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BATHYMETRIC DISTRIBUTION, SPAWNING PERIODICITY, SEX RATIOS, AND SIZE COMPOSITIONS OF THE MANTIS SHRIMP, *SQUILLA EMPUSA*, IN THE NORTHWESTERN GULF OF MEXICO[1]

The mantis shrimp, *Squilla empusa*, ranges in the western Atlantic Ocean from Maine through the Gulf of Mexico (Gulf) to Surinam (Manning 1969). This stomatopod occurs in high-salinity waters (Gunter 1950; Franks et al. 1972) and is one of the more common macrocrustaceans in the northern Gulf (Hildebrand 1954). *Squilla* sp. may be important predators of other crustaceans, polychaetes, and fish (Camp 1973; Caldwell and Dingle 1976), but they also serve as food for many fishes including *Rachycentron canadum, Lutjanus campechanus, Sciaenops ocellatus, Micropogonias undulatus*, and *Rhomboplites aurorubens* (Knapp 1951; Moseley 1966; Overstreet and Heard 1978a, b; Grimes 1979).

Despite its importance, little detail is known of the life history of *Squilla empusa*. The pelagic larval stages have been described (Morgan and Provenzano 1979; Morgan 1980), and much information has been published recently on the worldwide zoogeography and distributional interrelationships, evolutionary ecology, and life history patterns of stomatopods, primarily coral-dwelling taxa (Reaka 1979, 1980; Reaka and Manning 1980). However, the latter information does not deal with *S. empusa*, and it may not be valid to extrapolate to this species. Reaka (1979: table 5) reported that the coral-dwelling taxa were long-lived and gave estimates of 26-34 yr to reach median size (using mean growth increments and mean molting frequencies), 12-14 yr (using mean growth and maximum molting), or 4-8 yr (using maximum growth and molting). Although we could not determine age of *S. empusa* readily from length-frequency analysis, a much shorter maximum life span (1-3 yr) is part of what appears to be a common pattern of population dynamics in the white and/or brown shrimp communities where *S. empusa* occur (Chittenden and McEachran 1976; Chittenden 1977).

This paper describes bathymetric distribution, size at maturation, spawning periodicity, sex ratios, size compositions, and morphometric relationships for *S. empusa* collected in the northwestern Gulf during routine trawling operations.

[1]Technical article TA 18359 from the Texas Agricultural Experiment Station, Texas A&M University, College Station, TX 77843.

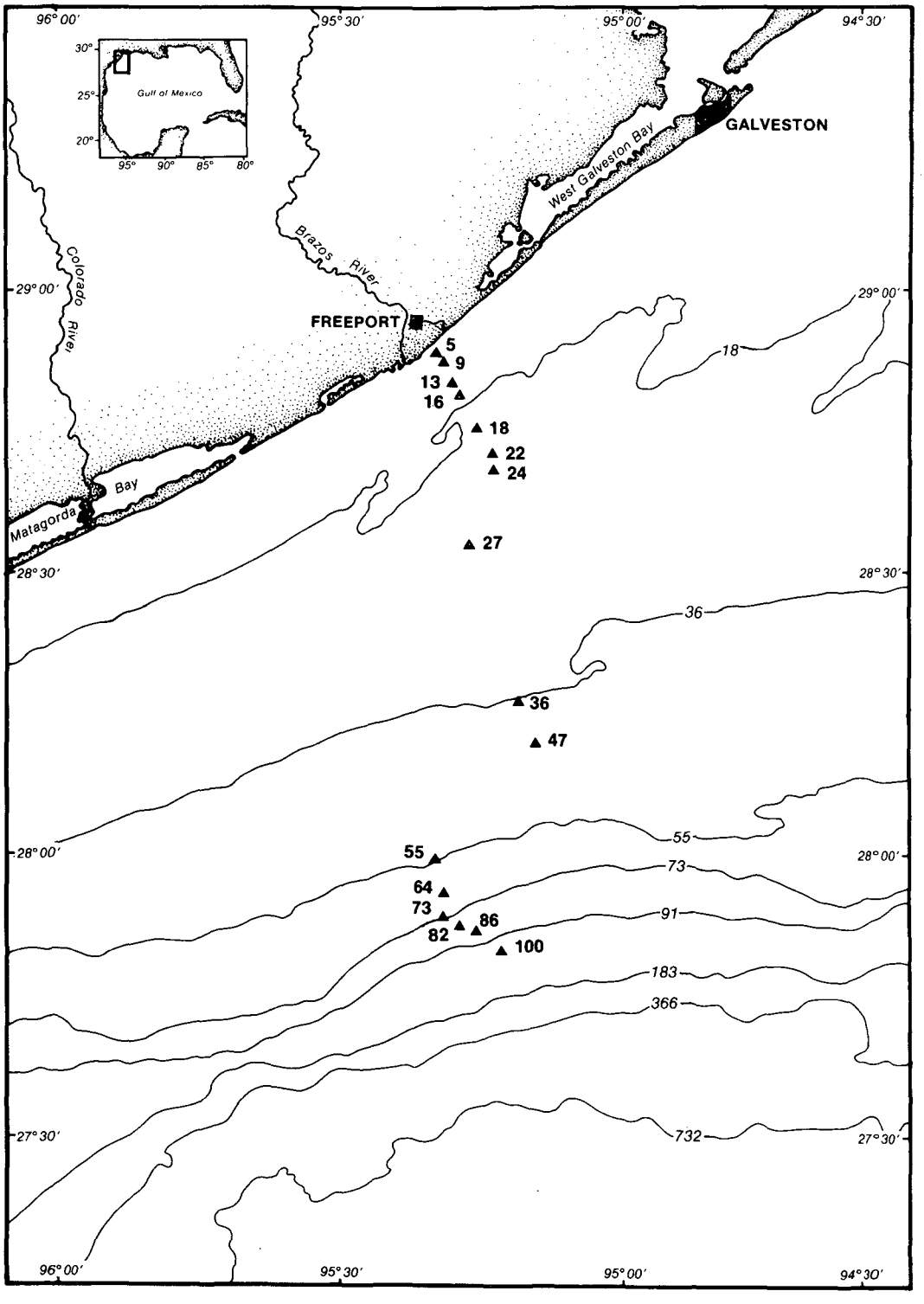

FIGURE 1.—Location of sampling areas. Station depths and bathymetric contours are indicated in meters.

Methods

Squilla empusa were collected fortnightly 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 tickler chain. Except for August and September 1979, a day and a night cruise were made each month in the period July 1979-October 1980 (Table 1). Data for *Squilla* were obtained from the first of two 10-min tows (bottom time) made at depths of 5, 9, 13, 18, 24, 27, 36, 47, 55, 64, 73, 82, 86, and 100 m, from 4 tows at 16 m, and from 12 tows at 22 m.

All *S. empusa* were culled from the catch, preserved in 10% Formalin[2], washed in fresh water, then stored in 70% ethanol. Specimens from the period July 1979-June 1980 were later processed to determine sex, total length (TL), and total wet weight (TW). Carapace length (CL), abdominal length (AL), abdominal width (AWD), and abdominal wet weight (AW) were measured on all specimens collected during seven cruises. Measurements follow Manning (1969), except that abdominal length was measured along the dorsal midline from the anteriormost portion of the first abdominal somite to the apices of the submedian teeth of the telson. Females collected during the period July 1979-October 1980 were assigned gonad maturity stages described in Table 2. Typical maximum size was approximated as a length l_L correlated with the Beverton-Holt yield model parameter t_L (Gulland 1969) following Alverson and Carney's (1975) definition that only 0.5-1% of the catch exceeds age t_L. All length measurements presented herein are total length unless stated otherwise.

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

TABLE 1.—Total length composition statistics (mm) by cruise for *Squilla empusa* from the Gulf of Mexico off Freeport, Tex., July 1979-October 1980. Night and day cruises are indicated by N and D.

Collection	*n*	Length (mm) Range	Mean	*s*	99% confidence limits of observations
5-9 July 79 N	695	26-132	85.7	17.1	41.7-129.7
19-22 July 79 D	6	77-108	88.2	14.0	31.8-144.6
22-25 Aug. 79 D	2	76-91	83.5	10.6	—
22-25 Sept. 79 D	491	37-124	71.7	14.3	34.9-108.5
2-6 Oct. 79 N	1,049	40-113	75.2	12.4	43.3-107.1
16-19 Oct. 79 D	458	47-109	75.0	11.1	46.4-103.6
3-6 Nov. 79 N	614	38-112	76.2	12.1	45.0-107.4
15-18 Nov. 79 D	72	51-96	71.0	9.5	46.5- 95.5
1-4 Dec. 79 N	137	53-102	75.4	11.9	44.7-106.1
14-19 Dec. 79 D	96	32-115	83.8	14.7	45.9-121.7
3-6 Jan. 80 N	857	29-123	77.0	15.5	37.1-116.9
16-20 Jan. 80 D	71	49-116	82.9	14.5	45.5-120.3
4-11 Feb. 80 N	948	33-116	78.6	15.1	39.7-117.5
15-20 Feb. 80 D	236	35-109	77.6	13.4	43.1-112.1
5-8 Mar. 80 N	680	34-113	79.2	11.8	48.8-109.6
19-23 Mar. 80 D	447	40-110	75.5	12.5	43.3-107.7
1-5 Apr. 80 N	197	37-106	77.1	12.7	44.4-109.8
16-20 Apr. 80 D	313	33-110	76.0	13.6	41.0-111.0
5-10 May 80 N	914	37-117	74.1	14.7	36.2-112.0
19-22 May 80 D	215	46-113	72.9	13.4	38.4-107.4
2-6 June 80 N	872	42-126	82.1	10.9	54.0-110.2
19-24 June 80 D	56	65-115	85.3	10.5	58.3-112.3
7-11 July 80 N	335	63-114	89.0	8.5	67.1-110.9
21-24 July 80 D	1	61	61.0	—	—
5-15 Aug. 80 N	478	32-122	75.5	15.6	35.3-115.7
26-29 Aug. 80 D	0	—	—	—	—
7-11 Sept. 80 N	74	54-115	84.2	11.9	53.5-114.9
22-25 Sept. 80 D	45	26-114	73.9	19.4	23.9-123.9
6-9 Oct. 80 N	60	46-117	83.2	12.3	51.5-114.9
20-31 Oct. 80 D	77	28-118	82.2	20.1	30.4-134.0

TABLE 2.—Descriptions of gonad maturity stages assigned to female *Squilla empusa*.

Stage	Description
1. Immature, Spent, or Resting	Ovaries narrow transparent tubes. We could not distinguish visually between immature, spent, or resting individuals, nor assign age based on length frequency analysis.
2. Early Developing	Ovaries with slight yellow coloration occupy 0-25% of abdominal cavity.
3. Late Developing	Ovaries with orange coloration occupy 25-50% of abdominal cavity; little or no expansion of ovaries within each segment.
4. Gravid	Ovaries deep orange in color occupy 50-100% of abdominal cavity; ovaries in each segment definitely expanded.

Results

Bathymetric Distribution and Diel Periodicity

Squilla empusa were collected from 5 to 86 m depths. Maximum abundance (male: 14.4-16.2 individuals/tow; female: 17.5-19.6 individuals/tow) occurred at 9-16 m (Fig. 2). Abundance was much lower at 5 m (male: 4.6 individuals/tow; female: 5.9 individuals/tow) and approximated that at 27 m. Abundance was even lower but uniform (<2.0 individuals/tow) from 36 to 55 m; only one specimen each was collected at 64 and 86 m.

Size compositions of *S. empusa* varied with depth, although trends were similar for each sex. Individuals from the entire observed size range (26-132 mm) occurred in depths of 5-27 m (Fig. 3); size compositions of each sex were similar throughout these waters. Deeper waters were occupied primarily by individuals in each sex greater than the average size of 77 mm. Few individuals <80 mm (<1%) occurred deeper than 27 m, and no individuals <80 mm occurred deeper than 55 m.

Catches of *S. empusa* were greatest at night. Mean catch/tow during the 1-yr period October 1979-September 1980, when both day and night

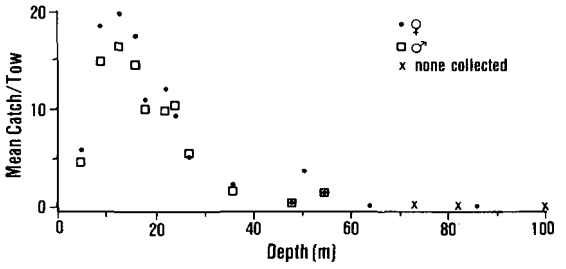

FIGURE 2.—Mean catch/tow (numbers) of *Squilla empusa* by depth for each sex.

cruises were made each month, was 6.79 during the day but 23.93 at night. The difference is significant at $\alpha = 0.01$ using a one-way analysis of variance ($F = 15.13$; 22 df), even though this simple model maximizes the error mean square in comparison to more complex models.

Size at Maturity and Spawning Periodicity

Squilla empusa begin to mature at 70 mm. No individuals <70 mm were in Early-Developing, Late-Developing, or Gravid stages (Fig. 4). Only a small fraction of all Gravid females (15%) were 70-80 mm, but half were gravid by 90 mm. There was little difference in size between individuals in the Early-Developing, Late-Developing, or Gravid stages, respective means being 88, 90, and 91 mm.

Spawning apparently occurs over an 8-mo period that begins in January and ends in July-August. Few or no Early-Developing, Late-Developing, or Gravid individuals were captured from September through December either year (Fig. 5). Individuals in these stages were abundant in January and remained so through July-August. Immature and Spent or Resting individuals greatly predominated during the period September-December each year.

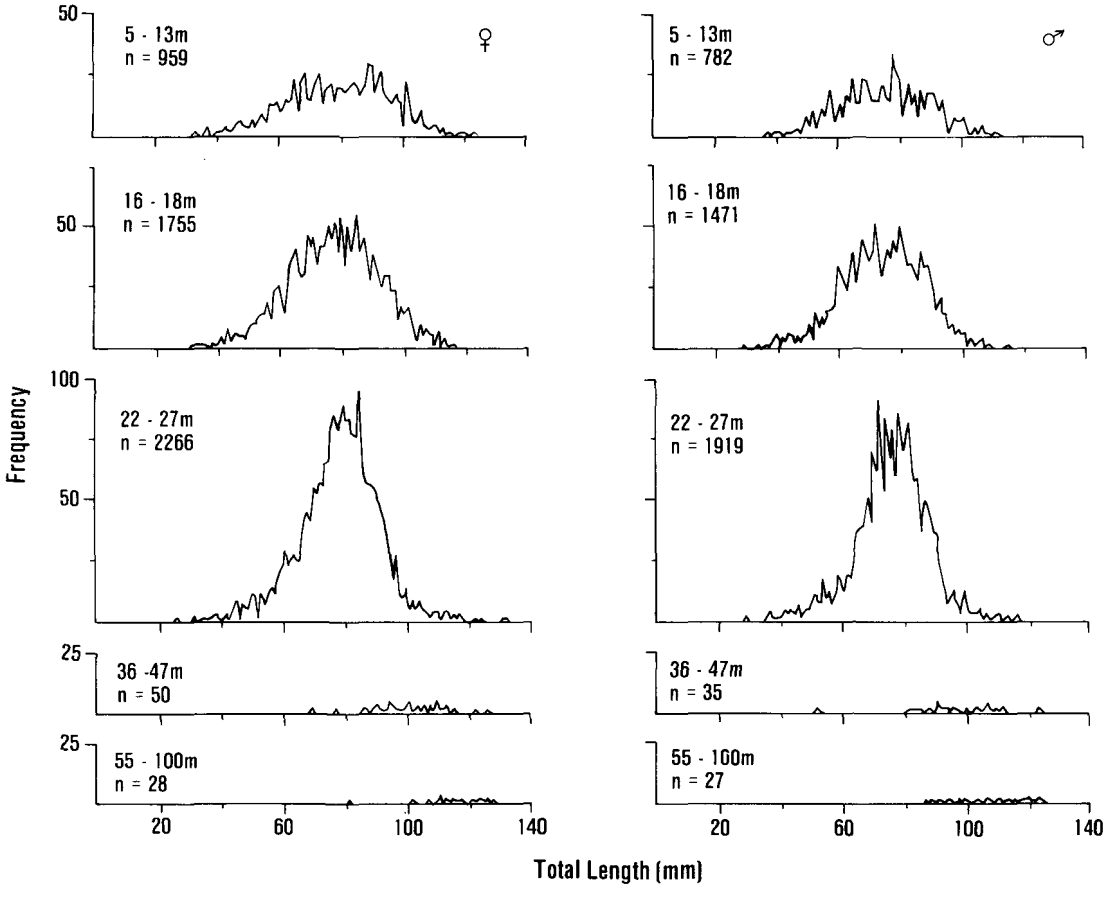

FIGURE 3.—Length frequencies of *Squilla empusa* by depth for each sex.

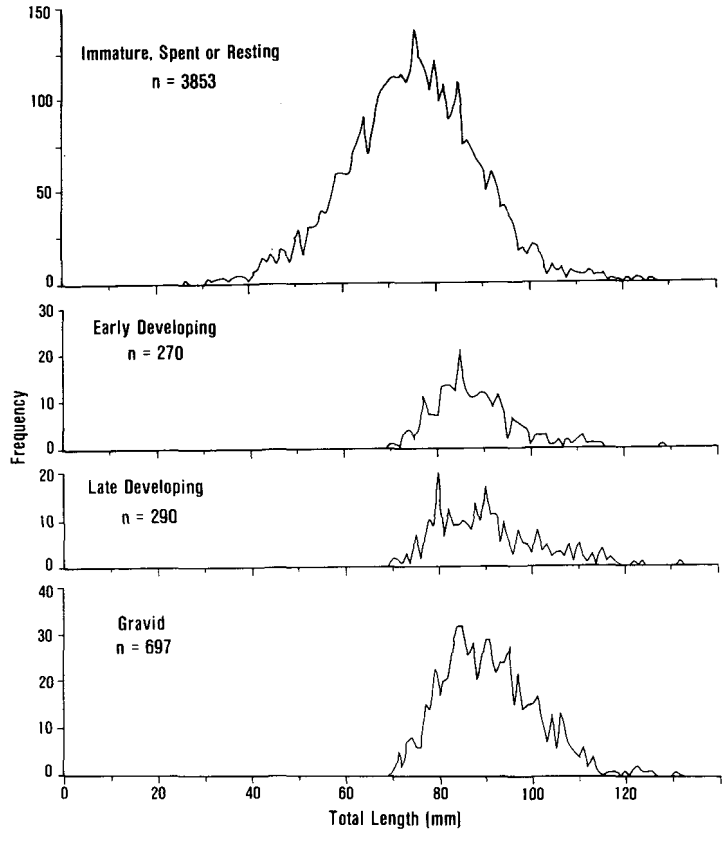

FIGURE 4.—Size of female *Squilla empusa* by maturity stage. Maturity stages are described in Table 2.

Sex Ratios

Females made up 54% of the overall catch of *S. empusa* and were significantly more abundant than males ($\chi^2 = 71.53$, $P < 0.05$). Except in August 1979 when only two individuals were caught, females predominated and made up 52-63% of the 500-1,000 *S. empusa* usually caught each month. Sex ratios did not differ significantly between depths ($\chi^2 = 1.82$, 4 df, $P > 0.05$). Sex ratios generally were equal from 30 to 80 mm, but females increasingly predominated at larger sizes (Fig. 6). Sex ratios did not differ significantly from a 1:1 ratio until *S. empusa* exceeded 80 mm (Table 3).

TABLE 3.—Observed sex ratios and chi-square statistics for *Squilla empusa* divided into 10 mm length groups, July 1979-June 1980. Asterisks indicate significant χ^2 at $\alpha = 0.05$.

Length range (mm)	No. individuals		χ^2
	Male	Female	
21-30	3	1	1.00
31-40	28	29	0.02
41-50	117	138	1.73
51-60	381	382	0.00
61-70	835	837	0.00
71-80	1,353	1,357	0.01
81-90	1,069	1,339	30.27*
91-100	387	699	89.64*
101-110	94	241	32.25*
111-120	19	69	28.41*
121-130	4	16	7.20*
131-140	—	2	2.00
Total	4,290	5,110	—

Maximum Size and Intrayear Variations in Size

Typical maximum size reached by *S. empusa* in the northwestern Gulf is 110-115 mm. The largest of 9,400 specimens we captured was only 132 mm, 99% were <110 mm, and 99.5% were <114 mm (Fig. 7).

Size compositions showed little change throughout the sampling period. Except for the

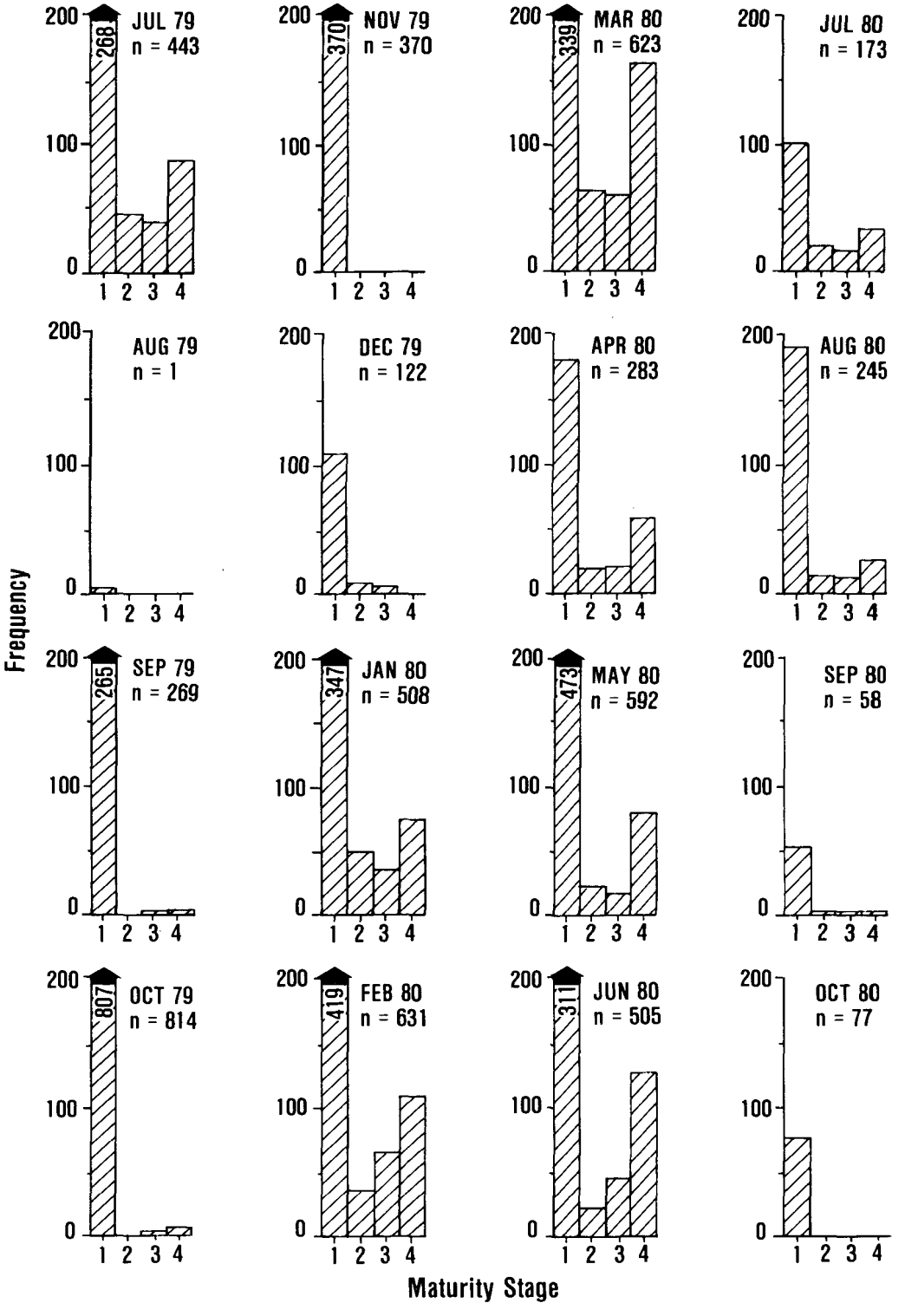

FIGURE 5.—Monthly numbers of female *Squilla empusa* by maturity stage for the period July 1973-October 1980. Stages (see Table 2) are 1) Immature, Spent or Resting, 2) Early Developing, 3) Late Developing, 4) Gravid.

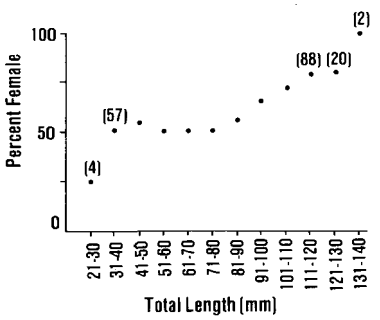

FIGURE 6.—Percentage of female *Squilla empusa* by size. Sample sizes are 255-2,710/size class, except where indicated.

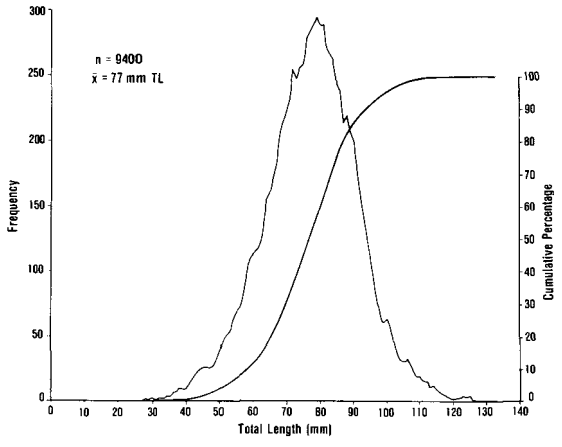

FIGURE 7.—Length frequency (moving averages of three) and cumulative percentage of all *Squilla empusa* collected off Freeport, Tex., July 1979-June 1980.

21-24 July 1980 day cruise when only one specimen was captured, mean sizes on each cruise ranged between only 71 and 89 mm (Table 1). In addition, 99% confidence limits for observations also showed little variation during this period.

Length-Weight-Width-Relationships

Length-length, length-weight, and length-width relationships are presented in Table 4. Length-weight regression coefficients were significantly different between the sexes ($F = 5.03$; 1, 9, 381 df; $P < 0.05$). However, the minor difference ($b = 2.94$ vs. 2.96) may have little biological meaning, thus pooled regression statistics are also presented to simplify stock assessment. Calculated length-weight regression coefficients significantly exceeded $\beta = 3.0$ at $\alpha = 0.05$ (data pooled, $t = -12.23$; males, $t = -5.89$; females, $t = -10.42$).

Discussion

Bathymetric Distribution and Diel Periodicity

Squilla empusa occur on a mud or sandy-mud bottom (Franks et al. 1972) as do several of its congeners (Reaka and Manning 1980). This species ranges on such bottoms across most of the continental shelf in the northern Gulf. We captured *S. empusa* to depths of 86 m in agreement with Hildebrand (1954) and Franks et al. (1972), who captured specimens to 82 and 91 m, respectively. Our findings that *S. empusa* were common

TABLE 4.—Length-length, length-weight, and length-width regressions for *Squilla empusa*, sexes pooled unless indicated, with supporting statistics. Measurements are in grams and millimeters. Size range for each equation is 26-132 mm TL. All regressions are significant at $\alpha = 0.001$. Corrected total sum of squares is for y unless x is designated; ν is from Ricker's (1973) GM functional regression. See below for definition of symbols.

	Equation	n	$100\,r^2$ (%)	Residual Mean square	Corrected total sum of squares	ν	$\bar{x}$
[1]CL	= 0.82 + 0.20 TL	1,021	93.4	0.4345	6,728.42	0.21	76.74
TL	= 1.21 + 4.70 CL	1,021	93.4	10.2521	158,764.13	4.86	16.09
AL	= −0.36 + 0.62 TL	1,023	97.6	1.4486	62,048.05	0.63	76.70
TL	= 2.40 + 1.58 AL	1,023	97.6	3.7213	159,395.26	1.60	46.92
AW	= −0.01 + 0.63 TW	1,026	99.1	0.0423	4,963.75	0.63	7.13
TW	= 0.08 + 1.58 AW	1,026	99.1	0.1067	12,505.14	1.59	4.46
AWD	= −0.11 + 0.38 AL	1,028	94.6	0.5012	9,555.32	0.39	46.87
AL	= 2.81 + 2.49 AWD	1,028	94.6	3.2828	62,590.81	2.56	17.70
AWD	= −0.41 + 0.24 TL	1,023	93.9	0.5669	9,486.92	0.25	76.70
TL	= 6.33 + 3.97 AWD	1,023	93.9	9.5249	159,395.26	4.10	17.72
All Data							
$\log_{10}$ TW	= −4.7725 + 2.9430 $\log_{10}$ TL	9,383	97.7	0.0014	581.99; 65.65(x)	2.9774	1.88(TL) 0.76(TW)
Males							
$\log_{10}$ TW	= −4.7974 + 2.9574 $\log_{10}$ TL	4,280	97.7	0.0014	247.66; 27.61(x)	2.9950	1.87(TL) 0.74(TW)
Females							
$\log_{10}$ TW	= −4.7615 + 2.9362 $\log_{10}$ TL	5,103	97.8	0.0014	330.23; 37.47(x)	2.9686	1.89(TL) 0.78(TW)

[1]CL = Carapace length; TL = total length; AL = abdominal length; AW = abdominal wet weight; TW = total wet weight; AWD = abdominal width.

inshore of 24 m and most abundant at 9-16 m agree with Camp's (1973) data off west central Florida, but contrast with the data of Hildebrand (1954), who found greatest abundance at 35-42 m off Louisiana. *Squilla empusa* apparently reach peak abundance in much deeper water in the north central Gulf than off Texas, which may simply reflect the phenomenon that the inshore white shrimp community penetrates into deeper water there than it does in the northwestern area (Chittenden and McEachran 1976).

We captured greater numbers of *S. empusa* at night as did Hoese et al. (1968), who suggested that *S. empusa* retreat to burrows during the day and consequently are more likely to avoid trawls.

Spawning Periodicity

The prolonged spawning period of January to July-August that we found agrees, in part, with Franks et al. (1972), who collected stomatopod larvae in the plankton from April through September off Mississippi, and with Swingle (1971), whose limited data from Mobile Bay, Alabama, suggested winter and spring spawning. In addition, *S. empusa* 10-25 mm long occurred May-December in the stomachs of *Centropristis philadelphica* collected in conjunction with our study (Pavela and Ross[3]); *S. empusa* were most abundant in these stomachs in September and October. About 4-5 mo elapsed between our first collection of gravid *S. empusa* and their first appearance in *C. philadelphica* stomachs. These data suggest *S. empusa* spawn over an extended period of time and spend an extended time in the egg mass, propelagic, or pelagic stages of development, as occur in other closely related stomatopod species (Reaka 1979; Senta 1967 and Pyne 1972 cited in Morgan 1980).

Sex Ratios and Maximum Size

The change in sex ratio we observed at 80 mm, which is about the size at which females mature, may reflect different mortality rates between the sexes after maturity or growth cessation in larger males. Our data do not permit a choice between these possibilities.

The maximum size of 132 mm that we observed is similar to other maximum sizes for this species reported from the northern Gulf (Hoese et al. 1968, 120 mm SL; Christmas and Langley 1973, 145 mm). Much larger specimens have been reported from the Atlantic coast north of Cape Hatteras, N.C. (Bigelow 1941, 180 mm, type of length not given). These geographic differences in maximum sizes of *S. empusa* appear similar to differences in size that are found in many fishes (White and Chittenden 1977; Shlossman and Chittenden 1981; Geoghegan and Chittenden 1982; Murphy and Chittenden[4]). Therefore, our findings may reflect the zoogeographic change in population dynamics that these authors suggest occurs in the area of Cape Hatteras. Fishes, and possibly other taxa, as our data on *S. empusa* suggest, show smaller sizes, shorter life spans, higher mortality rates, younger age at maturity, more rapid turnover of biomass, and greater ability to avoid growth overfishing (see Gulland 1980) in the warm-temperate Carolinean Province waters of the Gulf of Mexico and South Atlantic Bight than do their conspecifics and congeners in the cold-temperate waters north of Cape Hatteras.

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