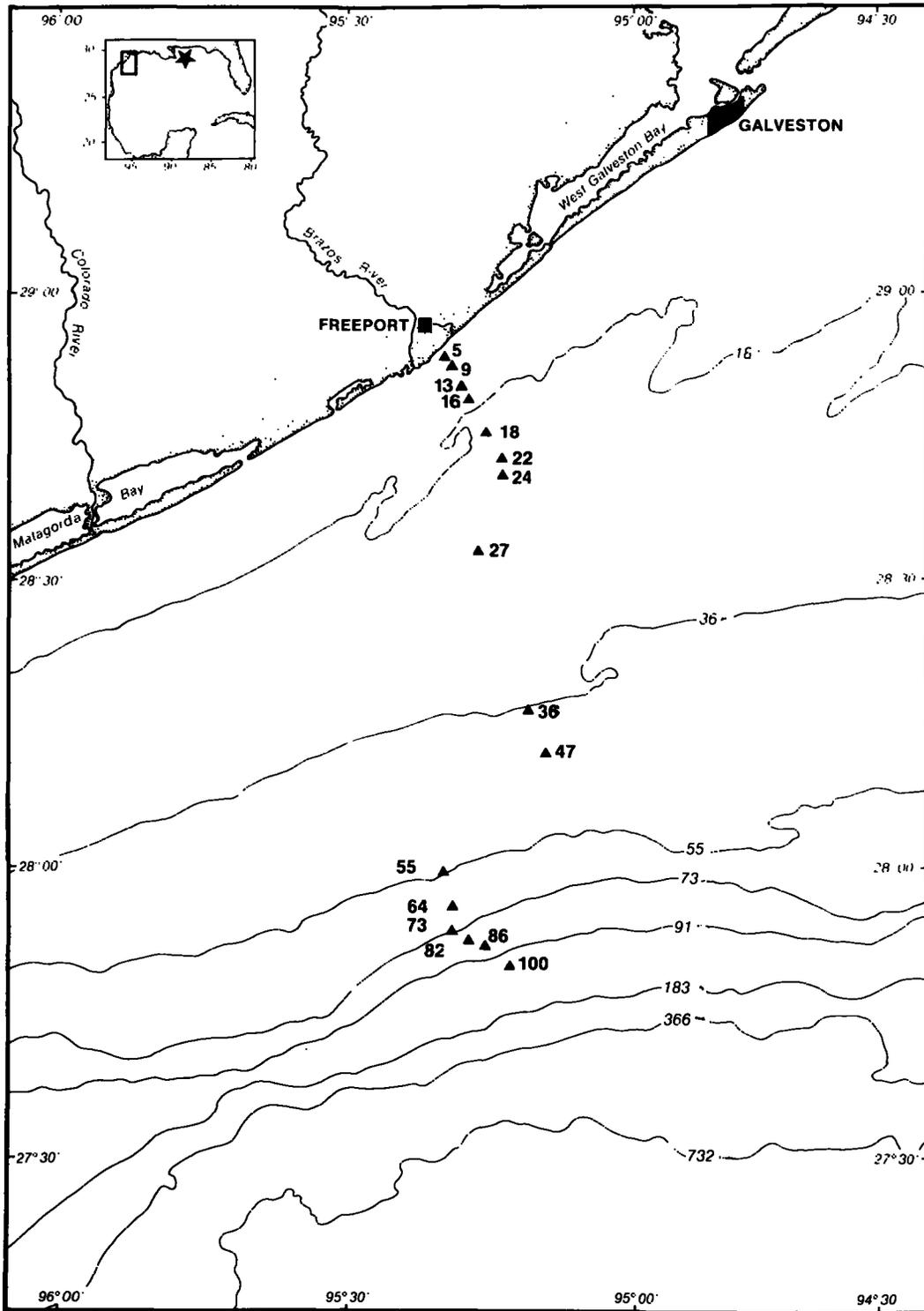
FIGURE 1.—Location of sampling area off Freeport, Tex. Station depths and bathymetric contours are indicated in meters. Starred area in insert indicates where collections were made in the north central Gulf.

m after November 1978 and at 55, 64, 73, 82, 86, and 100 m after May 1979. Collections were made during the day through September 1978; thereafter, a day and a night cruise usually were made each month. Two 10-min tows (bottom time) were made at each depth except that 1 tow was made at most depths prior to October 1978, usually 8 tows were made at 16 m, and usually 24 tows were made at 22 m.

All *L. fasciatus* were culled from the catch, measured to the nearest millimeter total length, fixed in 10% Formalin[5], and later preserved in 70% ethanol. For the period October 1979-April 1981, if available, 300 fish each month were selected for intensive processing using stratified random sampling in which a stratum included an individual spawned group (Standard 1983: app. 1). The following data were taken on the first 200 fish selected: total length (TL), standard length (SL), girth at origin of dorsal fin (G), total weight (TW), gonad weight (GW), sex, and ovary maturity stage. Only sex and ovary maturity stage were recorded for the remaining 100 fish. Maturity stages (Table 1) were assigned to immature and female fish using a slight modification of Kesteven's system (Bagenal and Braum 1971). Gonadosomatic indices (GSI) were calculated for individual females as GSI = 100 GW/TW.

Supplemental collections were made in the north central Gulf from 24 October to 5 November 1982 aboard the FRS *Oregon II* (NMFS) using standard 12.2 m (40-ft) 4-seam semiballoon shrimp trawls at depths of 9-91 m between long. 88°00' and 89°00'W and at depths of 347-549 m between long. 87°50' and 88°00'W (Rohr et al.[6]). Total length was measured on all *L. fasciatus* cap-

TABLE 1.—Description of gonad maturity stages assigned to *Larimus fasciatus*.

Stage and name	Description
1 Immature	Gonads barely or not visible, sexes indistinguishable to the naked eye.
2 Maturing Virgin	Ovaries small, thin, confined to posteriodorsal wall of body cavity.
3 Early Developing	Ovaries solid, opaque, occupy <30% of body cavity. Individual eggs not visible to naked eye.
4 Late Developing	Ovaries occupy >30% of body cavity. Individual eggs opaque, distinguishable to naked eye by close examination.
5 Gravid	Ovaries occupy >50% of body cavity. Individual eggs distinct, <50% translucent.
6 Ripe	Ovaries completely fill body cavity, >50% of the eggs translucent.
7 Spawning/Spent	Ovaries flaccid, remaining eggs translucent.
8 Resting	Ovaries firm, occupy <30% of body cavity, translucent eggs may persist. Fish large enough to have spawned.

tured to compare with size compositions from the northwestern Gulf.

Age in years was determined by length-frequency analysis, e.g., the Petersen Method (Lagler 1956). Spawned groups (intrayear class cohorts) were specified by the season and year when they hatched, e.g., fall 1980. Descriptions of spawning periodicity (beginnings and ends) using length frequencies assume the following size and age combinations predicted from quadratic regression of total length on age, years pooled, noted below: 15 mm TL at 1 mo, 30 mm at 2 mo, and 45 mm at 3 mo. The same combinations were predicted from regressions for individual fall-spawned groups.

Duration of the spawning period was approximated for fall-spawned groups following Geoghegan and Chittenden (1982) as

$$\frac{\text{Time-specific mean size range early in life}}{\text{Mean growth/day early in life}}.$$

Calculations were based on April-June data, the first months when fall groups appeared fully recruited. Time-specific size range was estimated for each fall group as the mean of the 99% confidence intervals for observations in April-June (Table 2). Growth per day was estimated as the mean of the growth per day values between successive collections in the April-June period (Table 2). This procedure assumes large fish hatch before small ones and that all grow at the same rate (Geoghegan and Chittenden 1982). The latter assumption appears valid because 99% confidence intervals for observations (Table 3) were fairly constant within cruises in the April-June period when sample sizes were large.

Hatching dates used to set time scales to calculate growth of fall-spawned fish were determined by a one-step iteration process. A hatching date of 1 October was assigned to start the process because 1) fish 20-40 mm TL, which we assumed were 1-3 mo old, first appear in November-December, and 2) slopes for regressions of ovary weight on total length (Fig. 2) and mean GSI (Fig. 3) were greatest in September-October. Quadratic regressions of total length on age in days were then used as a simple model to estimate initial *x*-intercepts for each fall-spawned group. Final hatching dates

TABLE 2.—Calculations (see Methods) to estimate duration of fall spawning periods of *Larimus fasciatus* during 1977, 1978, 1979, and 1980. Collection dates, sample sizes, means, and 99% confidence limits for observations were obtained from Table 3.

Group and collection date	n	Mean total length	99% confidence limits of observations	Growth increment between first and last date	Time (days)	Growth/Day (mm)
1977 fall-spawned group						
14 Apr. 1978	5	69.0	33.9-104.0	18.5	24	0.77
8 May 1978	37	87.5	63.9-111.1			
Means			58.65 (interval)	18.5	24	0.77
Spawning period = 58.65/0.77 = 76 d						
1978 fall-spawned group						
5 Apr. 1979	197	67.6	39.3-95.9	11.1	15	0.74
20 Apr. 1979	328	78.7	50.6-106.8	16.1	24	0.67
14 May 1979	490	94.8	68.0-121.6	20.5	23	0.89
6 June 1979	65	115.3	85.3-145.3	7.1	15	0.47
21 June 1979	151	122.4	104.0-140.8			
Means			52.64 (interval)	13.7	19	0.69
Spawning period = 52.64/0.69 = 76 d						
1979 fall-spawned group						
1 Apr. 1980	746	72.6	49.3-95.9	7.0	15	0.47
16 Apr. 1980	437	79.6	53.1-106.0	0.1	19	0.01
5 May 1980	1,202	79.7	55.2-104.2	9.1	14	0.65
19 May 1980	239	88.8	59.8-117.8	15.0	14	1.07
2 June 1980	614	103.8	81.3-126.3	12.1	17	0.71
19 June 1980	254	115.9	90.2-141.6			
Means			50.48 (interval)	8.7	16	0.58
Spawning period = 50.48/0.58 = 87 d						
1980 fall-spawned group						
7 Apr. 1981	110	60.0	33.1-86.9	14.2	13	1.09
20 Apr. 1981	69	74.2	45.7-102.7	6.2	14	0.44
4 May 1981	97	80.4	57.0-103.8	9.3	15	0.62
19 May 1981	165	89.7	68.8-110.6	12.8	14	0.91
2 June 1981	128	102.5	77.9-127.1	9.3	13	0.72
15 June 1981	174	111.8	90.4-133.2			
Means			48.57 (interval)	10.4	14	0.76
Spawning period = 48.57/0.76 = 64 d						

TABLE 3.—Growth data (mm TL) by spawned group for *Larimus fasciatus* from the Gulf off Freeport, Tex. Night and day cruises are indicated by night (N) and day (D). Observed size ranges delineate spawned group boundaries used in growth and mortality calculations and indicated in Figure 6. Collection dates with asterisks indicate collections pooled to estimate mean size at age.

Group and 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)
1976 fall-spawned group							
1 Oct. 1977 D*	9	120-143	133.6	46.5	128.4-138.8	110.7-156.5	+ 4.9
3 Dec. 1977 D	2	136-141	138.5	12.5	106.7-170.3	-86.6-363.6	
1977 fall-spawned group							
21 Mar. 1978 D	10	47-97	62.3	261.3	50.7-73.9	9.8-114.8	+ 6.7
14 Apr. 1978 D	5	62-78	69.0	58.0	59.5-78.5	33.9-104.0	+18.5
8 May 1978 D	37	70-104	87.5	75.0	84.6-90.4	63.9-111.1	+40.0
15 July 1978 D	286	113-141	127.5	26.5	126.9-128.1	114.2-140.8	+20.5
15 Sept. 1978 D*	8	145-152	148.0	8.6	145.5-150.5	137.7-158.3	+ 1.2
1 Dec. 1978 N	14	141-162	149.2	33.3	145.9-152.5	131.8-166.6	+ 5.8
13 Dec. 1978 D	1	155	155.0	—	—	—	+ 1.0
6 June 1979 N	1	156	156.0	—	—	—	+18.0
21 June 1979 D	1	174	174.0	—	—	—	
1978 fall-spawned group							
1 Dec. 1978 N	98	34-99	64.3	220.7	61.3-67.3	25.3-103.3	+ 9.5
13 Dec. 1978 D	51	34-98	73.8	266.6	69.2-78.4	30.1-117.5	- 7.5
24 Feb. 1979 D	19	40-97	66.3	343.8	57.4-75.2	12.9-119.7	+ 1.3
5 Apr. 1979 N	197	45-98	67.6	120.3	66.1-69.1	39.3-95.9	+11.1
20 Apr. 1979 D	328	51-115	78.7	118.7	77.5-79.9	50.6-106.8	+16.1
14 May 1979 N	490	68-134	94.8	108.0	93.9-95.7	68.0-121.6	+20.5
6 June 1979 N	65	78-130	115.3	128.1	112.5-118.1	85.3-145.3	+ 7.1
21 June 1979 D	151	95-140	122.4	51.3	121.3-123.5	104.0-140.8	- 1.4
5 July 1979 N	3	115-131	121.0	76.0	99.3-142.7	34.5-207.5	+ 2.5
19 July 1979 D	83	111-138	123.5	42.7	122.1-124.9	106.3-140.7	+15.6
22 Aug. 1979 D	83	111-155	139.1	54.5	137.5-140.7	119.6-158.6	+ 5.7
22 Sept. 1979 D*	23	132-164	144.8	38.8	142.1-147.5	127.2-162.4	+ 0.8
2 Oct. 1979 N*	59	133-156	145.6	29.8	144.2-147.0	131.1-160.1	- 1.5
16 Oct. 1979 D*	198	127-164	144.1	34.6	143.3-144.9	128.9-159.3	+ 2.0
3 Nov. 1979 N	9	138-158	146.1	43.4	141.0-151.2	124.0-168.2	+ 2.8
15 Nov. 1979 D	7	144-155	148.9	13.8	145.5-152.3	135.1-162.7	+ 2.8

TABLE 3.—*Continued*

| Group and collection date	n	Observed size range (mm)	Mean length (mm)	s²	95% confidence limits of the mean	99% confidence limits of observations	Unadjusted growth increment (mm)
1 Dec. 1979 N	3	148-155	151.7	12.3	143.0-160.4	116.9-186.5	
							+11.3
14 Dec. 1979 D	1	163	163.0	—	—	—	
							− 6.0
3 Jan. 1980 N	1	157	157.0	—	—	—	
							−11.0
4 Feb. 1980 N	1	146	146 0	—	—	—	
							+ 4.0
5 Mar. 1980 N	1	150	150.0	—	—	—	
							+ 1.8
19 Mar. 1980 D	45	135-163	151.8	29.8	150.2-153.4	137.1-166.5	
							− 1.3
16 Apr. 1980 D	8	132-166	150.5	91.4	142.5-158.5	117.0-184.0	
							+21.0
19 May 1980 D	2	161-182	171.5	220.5	38.1-304.9	−773.8-1,116.8	
							−13.0
2 June 1980 N	22	146-174	158.5	37.4	155.8-161.2	141.2-175.8	
							− 1.3
19 June 1980 D	26	147-180	157 2	50.8	154.3-160.1	137.3-177.1	
							+ 2.0
7 July 1980 N	45	150-172	159.2	26.1	157.7-160.7	145.4-173.0	
							+ 4 1
5 Aug. 1980 N*	11	156-175	163.3	31.6	159.5-167 1	145 5-181 1	
							+13.7
7 Sept. 1980 N*	1	177	177.0	—	—	—	
1979 fall-spawned group							
3 Nov. 1979 N	4	21-41	32.5	70.3	19.2-45.8	−16.5-81.5	
							+ 8.0
15 Nov. 1979 D	2	36-45	40.5	40.5	−16.7-97.7	−364.6-445.6	
							+14.8
1 Dec. 1979 N	24	33-87	55.3	269.6	48.4-62.2	9.2-101.4	
							− 4.5
14 Dec. 1979 D	74	29-88	50.8	146.4	48.0-53.6	18.8-82.8	
							+ 5.8
3 Jan. 1980 N	39	34-110	56.6	313.2	50.9-62.3	8.7-104.5	
							− 2.5
16 Jan. 1980 D	246	31-124	54.1	108.8	52.8-55.4	27.2-81.0	
							+ 4.0
4 Feb. 1980 N	581	33-109	58.1	99.2	57.3-58.9	32.4-83.8	
							+ 2.0
15 Feb. 1980 D	1723	30-97	60.1	77 3	59.7-60.5	37.5-82.7	
							+ 0.9
5 Mar. 1980 N	507	39-95	61.0	80.5	60.2-61 8	37 9-84.1	
							+10.9
19 Mar. 1980 D	217	47-121	71 9	103.5	70.5-73.3	45.7-98.1	
							+ 0 7
1 Apr 1980 N	746	45-115	72.6	81.7	72 0-73.2	49.3-95.9	
							+ 7.0
16 Apr 1980 D	437	44-108	79.6	105.1	78.6 80.6	53.1-106.0	
							+ 0.1
5 May 1980 N	1202	54-114	79.7	90.5	79.2-80.2	55.2-104.2	
							+ 9.1
19 May 1980 D	239	59-116	88.8	127 1	87.4-90.2	59.8-117 8	
							+15.0
2 June 1980 N	614	72-139	103.8	76.5	103.1-104.5	81.3-126.3	
							+12.1
19 June 1980 D	254	86-139	115.9	99.6	114.7-117.1	90.2-141 6	
							+ 4.6
7 July 1980 N	750	90-149	120.5	84 2	119.8-121.2	96.9-144.1	
							+ 3.8
21 July 1980 D	142	104-153	124.3	84.6	122.8-125.8	100.6-148.0	
							+ 6.6
5 Aug 1980 N	794	102-155	130.9	73.0	130.3-131.5	108.9-152.9	
							+26.1
26 Aug. 1980 D	1	157	157.0	—	—	—	
							−11.0
7 Sept. 1980 N*	116	123-158	146.0	42.1	144.8-147.2	129.0-163.0	
							+ 5.7
22 Sept. 1980 D*	12	143-162	151.7	39.2	147.7-155.6	132.3-171.1	
							− 3.0
6 Oct 1980 N*	82	137-168	148.7	36.7	147.4-150.0	132.7-164.7	
							− 7.7
20 Oct. 1980 D*	5	118-156	141.0	251.0	121.3-160.7	48.5-233.5	
							+11.9
3 Nov. 1980 N	27	140-173	152.9	67.1	149.7-156.1	130.1-175.7	
							− 1.0
18 Nov. 1980 D	18	143-157	151.9	14.6	150.0-153.8	140.8-163.0	
							− 0.4
1 Dec 1980 N	4	149-153	151.5	3.7	148.4-154.6	140.3-162.7	
							− 4.5
15 Dec. 1980 D	1	147	147.0	—	—	—	
							− 4.0
7 Jan. 1981 N	7	127-167	143.0	211 7	129.5-156.5	89.1-196.9	
							+14.0
2 Feb. 1981 N	1	157	157.0	—	—	—	
							−17.0
16 Feb. 1981 D	2	130-150	140.0	200.0	12.9-267.1	−760.2-1,040.2	
							+ 5.5
7 Apr. 1981 N	2	145-146	145.5	0.5	139.1-151.9	100.5-190.5	
							− 4.5
20 Apr 1981 D	3	133-148	141.0	57.0	122.2-159.8	66.1-215.9	
							+14.8
4 May 1981 N	20	148-167	155.8	23.5	153.5-158.1	141.9-169.7	
							− 2.8
2 June 1981 N	5	143-161	153.0	43 5	144.8-161.2	122.6-183.4	
							+ 6.0
15 June 1981 D	11	146-174	159.0	53.2	154.1-163.9	135.9-182.1	
							0.0
1 July 1981 N	9	143-171	159.0	85.0	151.9-166.1	128.1-189.9	
							− 0.5
20 July 1981 D	199	146-176	158.5	40 5	157.6-159.4	142.1-174.9	
1980 spring-spawned group							
3 Aug 1980 N	7	58-80	65.4	64.0	58.0-72.8	35.7-95.1	
1980 fall-spawned group							
18 Nov. 1980 D	1	68	68.0	—	—	—	
							−15.4
1 Dec. 1980 N	62	22-108	52.6	267.0	48.4-56.8	15.0-90 2	
							−20.1
15 Dec. 1980 D	2	29-36	32.5	24.5	−12.0-77.0	−282.6-347.6	
							+19.6
7 Jan. 1981 N	191	31-91	52.1	231.2	49.9-54.3	12.9-91.3	
							+ 2.2
21 Jan. 1981 D	25	33-82	54.3	214.0	48.3-60.3	13.4-95.2	
							− 7 5
2 Feb. 1981 N	255	21-118	46.8	93.7	45.6-48.0	21.9-71.7	
							+15.3
16 Feb. 1981 D	49	33-108	62.1	330.2	56.9-67.3	13.4-110.8	
							− 6.4
2 Mar. 1981 N	32	42-86	55.7	156.5	51.2-60.2	21.4-90.0	
							+ 0.5
16 Mar. 1981 D	11	43-87	56.2	129.8	48.5-63.9	20.1-92.3	
							+ 3.8
7 Apr. 1981 N	110	39-87	60.0	105.7	58.1-61.9	33.1-86.9	
							+14.2
20 Apr. 1981 D	69	56-107	74.2	115.7	71.6-76.8	45.7-102.7	
							+ 6.2
4 May 1981 N	97	64-107	80.4	79.7	78.6-82.2	57.0-103.8	
							+ 9.3
19 May 1981 D	165	70-115	89.7	66.0	88.5-90.9	68.8-110.6	
							+12.8
2 June 1981 N	128	78-129	102.5	91.1	100.8-104.2	77.9-127.1	
							+ 9.3
15 June 1981 D	174	92-133	111.8	68.8	110.6-113.0	90.4-133.2	
							+ 8.4
1 July 1981 N	48	106-137	120.2	39.8	118.4-122.0	103.3-137.1	
							+13.0
20 July 1981 D	152	107-145	133.2	41.8	132.2-134.2	116.5-149.9	
							+ 8.3
3 Aug. 1981 N	132	120-166	141.5	62.0	140.2-142.8	121.2-161.8	
							+ 1.8
16 Aug. 1981 D	428	105-170	143.3	49.3	142.6-144.0	125.2-161.4	
1981 spring-spawned group							
15 June 1981 D	2	42-47	44.5	12.5	12.7-76.3	−180.6-269.6	
							+ 9.5
20 July 1981 D	9	41-72	54.0	110.8	45.9-62.1	18.7-89.3	
							+14.5
3 Aug. 1981 N	2	58-79	68.5	220.5	−64.9-201.9	−876.8-1,013.8	
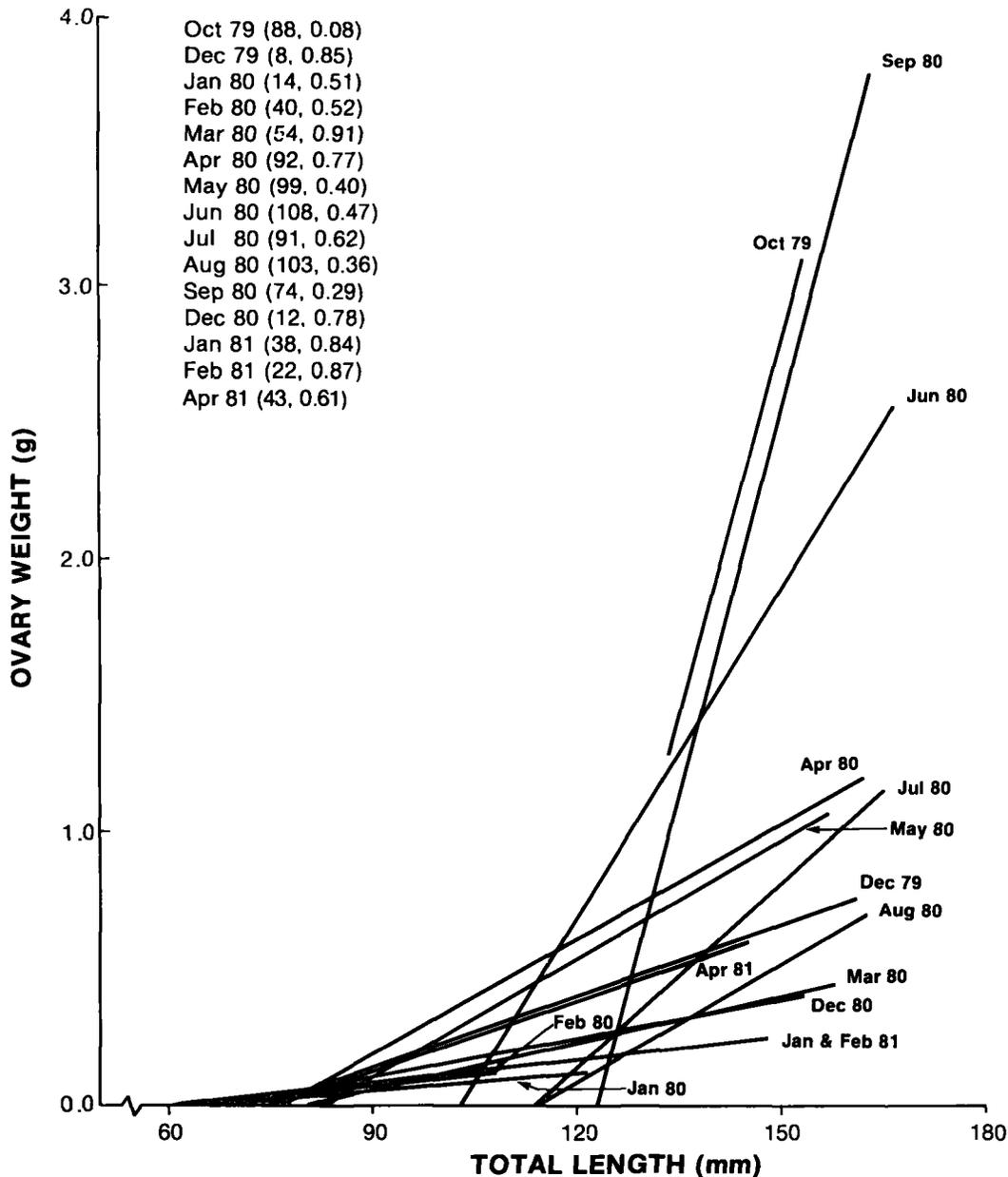
FIGURE 2.—Monthly regressions of ovary weight on total length for *Larimus fasciatus*. Length of each line shows the observed size range. Sample sizes and r^2 values are tabulated for each period. Regressions presented were significant at α = 0.05.

were calculated by using initial x-intercepts to readjust the initial x-variable (time) scale, so that each final growth curve passed through the origin (Table 4). Final calculated hatching dates are mean values because regressions predict averages. Rate parameters—e.g., regression coefficients, growth/30 d, and von Bertalanffy K values—fitted to observed size data are the same

within rounding error regardless of the hatching dates used, because curves are fitted to the same time dimension between the initial and last collection of a cohort.

Total annual mortality rates (1 − S) were calculated on a time-specific and cohort-specific basis from the expression $S = N_t/N_0$ where S = rate of survival, and N_t and N_0 are the numbers of fish at
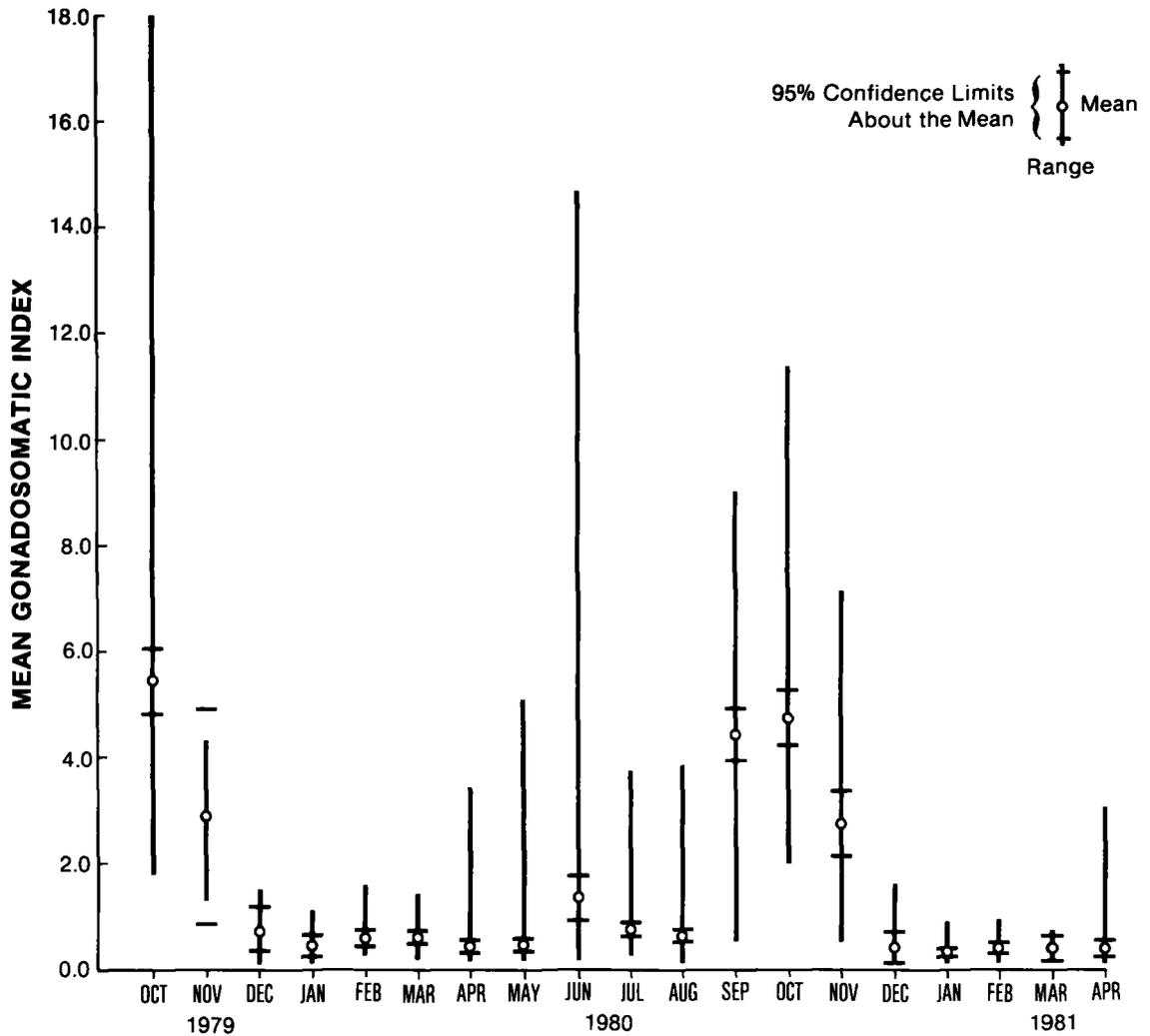
FIGURE 3.—Monthly mean gonadosomatic indices, ranges, and 95% confidence limits about means for female *Larimus fasciatus*, spawned groups pooled, October 1979-April 1981.

TABLE 4.—Summary of iterative process used to calculate final hatching dates and set time scales for growth calculations. Equations describe regressions of observed mean total length (TL) on age in days. Initial age values and growth equations were scaled to a 1 October hatching date. Final fitted regressions are in Figure 7.

Spawned group	Initial growth equation	Initial x-intercept	Final growth equation	Final calculated hatching date
Fall 1978	$y = 28.59 + 0.40825x - 0.00031x^2$	−67	$y = -0.13 + 0.44924x - 0.00031x^2$	27 July 1978
Fall 1978, initial two collections deleted	$y = -8.28 + 0.58365x - 0.00049x^2$	14	$y = -0.21 + 0.56983x - 0.00049x^2$	15 Oct. 1978
Fall 1979	$y = 7.41 + 0.51937x - 0.00045x^2$	−14	$y = 0.13 + 0.53162x - 0.00045x^2$	17 Sept. 1979
Fall 1980	$y = 12.94 + 0.36704x$	−35	$y = 0.09 + 0.36704x$	27 Aug. 1980
Fall 1980, initial two collections deleted	$y = -7.47 + 0.45303x$	16	$y = -0.22 + 0.45303x$	17 Oct. 1980

age each month. Analyses excluded several months in which estimates were not reliable because of incomplete recruitment (2 mo, time-specific; 6 mo, cohort-specific), seeming immigration (1 mo, time-specific), or some stations were not occupied in one cruise (1 mo, cohort-specific). Pooled estimates of S were calculated using Heincke's procedure (Ricker 1975) and were converted to $1 - S$ and Z using relationships in Gulland (1969:59). Observed estimates were compared against theoretical values calculated from the expression $\overline{Z}$ = 4.6/number of years in life span (Royce 1972:238). Typical maximum life span was approximated by the Beverton-Holt yield model parameter t_L (Gulland 1969), and typical maximum size was approximated as a corresponding length (l_L) following Alverson and Carney's (1975) definition that only 0.5-1% of the catch exceeds age t_L. Values of l_L were calculated from the cumulative length frequency for all fish captured in the period October 1977-August 1981. We calculated specific values of t_L from l_L by solving for time in von Bertalanffy (Gulland 1969:40) and quadratic regression equations. Total mortality rates and growth data presented are termed *apparent* because they may be affected by emigration as noted; if so, they overestimate mortality but underestimate sizes at age.

Ovaries were prepared to estimate fecundity (FEC) using procedures similar to Bagenal (1957) and Simpson (1959). Entire ovaries of 60 Early Developing, Late Developing, Gravid, or Ripe fish were removed, split, everted, placed in Gilson's solution for 1-3 mo, and agitated using a magnetic stirrer to enhance separation of ova from connective tissue. Connective tissue was removed and supernatant siphoned off until only ova remained. Eggs were then placed in a beaker, filled to 200 ml with water, and magnetically stirred to be uniformly dispersed. Fecundity was determined for each fish by taking a 2 ml sample from each of three fixed levels in the beaker (at 25, 100, 175 ml) to enumerate eggs. Samples were pooled to calculate a mean/2 ml for each fish because, although significant, differences in mean egg count per level over all fish were small (627, 592, and 598, respectively; n = 60 for each level). Mean counts/2 ml were expanded to determine fecundity as the number of eggs in the total water volume.

Regression relationships were calculated following standard procedures (Helwig and Council 1979; Snedecor and Cochran 1980). Von Bertalanffy growth was calculated using Fabens' (1965) program. All length measurements pre-

sented herein are total length unless stated otherwise, and all length frequencies are moving averages of three. Conversions between standard length and total length used regressions presented herein.

We use the verb "recruit" and the noun "recruitment" herein to describe areas in which young *L. fasciatus* descend to the bottom from their pelagic (Johnson 1978) early stages. This usage conforms to Beverton and Holt's (1957) meaning of recruitment, because these bottom areas are exploited, and to Ricker's (1975) meaning, because fish also then enter the exploited phase of life.

RESULTS

Maturation and Spawning Periodicity

Larimus fasciatus from the northwestern Gulf mature at 80-130 mm as they approach age I. Gonad development was distinct at 80-150 mm when most females entered the Early Developing stage (Fig. 4). All fish in Late Developing and later stages were >130 mm. These data are supported by regressions of ovary weight on length (Fig. 2) in which extrapolated x-intercepts were 75-125 mm during the April-October period when spawning occurs. Age compositions and sizes presented later indicate *L. fasciatus* mature to first spawn at 12-14 mo.

Little somatic growth seemingly occurs after *L. fasciatus* enter late stages of gonad development. Mean lengths of fish were 146 mm in the Late Developing stage, 147 mm when Gravid, 149 mm when Ripe and Spawning/Spent, and 150 mm when Resting (Fig. 4). Maximum and minimum sizes also remained constant through these stages.

Larimus fasciatus spawn within a broad period from April through November. Fish in Ripe or Gravid stages occurred throughout this period (Fig. 5), slopes and elevations of regressions of ovary weight on length generally were highest (Fig. 2), and GSI maximums usually were high (Fig. 3). Gonad analyses are supported by 1) recurrent collections of fish 20-40 mm from November through February each year in the period 1978-81 which probably were 1-3 mo old and indicate spawning from September through November (Fig. 6), and 2) collections of distinct groups of fish 40-80 mm in the period mid-June through August in 1980 and 1981 which probably were 3-5 mo old and indicate spawning from April through June.

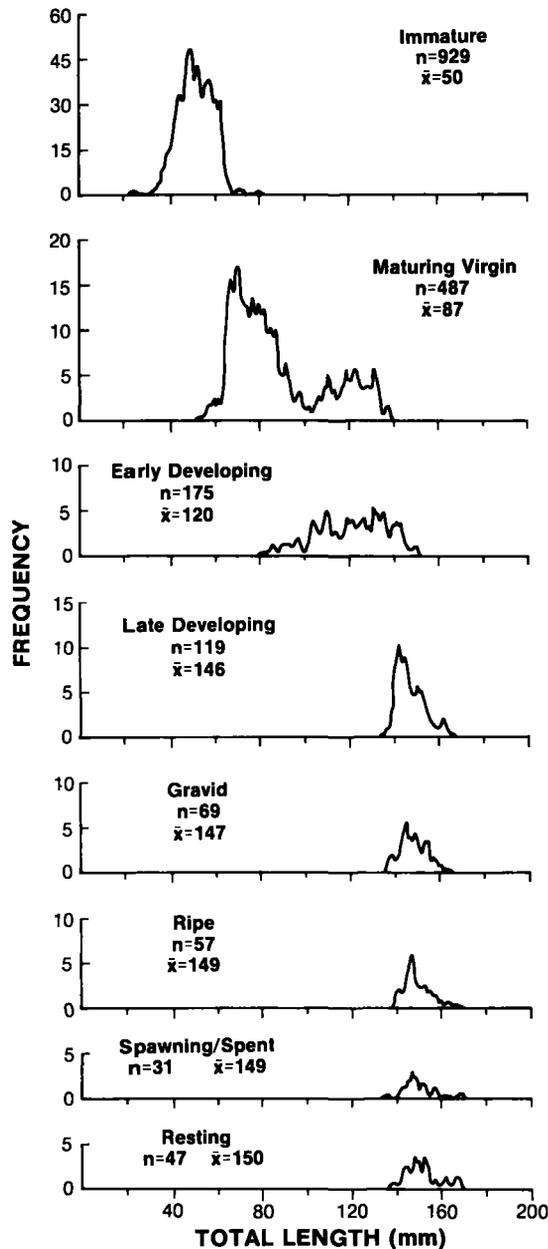Little or no spawning of *L. fasciatus* occurs from

FIGURE 4.—Length frequencies of immature and female *Larimus fasciatus* by gonad maturity stage. See Table 1 for maturity stage criteria.

December through March. Almost all fish were in the Immature, Maturing Virgin, Early Developing, or Resting stages in that period (Fig. 5). Few were in the Late Developing stage then and none were Gravid or Ripe. In addition, mean and maximum GSI values were lowest during the December-March period (Fig. 3) as were the slopes and elevations of regressions of ovary weight on length (Fig. 2). Gonad analyses are supported by the absence of fish 20-80 mm from late February to mid-June each year (Fig. 6) with the exception of fall-spawned fish whose growth in late winter and spring is clearly followed.

Although *L. fasciatus* spawn within a broad time period, spawning primarily occurs during what we interpret as two discrete periods, a major fall period (September-November) and a very minor spring period (April-June). Mean and/or maximum GSI values were highest in the periods May-June and September-November, and these peaks were separated by troughs in the periods July-August and December-April (Fig. 3). Although few fish were Ripe in August, nearly all were in Late Developing, Gravid, Ripe, and Spawning/Spent stages from September through November (Fig. 5); few were in Immature, Maturing Virgin, or Early Developing stages then. Fall-spawned fish greatly predominated each year and formed length-frequency modes easily followed through the spring and summer after their recruitment in fall and winter (Fig. 6). A minor spring spawn is indicated by distinct, but not abundant, groups of fish 40-80 mm in the periods August 1980 and June-August 1981 (Fig. 6) and by the occurrence of a few (14) Gravid and Ripe stage fish from April through June and Late Developing fish in March (Fig. 5). No recently recruited spring-spawned fish were evident after August (Fig. 6), but they may be represented by the few intermediate-sized fish from an unclear spawned group in January and March 1980 and February 1981.

Little or no spawning of *L. fasciatus* occurs in July and August. No fish 20-40 mm (1-3 mo old) were captured from July through October (Fig. 6). Only two fish were Gravid or Ripe during July and August and few were in the Late Developing stage then (Fig. 5).

Calculated hatching dates agree with the major fall-spawning period—September-November—indicated by gonad and length-frequency analyses. Depending on data points included, calculated hatching dates were 27 July or 15 October 1978, 17 September 1979, and 27 August or 17 October 1980 (Table 4). Hatching dates of 15 October and 17 October seem most realistic for 1978 and 1980. The earlier dates for those years are based on regressions fitted to all collections. The earliest two collections in those years, however, probably contribute upwardly biased size data
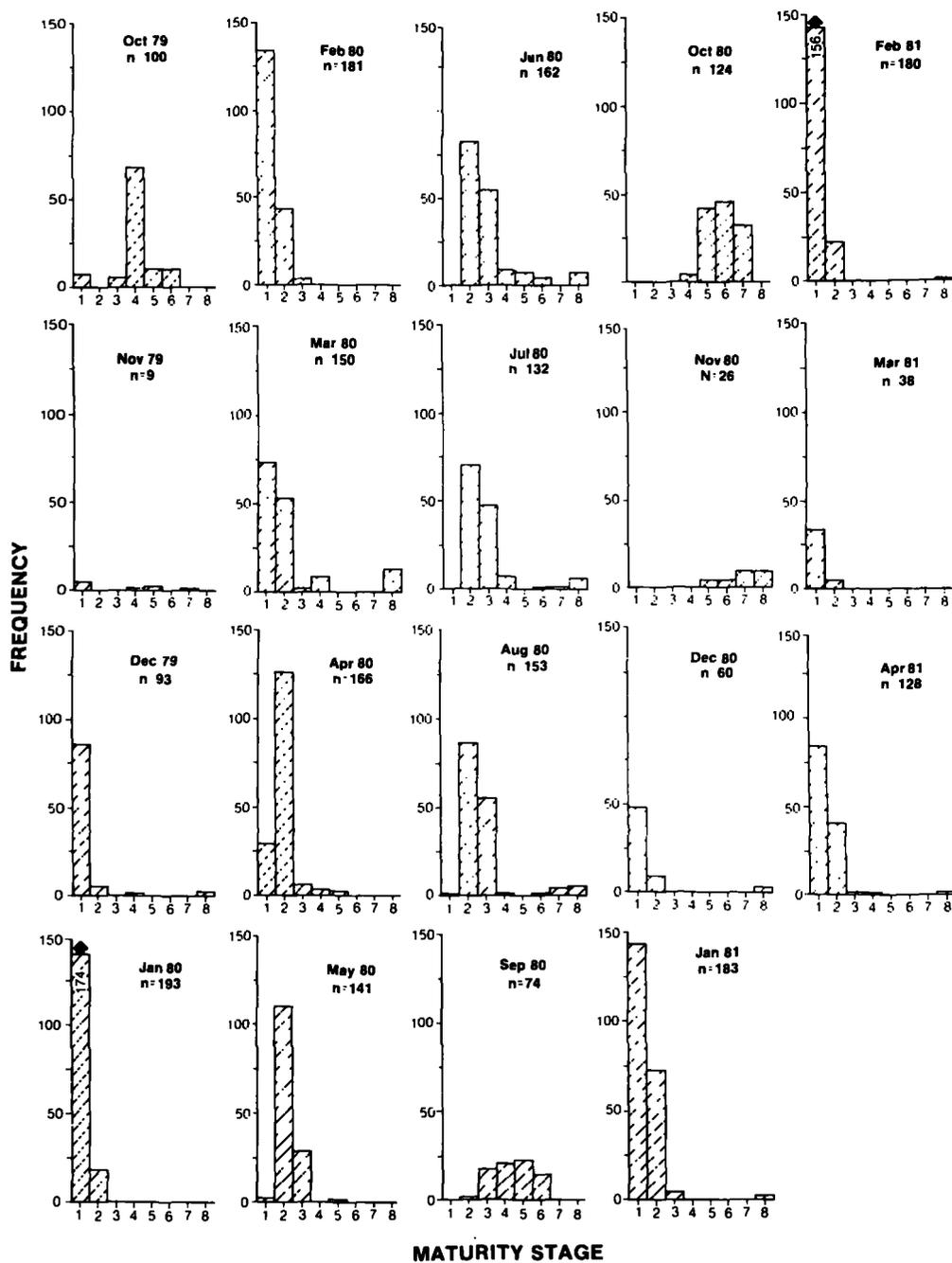
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FIGURE 5.—Monthly gonad maturity stages of immature and female *Larimus fasciatus*. Maturity stages (see Table 1) are 1 - Immature, 2 - Maturing Virgin, 3 - Early Developing, 4 - Late Developing, 5 - Gravid, 6 - Ripe, 7 - Spawning/Spent, and 8 - Resting.
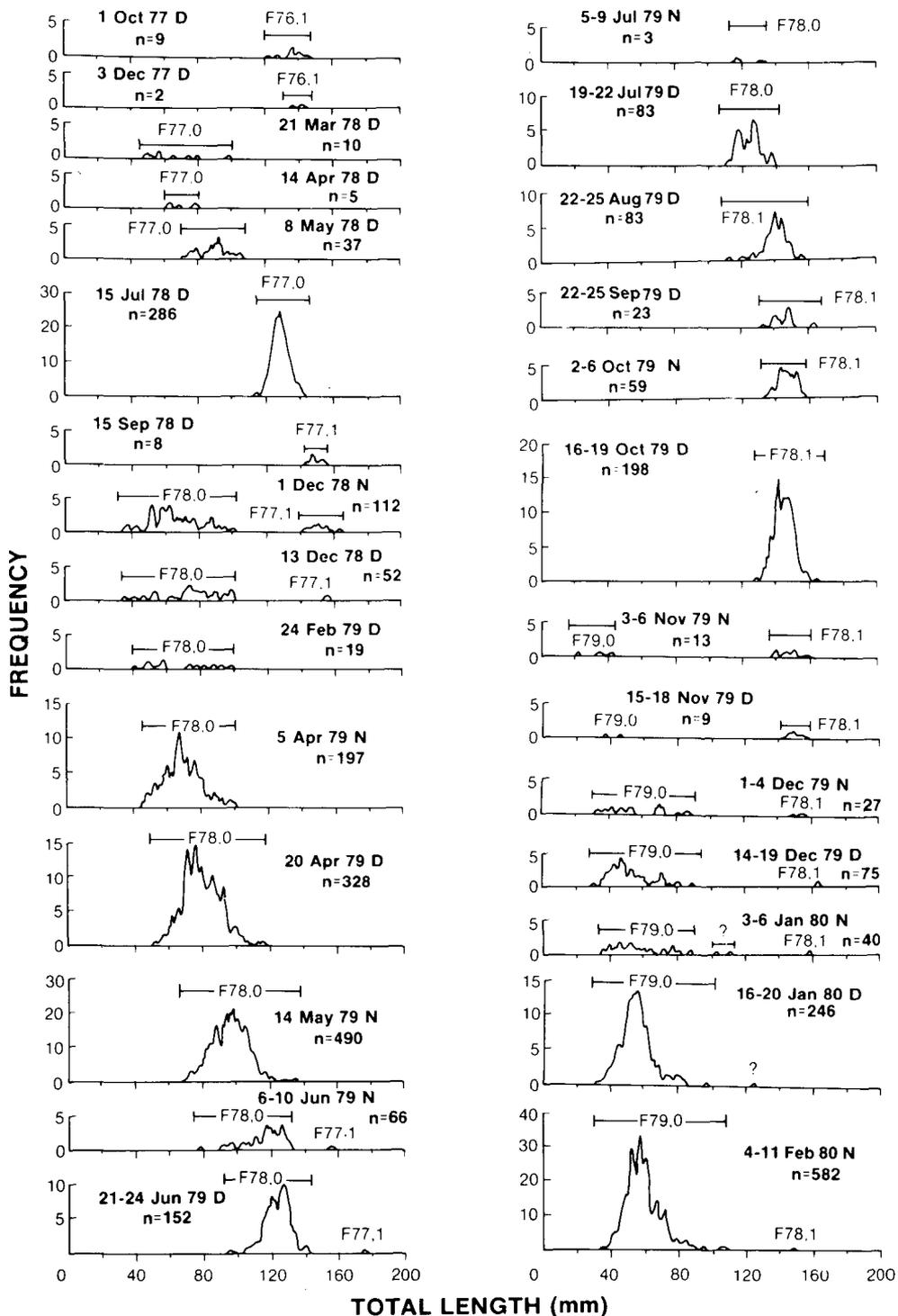
FIGURE 6.—Monthly length frequencies of *Larimus fasciatus* off Freeport, Tex. Day and night cruises are indicated by D and N. Bars in each panel depict size range of indicated spawned group; further detail is in Table 3. The letter and first two digits within a bar indicate spawned groups; the last digit is age in years, e.g., F77, 1
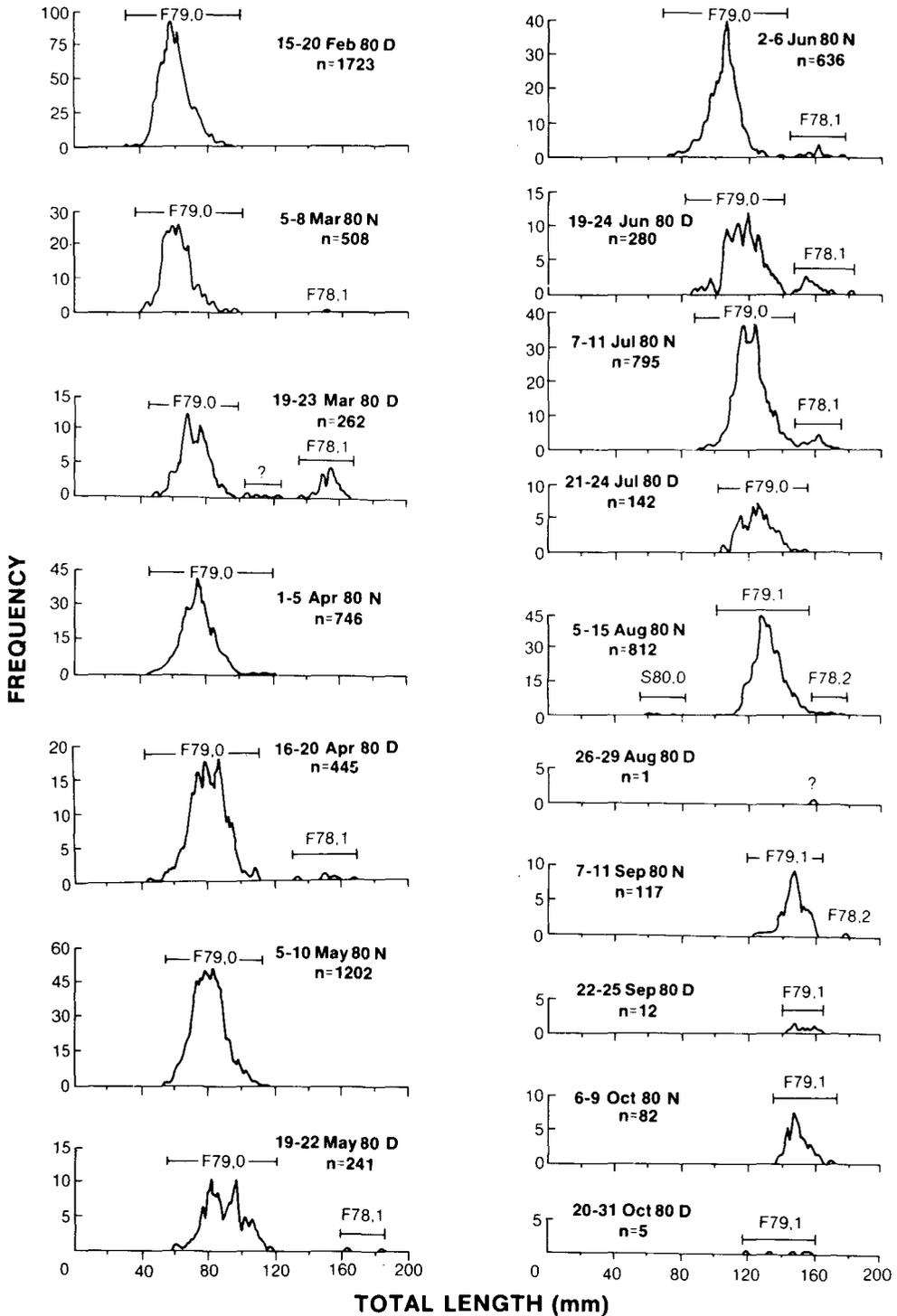
FIGURE 6.—*Continued*—represents the fall 1977-spawned group when age I. Age designation for each cohort changed in August to simplify reference between Figures 6 and 10 D; true ages in August only approach those indicated.

TOTAL LENGTH (mm)

FIGURE 6.— *Continued.*

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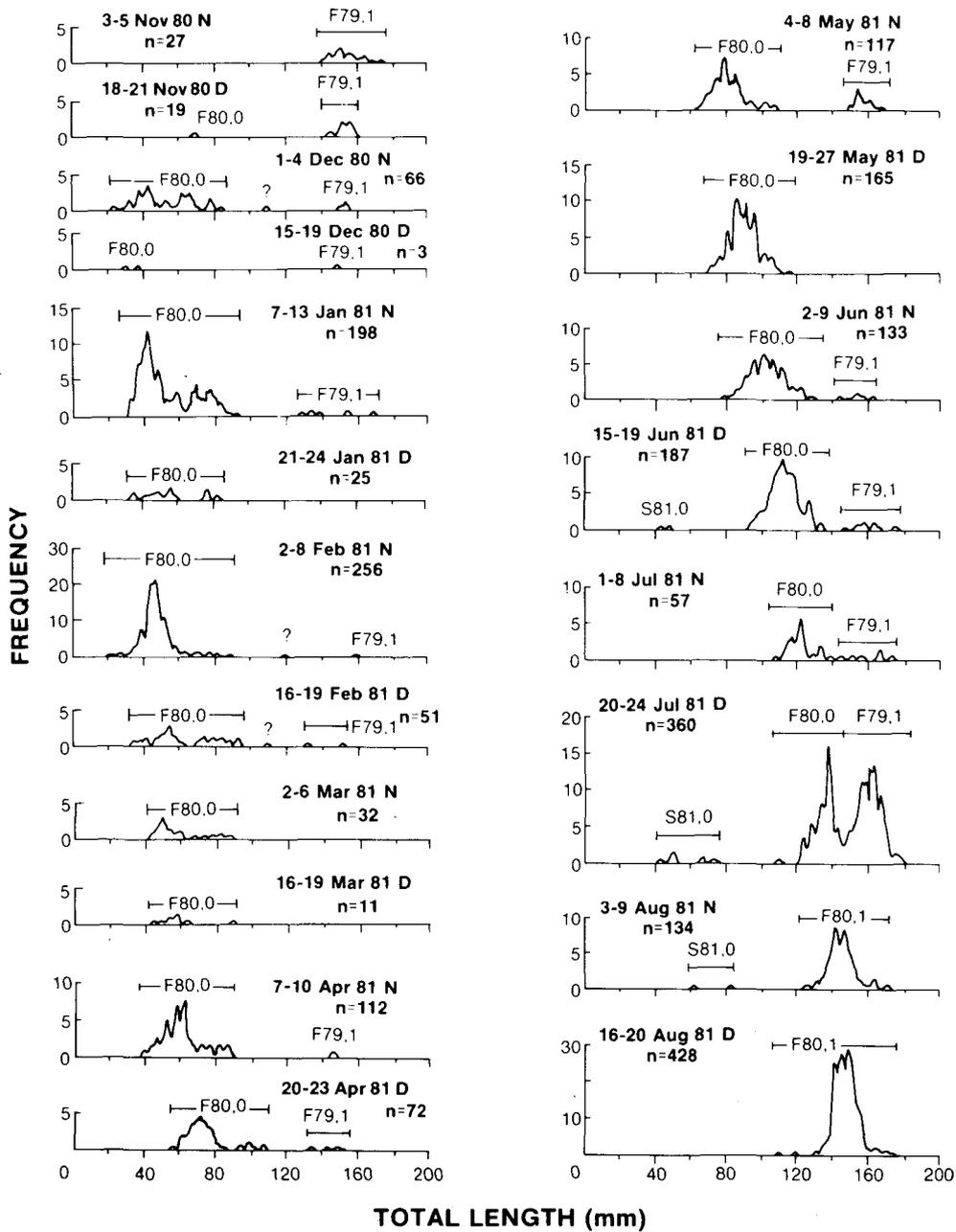
that reflect gear selection for large fish or incomplete recruitment of smaller fish; mean sizes in those collections were as large as or larger than means in subsequent collections and seem to be outliers (Fig. 7A, C). Coefficients of determination were higher when the earliest two collections were excluded (Fig. 7A, C).

The period of successful spawning spans 60-90 d within the major September through November interval. Based on mean 99% confidence limits for observations and growth per day in each April-

June period, calculated durations of fall spawning periods were 76 d in 1977, 76 in 1978, 87 in 1979, and 64 in 1980 (Table 2). These estimates fall within and agree with the broad 90-d duration of the fall-spawning period indicated by gonad maturity and weight data.

The predominant fall-spawned groups are produced by fish that first spawn when 12-14 mo old and the minor spring-spawned groups by fish 19-21 mo old. Fall-spawned fish apparently do not spawn when 5-7 mo old in their first spring, because GSI values for fall 1979 and fall 1980 fish remained low during their initial springs (Fig. 8B, C). Peaks in GSI values from September through November in 1979 and 1980 were formed by fall 1978 and fall 1979 fish, first spawning at 12-14 mo of age (Fig. 8A, B). Peaks in GSI values from April through June in 1980 and 1981 were formed by fall 1978 and fall 1979 fish that spawned when 19-21 mo old (Fig. 8A, B). We were not able to determine age when spring-spawned groups spawn, because these fish were clearly identifiable only until 3-5 mo old (see section on Age Determination and Growth).
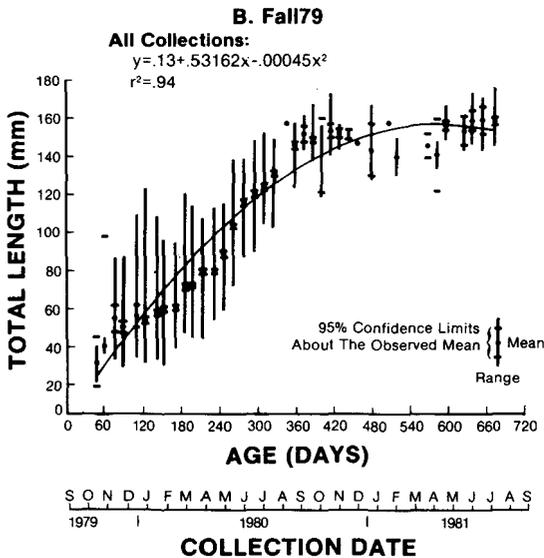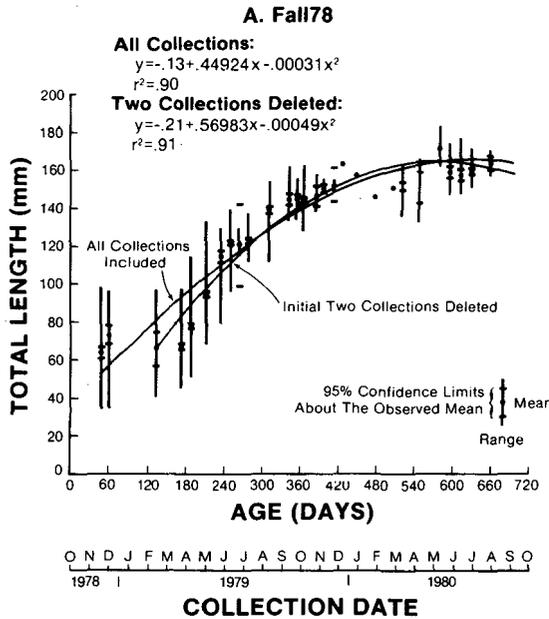
FIGURE 7.—Mean observed and predicted sizes at age (days) for the 1978 (A), 1979 (B), and 1980 (C) fall-spawned groups of *Larimus fasciatus*. Mean sizes at age were regressed on age scaled to calculated hatching dates of 27 July and 15 October 1978, 17 September 1979, and 27 August and 17 October 1980. Observed mean lengths and their confidence limits are from Table 3. Regressions were significant at $\alpha = 0.001$.
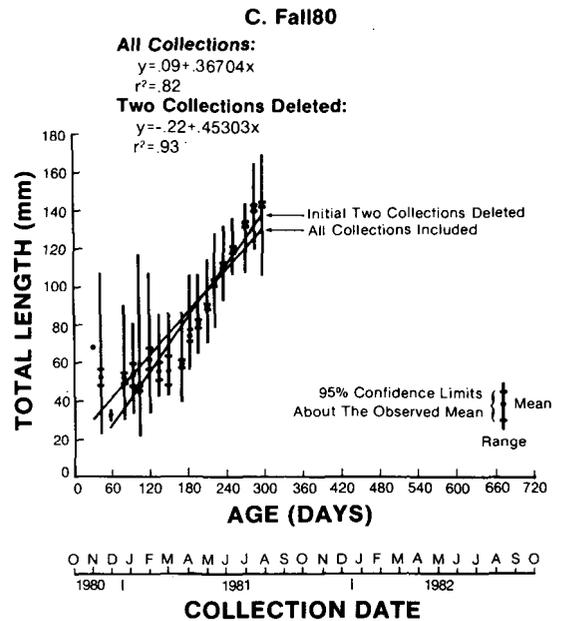
Bathymetric Distribution, Recruitment, and Movements

The bathymetric distribution of *L. fasciatus* in the northwestern Gulf off Freeport extends from <5 to 55 m. This species was most abundant at 5 m, the shallowest depth occupied (Fig. 9). Abundance declined sharply between 5 and 18 m and remained low from 18 to 36 m. Only one specimen was collected deeper than 36 m.

Young-of-the-year *L. fasciatus* in the northwestern Gulf recruit in waters <5-16 m when 2-4 mo old. Fall-spawned young 30-100 mm recruited almost exclusively in 5-16 m from November through April (Fig. 10A, B). Only four young-of-the-year specimens at 18-22 m were collected deeper than 16 m. Similarly, spring-spawned young 60-80 mm recruited only at 5-16 m in the period August-October (Fig. 10D).

Greatest recruitment of fall-spawned *L. fasciatus* occurred in the shallowest depths sampled. Recent fall-spawned recruits were most abundant by far at 5 m in November-April (Fig. 10A, B). Abundance then sharply declined with depth and was very low deeper than 16 m in that period.

FIGURE 8.—Monthly mean gonadosomatic indices, sample sizes, ranges, and 95% confidence limits about means for the 1978 (A), 1979 (B), and 1980 (C) fall-spawned groups of *Larimus fasciatus*. Age in months is indicated for each spring and fall spawning period.

FIGURE 9.—Catch/effort (mean number of individuals per 10 min tow) by depth for *Larimus fasciatus* off Freeport, Tex., each year and pooled, October 1977-August 1981.
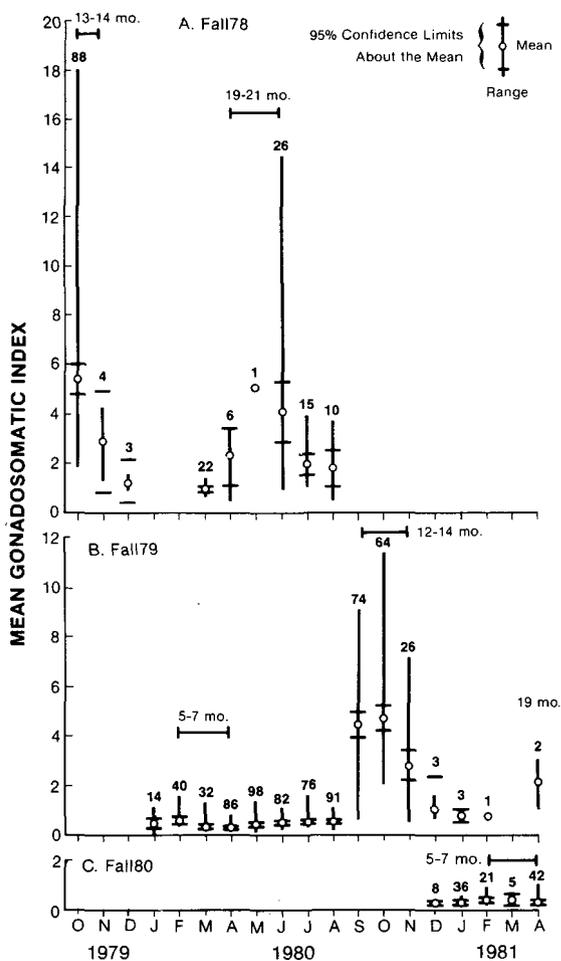
Fall-spawned *L. fasciatus* gradually disperse toward deeper water in late spring or summer. The distribution of young-of-the-year in May-July was similar to that in November-April (Fig. 10C). Fish approaching age I showed a clear offshore shift in distribution by August-October when abundance greatly declined at 5-13 m, became highest at 16-22 m, and was as high at 24-27 m as at 5-13 m (Fig. 10D). Fish approaching age I became distributed to 36 m, a depth they previously did not occupy, in August-October.

Larger *L. fasciatus* lead the offshore dispersal as they approach age I. Size compositions of the young-of-the-year were uniform with depth in November-April (Fig. 10A, B). They became skewed toward the right in May-July and show a gradient of increasing size with depth in August-October which suggests larger, presumably older, fish move offshore first.

Adult fall-spawned *L. fasciatus* in the northwestern Gulf occupy the 13-24 m bathymetric range from November through April while
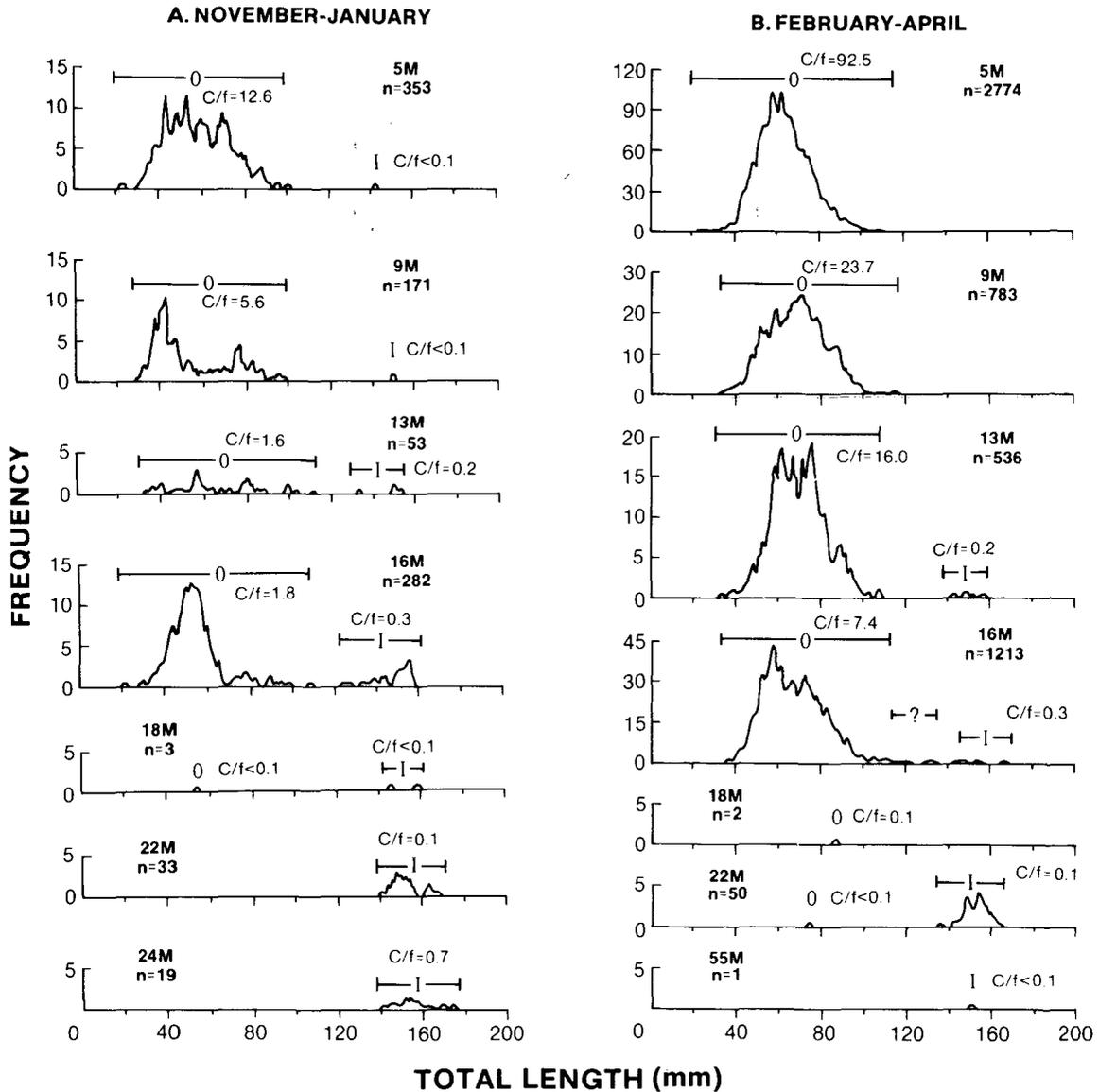
FIGURE 10.—Length frequencies and catch per effort (mean number of individuals per 10 min tow) by depth for *Larimus fasciatus* off Freeport, Tex.: A) November-January, B) February-April, C) May-July, and D) August-October. Data in each panel were pooled over the

young-of-the-year recruit inshore. Newly age I and older fish were most abundant at 13-24 m in November-April (Fig. 10A, B). Few were captured at 5-9 m then.

Age Determination and Growth

Few spawned groups of *L. fasciatus* exist at any

one time in the northwestern Gulf and only one normally predominates. No more than three spawned groups were present at any time (Fig. 6). This maximum occurred only in August 1980 and June-July 1981 when spring-spawned fish recruited to join two fall-spawned groups. These were the only occasions when spring-spawned fish were clearly identifiable and their abundance was
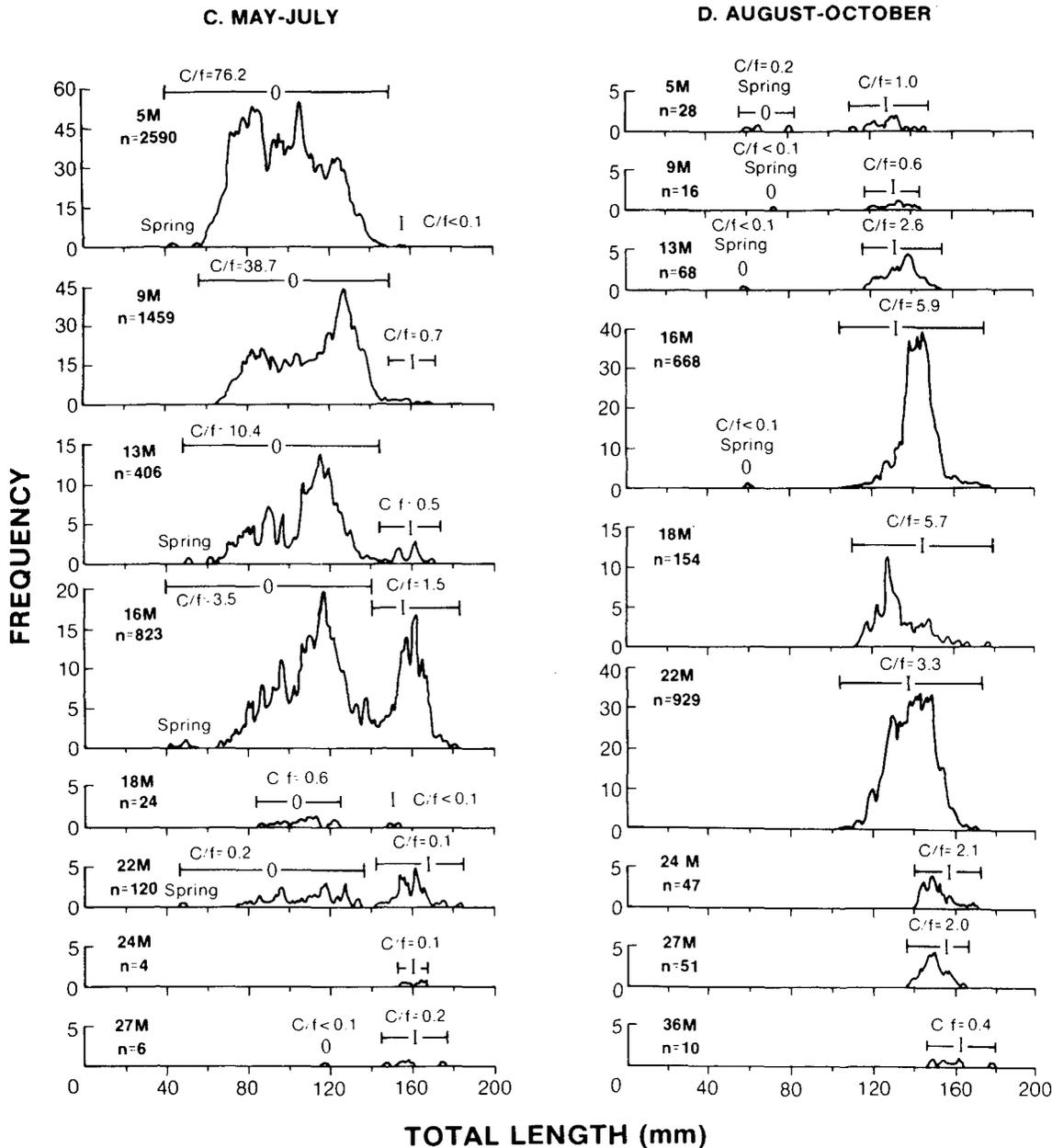
FIGURE 10.—*Continued*—period October 1977-August 1981 because length frequencies were similar each year. Designated ages are for fall-spawned fish except where noted. Age design' n for each cohort changed in August.

negligible even then. Although two fall-spawned groups, represented by young-of-the-year and age I fish, often were captured, only one predominated in any month except in July 1981 when fish approaching age II were abundant but disappeared thereafter. Once fully recruited, each fall-spawned group predominated to age I and then nearly disappeared as the next fall group began to recruit.

Larimus fasciatus is not abundant after 12 mo of age in the northwestern Gulf and reaches only 21-23 mo there. Fall-spawned fish were abundant after 12 mo of age (Fig. 6) only in July 1981 when they approached age II. Fall-spawned groups disappeared at 15-23 mo of age (Table 5, Fig. 6). The few spring-spawned fish captured were identifiable only until 3-5 mo of age (Table 5, Fig. 6). Fish of intermediate size between clearly defined fall-spawned groups in January and March 1980 and February 1981 could have been spring-spawned, but their identity is not clear.

Slightly larger *L. fasciatus* occur in the north central Gulf than in the northwestern area.

(Harding 1949), moreover, do not and cannot resolve this situation because of the original problem: the underlying length frequency is not absolutely clear. However, the 48 mm range of sizes (139-187 mm) for fish in the north central Gulf is only slightly larger than a 35 mm range (130-165 mm) that tightly brackets most fish in the northwestern Gulf where only one fall group predominated (Fig. 11). Moreover, sizes in the north central Gulf in the period October-November were only slightly larger than and greatly overlap those for northwestern Gulf fish which were just age I. These facts suggest only one or at most two spawned groups predominated in the north central Gulf, fish just age I and age II. This interpretation is supported by our findings noted later that 1) the largest fish we captured in the northwestern Gulf (182 mm) was only 20 mo old, 2) von Bertalanffy predictions indicated mean sizes of 164 and 181 mm at age II in the northwestern Gulf depending upon variation between fall-spawned groups, and 3) the observed size range was 143-176

TABLE 5.—Periods of time, sizes, and age when spawned groups of *Larimus fasciatus* were last captured.

Spawned group	Period last captured	Size (mm TL)	Age (mo)	Comments
Fall 1976	Early December 1977	136-141	15-16	Very few ever captured.
Fall 1977	Late June 1979	174	21-22	Few ever captured.
Fall 1978	Early September 1980	177	22-23	Few captured after October 1979.
Fall 1979	Mid-July 1981	146-176	22-23	Few captured after October 1980, except for late July 1981.
Spring 1980	Early August 1980	58-80	3-4	Collected only in August 1980.
Fall 1980	Mid-August 1981	105-170	10-11	Still dominant in last collection.
Spring 1981	Early August 1981	58-79	3-4	Very few ever collected.

Maximum and mean sizes were greater in the north central Gulf (max. = 187 mm, $\bar{x}$ = 160 mm) than in the northwestern area (max. = 173, $\bar{x}$ = 146) during the period October and November, ignoring the seven recently hatched recruits captured in the latter area (Fig. 11).

Only one or two spawned groups of *L. fasciatus* apparently predominate in the north central Gulf, probably fish that became age I and age II in the fall. We are not able to confidently identify modal groups to assign ages and, particularly, delineate sizes where age groups overlap in that area (Fig. 11), because we made only one cruise there, not the time-intensive series that permits confident age designations for the northwestern Gulf. Analyses such as linear transformation of cumulative percentage frequencies using probability paper
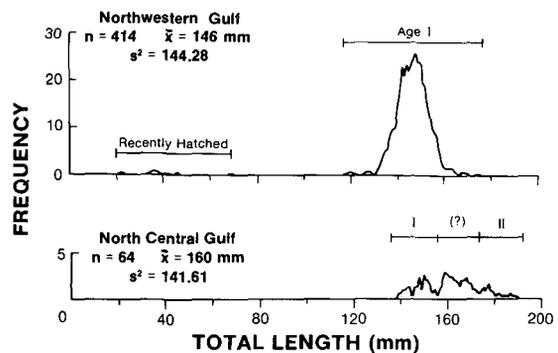

FIGURE 11.—Length frequencies and age designations for all *Larimus fasciatus* captured in the period October-November in the northwestern (1977-80) and north central (1982) Gulf of Mexico. Means, n, and s^2 ignore seven recent recruits (<70 mm) in the northwestern Gulf.

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mm in July for the abundant fall 1979-spawned group as it approached age II in the northwestern Gulf. We have assumed fish in the north central Gulf were produced in the major fall-spawning period, not the minor spring one, and that differences in size compositions do not reflect only possible intra-Gulf differences and greater size at age in the north central Gulf. Comprehensive collections in that area are needed to resolve the latter assumption.

Apparent growth of *L. fasciatus* in the northwestern Gulf was similar between fall-spawned groups, mean sizes being 130-150 mm at age I and 155-180 mm at or approaching age II. Observed mean sizes and ranges at age I, based on pooled data from September and October (Table 3), were 134 mm (120-143) for fall 1976 fish, 148 mm (145-152) for fall 1977 fish, 145 mm (127-164) for fall 1978 fish, and 147 mm (118-168) for fall 1979 fish. These sizes at age I agree with quadratic regression predictions of 142 and 134 mm (Fig. 7) and von Bertalanffy model predictions of 137 and 131 mm for fall 1978 and fall 1979 fish, respectively. Observed mean size and ranges at or approaching age II (Table 3) was 159 mm (150-172) in July 1980 for fall 1978 fish, 159 mm (143-176) in July 1981 for fall 1979 fish, and 164 mm (156-177) in August-September 1980 for fall 1978 fish. These values are only slightly larger than a quadratic regression prediction of 155 mm at age II for fall 1978 fish (Fig. 7A), and are the same as or a little smaller than von Bertalanffy model predictions of 164 and 181 mm at age II for fall 1979 and fall 1978 fish, respectively.

Fitted von Bertalanffy equations based on hatching dates of 15 October for fall 1978 fish and 17 September for fall 1979 fish were

$$\text{Fall 1978: } l_t = 201 (1 - e^{-0.003162(t - 1.574)})$$

$$\text{Fall 1979: } l_t = 176 (1 - e^{-0.003670(t + 4.696)})$$

where l_t = length in millimeters, and t = time in days. Annual K values were 1.15 and 1.34, respectively. Respective annual t_0 values (0.00431 and −0.01287) were small which may reflect our forcing the curve through the origin.

Apparent growth of fall-spawned *L. fasciatus* follows an S-shaped intrayear pattern and is greatest in the spring and summer. Observed mean sizes at age showed a clearly S-shaped pattern (Fig. 7). Adjusted growth increments were small early in life (Fig. 12) and may reflect cool-water temperatures then, gear selection for larger

young, or a pattern of incomplete recruitment in which smaller, younger fish gradually recruit to join early recruits that are slightly larger and older. Growth increments for age 0 fish were greatest in March-June, peaking in early June (26.7 and 32.1 mm/30 d). Growth increments decreased as maturation occurred from July through September, became small after spawning in October-January, and increased slightly in June-August as the fish approached age II.

Apparent sizes of *L. fasciatus* at or approaching age I in the northwestern Gulf reached a plateau in August-September and for many months later. Mean sizes of fish at or approaching age I remained constant then, and 99% confidence limits for observations generally remained uniform at 130-160 mm (Table 3, Fig. 6). This pattern suggests an exodus of larger individuals and/or cessation of growth coincident with gonad maturation (see section on Maturation and Spawning Periodicity).

Maximum Size, Life Span, and Mortality

The maximum size *L. fasciatus* reach in the northwestern Gulf is about 180 mm, but more typically individuals reach only 160-165 mm. The largest of the 13,676 fish we collected there was 182 mm; 99% were <161 mm and 99.5% were <164 mm (Fig. 13), these sizes being estimates of l_L.

Typical maximum life span of *L. fasciatus* appears to be only 1-2 yr in the northwestern Gulf. A value of t_L = 1-2 yr is reasonable for that area because 1) fish average 155-180 mm at or approaching age II and 130-150 mm at age I with the upper 99% confidence limits for observations at age I generally being 160-165 mm (Table 3), 2) l_L values of 161 and 164 mm predict t_L values of 1.3-2.0 yr (Table 6), 3) the largest specimen was 20 mo old when collected in May 1980, and 4) *L. fasciatus* disappeared off Texas at 15-23 mo of age (Table 5),

TABLE 6.—Values of t_L (yr) for *Larimus fasciatus* calculated from l_L (mm TL) using quadratic and von Bertalanffy equations scaled to hatching dates of 15 October for fall 1978 and 17 September for fall 1979 fish. The apex of the parabola for fall 1979 fish was 157 mm so that t_L values could not be calculated for that cohort.

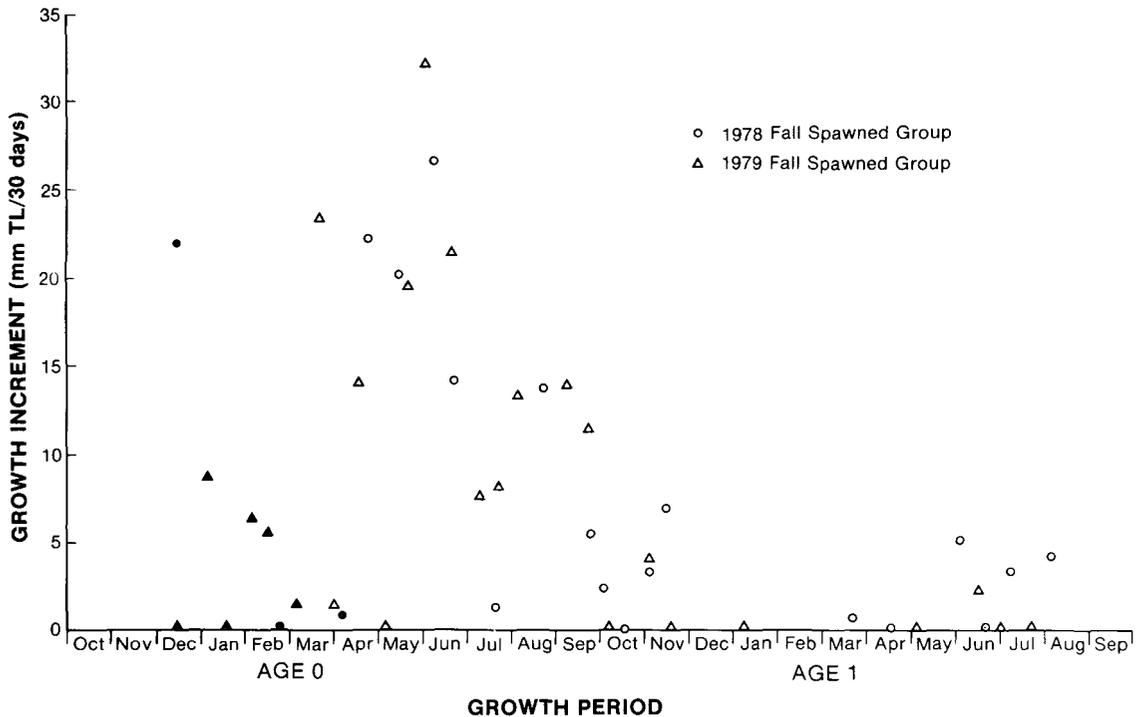| Spawned group	l_L	t_L calculated from:	
		Quadratic regression	von Bertalanffy equation
Fall 1978	161	1.33	1.40
Fall 1978	164	1.44	1.47
Fall 1979	161	—	1.83
Fall 1979	164	—	1.99

FIGURE 12.—Monthly growth increments for 1978 and 1979 fall-spawned *Larimus fasciatus*. Unadjusted growth increments (Table 3) were converted to growth/30 d, omitting collections of five or less fish. Negative growth is rounded to zero. Values denoted by darkened symbols may reflect incomplete recruitment, gear selection for larger young, or cool-water temperatures early in life.
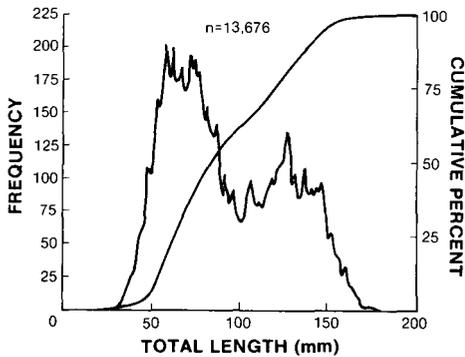

FIGURE 13.—Length frequencies and cumulative percentage of all *Larimus fasciatus* collected off Freeport, Tex., October 1977-August 1981.

and few ever approached age II except in July 1981 as previously noted. The latter instance suggests larger, older specimens of *L. fasciatus* may occur elsewhere; if so, our estimate of t_L may be too low for a stock that also ranges outside the northwestern Gulf.

Larimus fasciatus from fall-spawned groups have an *apparent* total annual mortality rate of 90-100% in the northwestern Gulf, mean time and cohort-specific values being 92-100%. Time-specific values of $1 - S$ were 100% in 17 of the 38 mo in which fish were collected (Fig. 6) because only one fall-spawned group was present and N_t was zero in the ratio N_t/N_0. Time-specific mortality estimates for the 18 remaining months gave ratios whose percentage values ranged from 89.93 to 99.96%; 14 exceeded 94%. Pooled estimates using Heincke's procedure were 97.18-100% depending on the spawned groups compared (Table 7). By pooling the Heincke numerators and denominators from each comparison an average time-specific $1 - S$ was 98.24%, or 96.86% if data from July 1981 are included. Cohort-specific values of $1 - S$ were 100% in 12 of the 24 mo for fall 1978 fish and in 2 of the 12 mo for fall 1979 fish because N_t was zero. Cohort-specific estimates for the remaining 6 mo in the fall 1978 cohort ranged from 97.83 to 99.81% except in June and July 1980 when estimates were 64.84 and 55.05%. Estimates for the remaining 7 mo in fall 1979 cohort ranged

TABLE 7.—Pooled time-specific and cohort-specific mortality estimates for *Larimus fasciatus* using Heincke's procedure (Ricker 1975). Symbols represent: N_0, youngest spawned group in Heincke's estimate; S, annual survival rate; $1 - S$, annual mortality rate; and Z, instantaneous mortality rate.

N_0	S	$1 - S$	Z
Time-specific			
Fall 1977	0	1.0000	∞
Fall 1978	0.0083	0.9917	4.79
Fall 1979	0.0180	0.9820	4.02
Fall 1980	0.0282	0.9718	3.57
Heincke's			
Pooled	0.0176	0.9824	4.04
Cohort-specific			
Fall 1978	0.0810	0.9190	2.51
Fall 1979	0.0317	0.9683	3.45

from 94.44 to 99.84% except in July 1981 when it was 74.43%. The low estimates in June and July reflect the unusual instance previously noted of immigration by fish approaching age II. Pooled cohort-specific estimates of $1 - S$ using Heincke's procedure were 91.90% for fall 1978 fish and 96.83% for fall 1979 fish (Table 7).

Sex Ratio and Fecundity

Male and female *L. fasciatus* appear equally abundant. The observed sex ratio of 1.00 males to 1.02 females among 2,502 mature or maturing fish examined in the period October 1979-April 1981 did not differ significantly from 1:1 ($\chi^2 = 0.19$; df = 1; $\alpha = 0.05$).

Mean fecundity of *L. fasciatus* in Gravid and Ripe stages was 70,453 eggs. Observed fecundity ranged from 32,333 to 143,800 eggs/female. Untransformed and log-log transformed linear regressions of fecundity on total length and total weight and related statistics are presented in Table 8; the former regression is depicted in Figure 14. The untransformed regression is a better fit

($100r^2$ being 29.7 vs. 27.1 for length and 35.1 vs. 28.4 for weight), but the transformed regression permits extrapolation over a broader size range. Fecundity statistics were based only on Gravid and Ripe fish, because residual plots for untransformed data indicated a relationship between fecundity and maturity stage (Fig. 15): maximum fecundity occurred in the Gravid and Ripe stages.

Weight, Girth, and Length Relationships

Total weight-total length, girth-total length, and standard length-total length regressions are presented in Table 8 with related statistics. Total length-total weight regressions for males and females were not significantly different in slope ($F = 0.35$, df = 1, 1936, $\alpha = 0.05$) or in elevation ($F = 1.62$, df = 1, 1936, $\alpha = 0.05$) so one pooled equation is presented for them. Total length-total weight regressions for males and females pooled and for immatures, males, and females pooled were significantly different in slope ($F = 44.87$, df = 1, 4808, $\alpha = 0.05$), but one equation that pools all sizes may be useful and is presented. Calculated slopes significantly exceeded $\beta = 3.0$ at $\alpha = 0.05$ for both length-weight relationships (males and females pooled, $t = 53.06$; immatures, males, and females pooled, $t = 60.41$).

DISCUSSION

Spawning Periodicity

We found that the broad April to November period within which *L. fasciatus* spawns generally agrees with many studies, including Hildebrand and Cable (1934), Miller (1965), Christmas and Waller (1973), and Ross (1978). However, our interpretation is new that little or no spawning oc-

TABLE 8.—Fecundity, total weight-total length, girth-total length, and standard length-total length regressions for *Larimus fasciatus* with supporting statistics. All regressions were significant at $\alpha = 0.01$; ν is from Ricker's (1973) GM regression. Measures are grams and millimeters. See Methods for symbols.

| Equation	n	TL range	$100r^2$	Residual MS	Corrected total SSx	Corrected total SSy	$\bar{x}$	$\bar{y}$	GM ν
FEC = −295,307 + 2,498.36 TL	40	136-163	29.7	$4,966 \times 10^5$	1,280.00	$2,686 \times 10^7$	146.4	70,453	4,581.2
$\log_{10}$FEC = −5.5049 + 4.7689 $\log_{10}$TL	40	136-163	27.1	0.0178	0.0111	0.9280	2.17	4.82	9.1573
FEC = −32,999 + 2,223.57 TW	40	136-163	35.1	$4,588 \times 10^5$	1,906.00	$2,686 \times 10^7$	46.5	70,453	3,753.7
$\log_{10}$FEC = 2.6564 + 1.3013 $\log_{10}$TW	40	136-163	28.4	0.0175	0.1554	0.9280	1.67	4.82	2.4435
$\log_{10}$ TW = −5.5981 + 3.3481 $\log_{10}$ TL (males + females)	1,938	52-179	99.3	0.0015	34.42	388.67	2.03	1.20	3.3605
$\log_{10}$ TW = −5.4761 + 3.2883 $\log_{10}$ TL (males + females + immatures)	2,874	22-179	99.4	0.0025	108.91	1,184.74	1.92	0.84	3.2983
G = −1.21 + 0.77 TL	2,871	22-179	99.2	7.75	2,628,914 (G)		92.09	69.35	0.77
TL = 2.35 + 1.29 G	2,871	22-179	99.2	13.09	4,439,633 (TL)		69.35	92.09	1.30
SL = −5.63 + 0.83 TL	2,875	22-179	99.8	2.23	3,066,599 (SL)		92.08	70.76	0.83
TL = 6.96 + 1.20 SL	2,875	22-179	99.8	3.24	4,446,964 (TL)		70.76	92.08	1.20
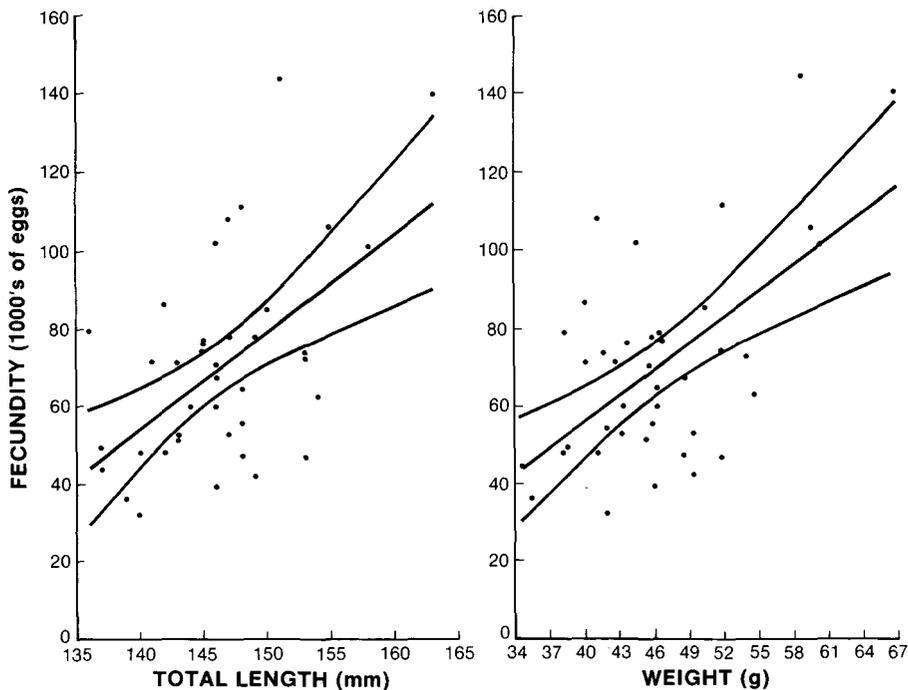
FIGURE 14.—Regressions of fecundity on total length and total weight with 95% confidence limits for $\bar{y}_x$ for *Larimus fasciatus*.
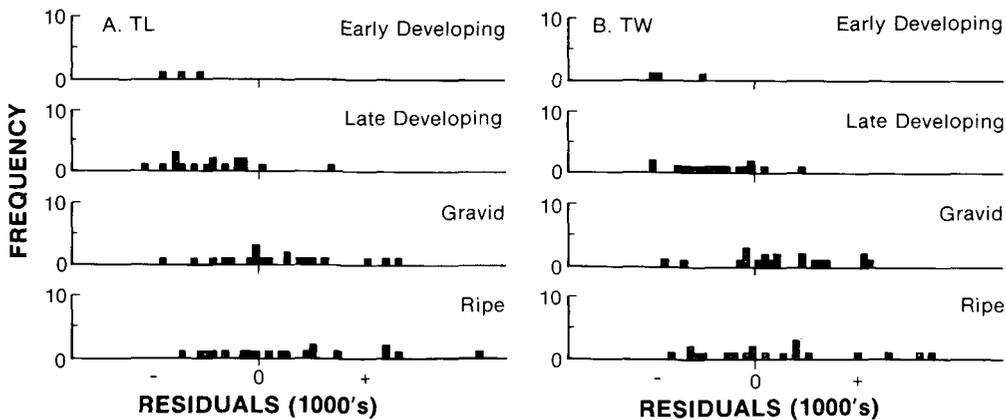

FIGURE 15.—Residual plots of maturity stages of *Larimus fasciatus* for relationship between fecundity and total length (A) and total weight (B) regressions.

curs in July and August and that spawning primarily occurs in two discrete periods, a major fall peak in September-November and a minor spring peak in April-June. The existence of distinct spring and fall spawning periods is supported by 1) Hoese's (1965) collection of larval fish only in June (11.5-25 mm SL modal length) and October (14-39 mm SL modal length) off Port Aransas,

Tex., 2) Ross's (1978) collection off North Carolina of presumably fall-spawned fish in February (79 mm modal TL = 60 mm SL) and what must be spring-spawned fish in July (75 mm modal TL = 57 mm SL), 3) Powles's (1980) collections of larval fish in the periods April-May and August-September but not in June-July between Cape Canaveral and Cape Fear, and 4) collections of

larval fish in the periods April-June and August-October between Cape Lookout and Chesapeake Bay (Berrien pers. commun. footnote 7 in Powles 1980). This bimodal pattern, moreover, is similar to findings of distinct spring- and fall-spawning periods in other Gulf fishes such as *Cynoscion arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), and *Peprilus burti* (Murphy 1981). Murphy and Chittenden[7] integrated biological findings with hydrographic data of Kelly and Randall[8] and suggested hydrographic reasons for this pattern in *P. burti* and *C. nothus*, which probably apply also to *L. fasciatus* and many other species: spawning is timed to coincide with the periodicity of downcoast alongshore currents (toward Mexico) and onshore Ekman transport at the surface. These phenomena probably transport pelagic eggs and larvae inshore and "downstream" to nurseries in the northwestern Gulf from spawning grounds located "upstream" in or toward the north central Gulf. Current transport mechanisms reverse in the summer (a variable period but about mid-June-early August) and would carry pelagic eggs and larvae offshore, which presumably is unfavorable to survival in many species, or toward the north central Gulf. If spawning is substantial, and successful, during summer, our length-frequency data and those for the other species cited indicate summer-spawned individuals do not subsequently appear in the northwestern Gulf. Presumably, their existence would be reflected as unimodal, or at least not clearly bimodal, length frequencies when adequate data become available for the north central Gulf.

Our finding that the few spring-spawned fish disappeared after August at 3-5 mo of age agrees with Hildebrand and Cable (1934) who collected what must have been spring-spawned fish in July ($\bar{x}$ = 34 mm, range 3-70 mm ?L) and August ($\bar{x}$ = 54 mm, range 3-77 mm ?L) off North Carolina and noted they were absent later. Because the magnitude of spring spawning appears so small, for practical stock assessment purposes, our data could just as well be interpreted as one long period

with little or no spawning from April to August. It seems more meaningful, however, to regard the spawning of *L. fasciatus* as occurring during two discrete periods because Murphy and Chittenden (footnote 7) suggested a hydrographic basis for that pattern.

Our findings are new that fall-spawned groups spawn in both spring and fall periods and that spring spawning is the product of fish about 20 mo old. Shlossman and Chittenden (1981) noted that temporal isolation of spawned groups in *C. arenarius* implied reproductive isolation and might indicate separate populations. The temporally separate spawned groups in *L. fasciatus*, however, are not reproductively isolated and apparently do not form separate populations because the same spawned group spawns in both periods. This simplifies management, because separate data may not be necessary for both spawning periods, especially considering that one is very small.

Shlossman and Chittenden (1981) and DeVries and Chittenden (1982) noted that the existence of two spawned groups in *C. arenarius* and *C. nothus* might buffer population stability as a multiple year class structure does in longer lived species. In *L. fasciatus*, however, the contribution that spring-spawned groups make to total population size is probably too small to buffer fluctuations at any reasonably "normal" stock size.

Bathymetric Distribution

Larimus fasciatus primarily is restricted to the inner continental shelf. Our finding, that they range from <5 to 55 m but are most common from 5 to 16 m, agrees with Hildebrand (1954), Miller (1965), Burns (1970), Milstein and Thomas (1976), and Wenner et al. (1979a, b). Franks et al. (1972) captured most specimens in 37-55 m off Mississippi which supports Chittenden and McEachran's (1976) suggestion that the white shrimp community, of which *L. fasciatus* is a member, penetrates into deeper water in the north central Gulf than it does in the northwestern area. However, Springer and Bullis (1956) collected fish at 106 m off both Mississippi and Texas.

Age Determination and Growth

Little literature exists on age determination and growth in *L. fasciatus*. We determined age by length-frequency analysis because our data came from a long-term set of cruises close enough together in time that modes were easily followed.

[7]Murphy, M. D., and M. E. Chittenden, Jr. Unpubl. manuscr. Reproduction, movements, and population dynamics of the gulf butterfish, *Peprilus burti*. 66 p. Marine Research Laboratory, Florida Department of Natural Resources, 100 Eighth Avenue, S.E., St. Petersburg, FL 33701.

[8]Kelley, F. J., Jr., and R. E. Randall. 1980. Physical oceanography. *In* R. W. Hann, Jr. and R. E. Randall (editors), Evaluation of brine disposal from the Bryan Mound site of the Strategic Petroleum Reserve Program, p. (1-1)-(1-93). National Technical Information Service, Springfield, VA 22150 (DOE/P010114-1).

Moreover, we observed so little overlap of lengths from different spawned groups that few individuals could have been incorrectly aged and basic conclusions on apparent growth and mortality would be little affected by such error. As Geoghegan and Chittenden (1982) found for *Stenotomus caprinus*, length-frequency analysis can be a superior method to age *L. fasciatus* because 1) little spawning occurs in other than one major discrete period each year, 2) length frequencies within spawned groups are reasonably described by a normal distribution, 3) growth of large and small fish within a spawned group appears uniform since the variance was generally constant between cruises, and 4) life span is short so age determination need be applied only to a few ages, the ideal situation for using length frequencies (Lagler 1956; Tesch 1971). Ross (1978) successfully used scales and otoliths to determine age of North Carolina fish, but we were not able to do so in limited trials and did not pursue these methods further because it seemed unnecessary.

Larimus fasciatus reach slightly larger sizes at age off North Carolina than apparent sizes we found in the northwestern Gulf. Von Bertalanffy predictions of size at age off North Carolina (Ross 1978) were 153 mm (121.3 mm SL) at age I, 188 mm (151.1 mm SL) at age II, and 209 mm (168.0 mm SL) at age III compared with quadratic and von Bertalanffy predictions of 130-150 mm at age I and 155-180 mm at or approaching age II for the northwestern Gulf. Our finding that growth is greatest in the spring and summer agrees with Ross (1978).

Maximum Size, Life Span, and Mortality

The largest *L. fasciatus* we found in the northwestern Gulf (182 mm) is smaller than most maximum sizes reported from the north central Gulf (Louisiana: 208 mm by Hildebrand 1954, 195 mm ?L by Dunham 1972, and Mississippi: 202 mm by Franks et al. 1972, 189 mm by Christmas and Waller 1973, 187 mm in our data), and much smaller than those reported from the Atlantic coast of the United States (New York to Florida: 220 mm by Wilk and Silverman 1976, Chesapeake Bay: 215 mm ?L by Hildebrand and Schroeder 1928, off North Carolina: 205 mm ?L by Hildebrand and Schroeder 1928, 206 mm ?L by Hildebrand and Cable 1934, and 225 mm = 182 mm SL by Ross 1978). The largest record is a 271 mm specimen collected off Mississippi (Franks 1970). The larger size off the Atlantic coast of the United

States may reflect greater longevity there, especially from about Cape Lookout or Cape Hatteras north where zoogeographic change in population dynamics may occur (White and Chittenden 1977). Ross (1978) collected age III fish off North Carolina, but the oldest fish we collected only approached age II.

The appearance of larger *L. fasciatus* in the north central Gulf than in the northwestern area follows a pattern apparent in a variety of species (Murphy and Chittenden footnote 7) including *C. nothus, P. burti, S. caprinus, Brevoortia patronus*, and *Micropogonias undulatus*. These authors suggested this could reflect 1) small but fundamental percentage composition and population dynamics differences between these areas, 2) greater biomass at all ages in the north central Gulf, not necessarily population dynamics differences, so that greater numbers of large fish might be captured there even if percentage compositions did not vary, and/or 3) probable permanent emigration from the northwestern to the north central Gulf by larger, older, spawning or postspawning fish as they approach age I. They suggested the last explanation applied to *C. nothus, P. burti*, and probably other fishes, and that it would be manifested as between area population dynamics differences. The following findings also suggest that *L. fasciatus* too more or less permanently emigrates from the northwestern to the north central Gulf as spawning and age I approaches 1) the plateaus in length formed in August and seeming cessation of somatic growth in later stages of gonad development, and 2) the appearance in the northwestern Gulf in July 1981 of an abundant fall-spawned group approaching age II. This older spawned group, and parallel spawned groups in other years, was absent or rare in all other months even though our data were based on 71 cruises and 3,390 tows over 4 yr.

Because larger, older *L. fasciatus* probably emigrate to the north central Gulf, the typical maximum life span of 1-2 yr we observed for the northwestern area may be a little low for a stock that ranges over both areas. With the exception of the very large specimen that Franks (1970) found, the largest individuals reported from the north central Gulf are only 189-208 mm as noted. This is not much larger than our largest specimen (182 mm) from the northwestern area, which was 20 mo old. Moreover, these maximums are similar to von Bertalanffy predictions of mean sizes at age II (165-185 mm) or at age III (175-195 mm) that we found, and sizes of 188 and 204 mm Ross (1978)

found at ages II and III, respectively. Therefore, a t_L value of 2-3 yr may be realistic for a stock that ranges over the north central and northwestern Gulf. We assume in suggesting this, that differences in size compositions do not reflect only possible intra-Gulf growth differences and greater size at age in the north central Gulf.

The mean *apparent* time-specific and cohort-specific total annual mortality rates we observed for the northwestern Gulf (92-100%) agree with theoretical estimates (Royce 1972:238) of 90-100% if maximum life span typically is only 1-2 yr as we found for that area. Because larger, older *L. fasciatus* probably emigrate to the north central Gulf, our observed mortality estimates are probably too high for a stock that ranges over both areas. Theoretical values of 80-90% based on a 2-3 yr typical maximum life span may be more realistic, a magnitude which agrees with the lowest values tenable for other sympatric species such as *C. arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *S. caprinus* (Geoghegan and Chittenden 1982), and *P. burti* (Murphy 1981). Even values of 80-90% are higher than the three lowest mortality rates we found for the northwestern Gulf (55-74%) and rates of 57 and 81% that Ross (1978) reported off North Carolina; the latter range of values is theoretically appropriate as an average over life spans of 3-5 yr, although present data suggest 4-5 yr is too large a value of t_L for the Gulf.

General

Population dynamics of *L. fasciatus* are similar to those reported from the northwestern Gulf for *M. undulatus* (White and Chittenden 1977), *C. arenarius* (Shlossman and Chittenden 1981), *C. nothus* (DeVries and Chittenden 1982), *S. caprinus* (Geoghegan and Chittenden 1982), *P. burti* (Murphy 1981; Murphy and Chittenden footnote 7), and in *Centropristis philadelphica* ignoring its hermaphroditism (Ross and Chittenden[9]). Our findings support the suggestions that 1) groundfishes of the white and brown shrimp communities in the Gulf have evolved a common pattern of population dynamics characterized by small size, early age at maturity, short life spans, high mor-

tality rates, and rapid turnover of biomass (Chittenden and McEachran 1976; Chittenden 1977), and 2) more or less permanent spawning or post-spawning emigration may occur from the northwestern Gulf to the north central area as fish approach age I (Murphy and Chittenden footnote 7). Because typical maximum life spans may be closer to 2-3 yr than 1-2 yr, these fishes may be a little more sensitive to growth overfishing than Chittenden's (1977) simulations, based on a 2 yr life span, suggest for *M. undulatus*.

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