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Abundance and Distribution of Two Species of *Squilla* (Crustacea: Stomatopoda: Squillidae) in the Northern Gulf of Mexico

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ABUNDANCE AND DISTRIBUTION OF TWO SPECIES OF *SQUILLA* (CRUSTACEA: STOMATOPODA: SQUILLIDAE) IN THE NORTHERN GULF OF MEXICO

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Abstract: Stomatopods (mantis shrimps) are predatory benthic crustaceans. Mantis shrimp in the genus *Squilla* are frequent bycatch animals unintentionally collected in conjunction with the shrimp fishery in the Gulf of Mexico (GOM). Their carcasses are discarded instead of being retained for human consumption, fish meal, or other protein-based food products. The size, depth, salinity, and temperature distributions of these species, as well as their abundance based on gender, were examined to gain biological information that would be necessary if a fishery were to develop in the GOM. I collected samples (n = 2,854) of *Squilla empusa* and *Squilla chydaea* in the northern GOM at depths of 1–96 m at 56 stations. *Squilla chydaea* was generally collected in greater abundance and in deeper water compared to *S. empusa*, even though the biomass of *S. empusa* collected in this study was larger than that of *S. chydaea*. For both species, individuals were larger in body length and wet weight in the winter, but more individuals were collected in the summer. Female *S. chydaea* dominated the catch in summer; there was no seasonal difference in sex ratio for *S. empusa*. The potential for commercial harvesting of mantis shrimp in the northern GOM is discussed and compared to other mantis shrimp fisheries.

Introduction

Mantis shrimp (Crustacea: Stomatopoda) are benthic crustaceans that can be divided into two groups based on the morphology of their raptorial appendages: smashers and spearers (Caldwell and Dingle 1976). Spearer stomatopods represent one of the most commonly found marine fauna collected during trawling activities on the continental shelves in tropical and subtropical regions (Hendrickx and Sanchez-Vargas 2005). Stomatopods are very common in marine waters around the world with around 500 species being described (Muller 1994), and this group is ecologically and economically important. They often prey upon commercially important penaeid shrimps, make up a large portion of the bycatch in the shrimping industry (Hendrickx and Sanchez-Vargas 2005), oxygenate and release nutrients to the benthic habitat by burrowing into the sediment, and are commercially harvested in Europe and Asia.

Stomatopods are fished commercially and used mainly in animal feed and pet food, as biomonitors for toxicity, and for human consumption. Analyses of the nutritional content of *Squilla* have determined the suitable uses and quantities needed for animal feed (Nandeesha et al. 1989, Lekshmy Nair et al. 1991, Reddy et al. 2004). Mantis shrimp in the genus *Squilla* are also used as biomonitors for heavy metals and are useful in determining the pollution levels in waters from environmental disasters and from industrial pollution (Blasco et al. 2002, Storelli and Marcotrigiano 2002). Because the abundance, recruitment, and diversity of stomatopods are negatively correlated with contaminated waters (Risk and Erdmann 2000), monitoring mantis shrimp populations may be an efficient way to estimate pollution levels.

Several species of mantis shrimp are commercially harvested and all are in the family Squillidae. *Squilla mantis* Linnaeus 1758 is commercially fished, consumed by humans in Europe (Abello and Martin 1993), and is of considerable economic importance as the largest crustacean fishery in the Adriatic Sea (5,000 tons/yr) (Froglia and Giannini 1989, Blasco et al. 2002, Chakraborty et al. 2002). *Oratosquilla neap* Latreille 1825, fished off the coast of India, is used in carp diets, poultry feed, and manure (Sukumaran 1987, Nandeesha et al. 1989). *Erugosquilla massavensis* Kossmann 1880 is fished commercially in the Mediterranean (Maynou et al. 2005), and *Kempina mikado* Kemp and Chopra, 1921 is currently fished in the East China Sea (Hamano et al. 1996). *Oratosquilla oratoria* de Haan 1844 is used in sushi and in animal feed, has been highly sought in a commercial fishery off of Japan for the last 40 years, and is the most commercially valuable species in the bottom-trawl fishery with a yearly landing of over 5,000 tons (Yamazaki 1986, Ohtomi et al. 1992, Kodama et al. 2004).

The northern GOM is a main commercial fishing area for penaeid shrimp, and *Squilla* is one of the most abundant bycatch organisms in this region and in the Atlantic Ocean (Wenner and Wenner 1988), and it is thought to prey heavily upon penaeid shrimp. Fishers discard *Squilla* caught in shrimp fisheries and most are dead when discarded (Kesavan Nair and Iyer 1990). *Squilla empusa* Say 1818 and *S. chydaea* Manning 1962 are distributed in the GOM and the Atlantic Ocean (Manning 1969). Both species are similar in morphology of the raptorial appendage and telson spination, inhabit muddy bottoms, are regularly captured in large quantities in trawls, and are a potential new commercial resource (Rudloe 1971). There is little published information on the ecology of *Squilla* in general (Rockett et al. 1984, Dittel 1991) and in particular of *S. chydaea* (Manning 1969, Perry and Larson 2004). This species has not been cited in reports of extensive collecting from the GOM (Chace 1954) and is believed to be an endemic species within the GOM.

In contrast, *S. empusa* has been studied extensively, with larval descriptions (Morgan and Provenzano 1979) and preliminary growth and distributional data (Chace 1954, Manning 1969, Rockett et al. 1984) being available. Wortham (2001) and Wortham-Neal (2002a, 2002b) have recently studied burrow and habitat preference, reproductive morphology and grooming behavior in *S. empusa*. *Squilla empusa* is benthic, nocturnal, has been found in habitats with penaeid shrimps, is very abundant over sand and muddy bottom (Rudloe 1971, Rockett et al. 1984), and is the most common mantis shrimp in the GOM (Manning 1969, Rudloe 1971). Its distribution has been reported off Texas to Florida in the GOM, in the Atlantic Ocean from New England to Brazil, and in waters near West Africa and South America (Chace 1954, Manning 1969). *Squilla empusa* is also the second most abundant crustacean in numbers and the fourth largest in biomass in the Atlantic Ocean (Wenner and Wenner 1988).

In this paper, I present results on the abundance, distribution, sizes, sex ratio, and habitat of two species of mantis shrimp in the genus *Squilla* in the northern GOM, as well as the first detailed biological information on *S. chydaea*. The objective was to develop and compare the biological and ecological understanding of these mantis shrimp in the GOM, so that if a fishery is established it can be regulated properly.

Materials and Methods

I collected mantis shrimp species off the coasts of Texas, Louisiana, Mississippi, and Alabama in summer and winter months between 1996-2003 on SEAMAP (Southeast Area Monitoring and Assessment Program) cruises aboard the RV *Tommy Munroe*. Some mantis shrimp were also collected in junction with Dauphin Island Sea Laboratory (DISL) in Alabama. Stations were randomly selected prior to the cruise and each was sampled once with a 12.2 m (40 foot) bottom otter trawl with a 2.54 cm (1 inch) mesh cod end; each trawl lasted a maximum of 30 min. Because spearer stomatopods burrow into the substrate, otter trawls likely underestimate their abundance, but can be used to provide relative estimates of sex ratio, size classes, and species diversity (Dittel 1991). Mantis shrimp were only collected from dusk to dawn when they are believed to be out of their burrows.

Bottom water was collected using a Niskin bottle and depth (m), temperature (°C), and salinity (ppt) were measured at each station. The stomatopods collected at each station were sorted by species and preserved in 10% formalin. In the laboratory, the mantis shrimp were measured (carapace length, CL, 0.1 mm) and weighed (WW, 0.01 g). Carapace length was used because Manning (1969), Hamano et al. (1996), and Torisawa et al. (1998) determined that CL is an accurate predictor of total length in spearer mantis shrimp. Gender was determined by identifying the penes at the base of the 8th walking appendage on males and a modified sixth ventral thoracic segment with a seminal receptacle on females (Wortham-Neal 2002a). Length frequencies were recorded for the most abundant species. Stomatopods were also collected in the GOM where water environmental data were not collected and these locations were not included in any calculations. The "winter" season included October through January while the "summer" season included April through July (Abello and Martin 1993). There were months when no collections were made due to weather and boat mechanical problems.

A Shapiro-Wilkes test was used on all data to determine if normality and homogeneity of variance assumptions were met. If normality and variance assumptions were met, linear regression was used to compare CL and WW within a species with gender pooled. If normality and homogeneity of variance assumptions were not met, the data were $\log_{10}$ transformed and if the transformation did not improve normality, then nonparametric Mann-Whitney test (M-W), Spearman's rho correlation, and chi-squared (χ^2) tests were used where appropriate (Siegal and Castellan 1988). I used ANCOVA to examine relationships between CL and WW by gender of each species and then by species with gender pooled, using CL as the covariate. If the parallelism of slopes was statistically upheld ($p > 0.05$), then the adjusted marginal means were compared between genders or between species. If parallelism of slopes was not upheld ($p < 0.05$), then weights between genders or between species could not be compared statistically. Abundances and distribution data were correlated with CL and WW. The data from males and females of the same species were combined if there was not a significant difference in the abiotic factors (salinity, temperature, depth) between gender. Relationships were considered significant if $p < 0.05$.

Results

Three species of Squillidae were collected with *S. empusa* and *S. chydaea* being the most abundant species. Only 3 *Gibbesia neglecta* Gibbes 1850 (formerly *Squilla;* see Manning and Heard 1997) were collected, so this species was not included in any analyses. Of the 55 specifically documented stations where trawling activities resulted in collections of at least one stomatopod, 69% of trawls contained *S. chydaea*, 78% of trawls contained *S. empusa*, and 49% of trawls contained both species. The more numerous species collected was *S. chydaea* (total n = 1,689 from 27 stations, mean =

TABLE 1. *Review of sex ratio (male:female) of different species in the family Squillidae. GOM = Gulf of Mexico.*

Species	***Ratio***	***Reference (Location of Study)***
Oratosquilla oratoria	1 : 1.56	calculated from Kubo et al. 1959 (Japan)
	1 : 1.63	Hamano and Matsuura 1987 (Japan)
	1 : 1.06	calculated from Ohtomi and Shimizu 1988 (Japan)
	1 : 1.21	calculated from Ohtomi et al. 1992 (Japan)
Oratosquilla nepa	1 : 1.65	calculated from Sukumaran 1987 (India)
Kempina mikado	1 : 1.64	Hamano et al. 1996 (China)
Squilla aculeate Bigelow 1893	1 : 1.9	Dittel 1991 (Costa Rica)
Squilla chydaea	1 : 1.11	Wortham this study (GOM)
Squilla empusa	1 : 1.17	calculated from Rockett et al. 1984 (GOM)
	1 : 1.04	Wortham this study (GOM)
Squilla hancocki Schmitt 1940	1.34 : 1	Hendrickx and Sanchez-Vargas 2005 (Gulf of California)
	1 : 1.06	Barbosa-Ledesma et al, 2000 (Mexico)
Squilla mantis	1 : 1.02	calculated from Abello and Martin 1993 (Mediterranean Sea)
	1 : 1.27	Froglia and Giannini 1989 (Adriatic Sea)
Squilla mantoidea Bigelow 1893	1.72 : 1	Hendrickx and Sanchez-Vargas 2005 (Gulf of California)
Squilla panamensis Bigelow 1891	1.23 : 1	Hendrickx and Sanchez-Vargas 2005 (Gulf of California)
Squilla parva Bigelow 1891	1 : 1.2	Dittel 1991 (Costa Rica)
	1 : 1.06	Barbosa-Ledesma et al. 2000 (Mexico)

13.9 ± 0.265) followed by *S. empusa* (total n = 1,198 from 56 stations, mean = 48.9 ± 0.517). Individuals collected at DISL were not included in analyses because of missing abiotic data.

Sex Ratio

The sex ratio of *S. chydaea* was biased toward females in the population with the ratio of males to females being 1:1.11 (n_{males} = 798, $n_{females}$ = 882; χ_1^2 = 4.4, $p < 0.05$); however, the sex ratio of *S. empusa* was equal (1:1.04; n_{males} = 577, $n_{females}$ = 598; χ_1^2 = 0.38, p > 0.25). Sex ratios of other spearer mantis shrimp in the family Squillidae are reported in Table 1. For *S. chydaea*, sex ratio varied by season. There were significantly more females than males in winter (M:F; 1:1.25; χ_1^2 = 7.03, p < 0.01) even though the sex ratio was nearly equal in summer (M:F; 1:1.05; χ_1^2 = 0.71, p > 0.25). For *S. empusa*, the sex ratio was nearly equal in both summer and winter (summer: 1.01:1 sex ratio, χ_1^2 = 0.04, p > 0.25; winter: 1:1.23 sex ratio, χ_1^2 = 2.77, p > 0.05). See Table 2 for specific frequencies of each gender by species and season. Overall, there were more females than males in *S. chydaea* compared to *S. empusa*, and this female bias was especially noticeable in the winter months.

Morphometric data

For *S. empusa*, there was no difference in the CL-WW relationship between males and females with the slopes being parallel (ANCOVA: parallelism, $F_{1, 1174}$ = 2.41, p = 0.121, WW adjusted means $_{female}$ = 8.93 ± 0.08 g, WW adjusted means $_{males}$ = 8.76 ± 0.08 g). For *S. chydaea*, this relationship differed with the slope of males being steeper (ANCOVA: parallelism, $F_{1, 1688}$ = 11.7, p = 0.001, WW adjusted means $_{female}$ = 5.36 ± 0.03 g, WW adjusted means $_{males}$ = 5.50 ± 0.03 g) (Figure 1).

Individuals of both species had significantly larger CL and WW in winter compared to the summer (Table 3). Carapace length of *S. chydaea* (pooled by gender) was significantly longer than that of *S. empusa* (M-W: *U* = -2.70, p = 0.007) (Figure 2). Even though the mean CL of *S. empusa* was statistically smaller, there was a greater range of CL than *S. chydaea* and more large size class individuals were collected of *S. empusa* than of *S. chydaea* (Table 4). With genders pooled, there was a difference in the CL-WW relationship between *S. chydaea* and *S. empusa*, with the slopes not being parallel, suggesting that the two species grow differently (ANCOVA: parallelism, $F_{1, 2863}$ = 4,144, p < 0.001, WW adjusted means $_{chydaea}$ = 5.24 ± 0.04 g, WW adjusted means $_{empusa}$ = 9.12 ± 0.05 g). Otherwise, *S. empusa* has a greater WW than *S. chydaea* when CL was held constant using ANCOVA. Both *S. chydaea* (r^2 = 0.918, $F_{1, 1687}$ = 18,956, p < 0.001) and *S. empusa* (r^2 = 0.947, $F_{1, 1173}$ = 21,018, p < 0.001) had positive relationships between CL and WW (Figure 3).

The largest WW sample of *S. empusa* collected at any one station was 1,476 g /30 min trawl; *S. chydaea* had 2,341 g/30 min trawl (Table 4). For *S. chydaea*, the station where the largest biomass of stomatopods were caught (i.e., station 3)

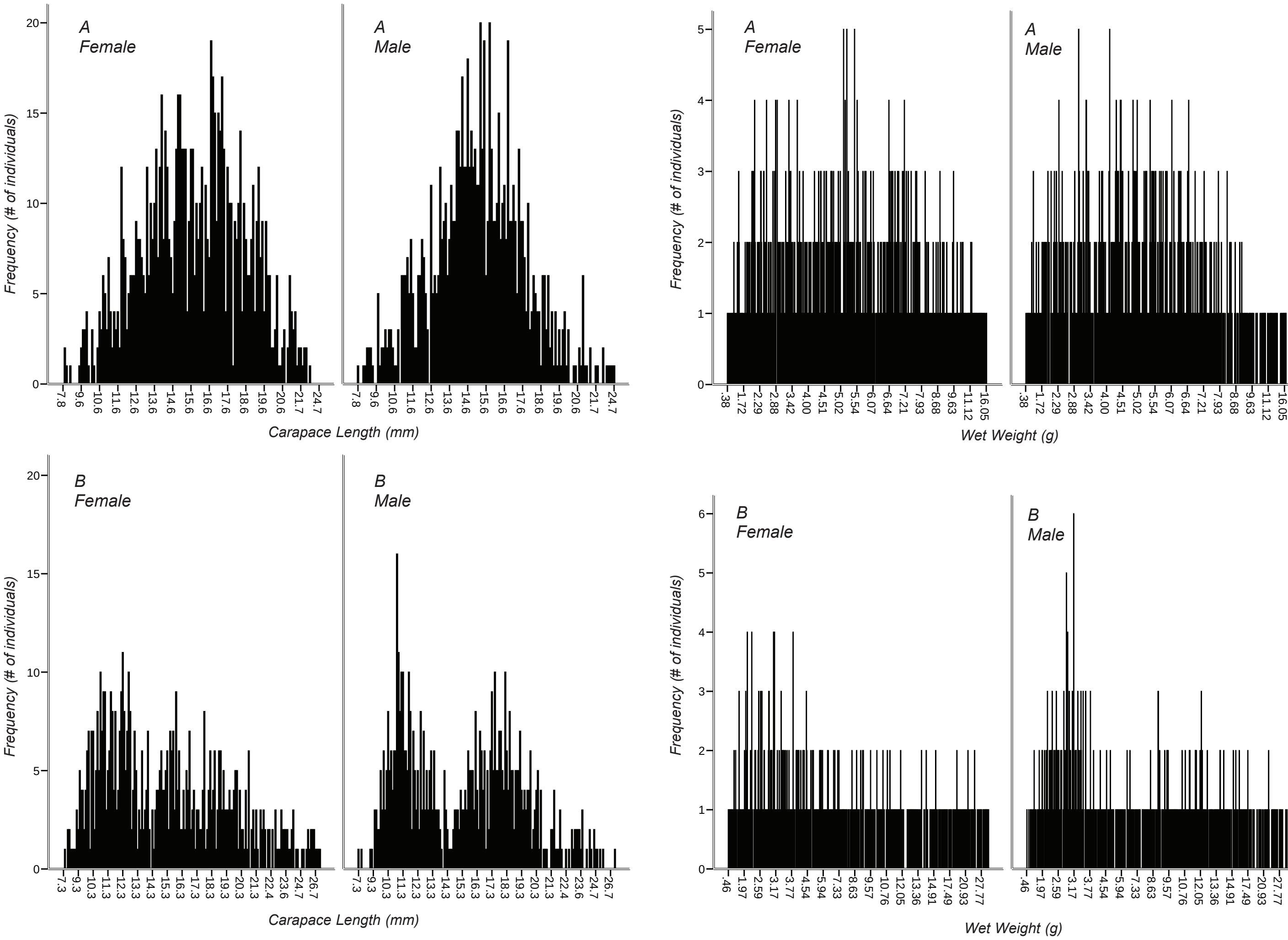

Figure 1.
Carapace length (mm) and wet weight (g) distributions by gender for all Squilla chydaea *(A) and* Squilla empusa *(B).*

was also the station where the largest number of individuals was caught (n = 329). However, in *S. empusa*, this was not the case. The station where the most individuals were caught (station 64; n = 409) had a mean WW of 3.5 ± 0.089 g and carapace length of 11.9 ± 0.093 mm; smaller individuals were collected at this station compared to the station with the largest WW (station 37, n = 125). Overall, both species were larger in the winter while *S. empusa* was larger in WW compared to *S. chydaea*.

Distribution and environmental parameters

Overall, males and females of both species of *Squilla* were distributed equally according to depth, temperature, and salinity (Table 5). *Squilla chydaea* was collected at greater depths than *S. empusa* (M-W: U = -37.9, p < 0.0001) (Table 6) and larger individuals were collected in deeper water for both species (*S. chydaea*: Spearman's *rho* = 0.580, p < 0.0001; *S. empusa*: Spearman's *rho* = 0.542, p < 0.0001). Individuals were collected at significantly different depths between the summer and winter seasons for *S. empusa* (Table 3E) and for *S. chydaea* (Table 3J). *Squilla empusa* apparently occurs in shallower waters in the winter, whereas *S. chydaea* apparently occurs in deeper waters in the winter. For both species, there were no significant difference among the depths at which males and females were collected (Table 5D).

Squilla empusa was collected in significantly warmer water than *S. chydaea* (Table 6) and larger individuals were collected in colder water (M-W: U = -33.5, p < 0.0001) (*S. chydaea*: Spearman's *rho* = -0.459, p <0.0001; *S. empusa*: Spearman's *rho* = -0.493, p <0.0001). Individuals were collected at significantly different temperatures between the summer and winter seasons for both species (Tables 3D and 3I). There were no significant difference among the temperatures where males and females were collected for *S. chydaea*; however, *S. empusa* males and females were collected at significantly different temperatures, even though the temperature difference was <1°C (Table 5C). For *S. empusa*, females were collected from significantly higher temperatures than males (Table 5); however, the mean temperature difference of <1 °C between males and females is not likely to be biologically significant.

TABLE 2. *Seasonal data of carapace length (CL, mm) and wet weight (WW, g) of* Squilla empusa *and* Squilla chydaea.

Species, Season, Sex, Measurement, % of total n	n	Mean	Median	Range by gender	Biomass Sum	% Total Biomass Sum
Squilla chydaea:						
Winter						
Female: (16.9%)						
WW	286	5.83	5.85	0.54 – 14.47	1,669	18.2
CL	286	16.3	16.8	7.9 – 22.0	–	–
Male: (13.4%)						
WW	226	5.58	5.13	1.0 – 17.27	1,262	13.8
CL	226	15.9	14.8	8.5 – 23.9	–	–
Totals: (30.3%)						
WW	512	5.72	5.48	0.54 – 17.27	2,931	32.0
CL	512	16.1	16.4	7.9 – 23.9	–	–
Summer						
Female: (35.7%)						
WW	603	5.49	5.13	0.38 – 16.60	3,313	36.2
CL	603	15.5	15.3	7.9 – 23.3	–	–
Male: (34.0%)						
WW	574	5.09	4.89	0.45 – 19.14	2,920	31.9
CL	574	14.9	15.0	7.8 – 24.7	–	–
Totals: (69.7%)						
WW	1,177	5.30	4.96	0.38 – 19.14	6,233	68.0
CL	1,177	15.2	15.2	7.8 – 24.7	–	–
Overall Totals						
Female: (52.6%)						
WW	889	5.60	5.26	0.38 – 16.60	4,982	54.4
CL	889	15.7	15.7	7.9 – 23.3	–	–
Male: (47.4%)						
WW	800	5.23	4.95	0.45 – 19.14	4,182	45.6
CL	800	15.2	15.2	7.8 – 24.7	–	–
Totals: (100%)						
WW	**1,689**	**5.42**	**5.13**	**0.38 – 19.14**	**9,164**	**100**
CL	**1,689**	**15.5**	**15.4**	**7.8 – 24.7**	**--**	**--**
Squilla empusa:						
Winter						
Female: (12.3%)						
WW	145	9.28	8.72	0.92 – 33.39	1,346	12.9
CL	145	15.9	15.9	7.9 – 26.0	–	–
Male: (10.0%)						
WW	118	9.47	8.32	1.63 – 24.52	1,117	10.7
CL	118	16.1	16.3	9.6 – 24.2	–	–
Totals: (22.4%)						
WW	263	9.36	8.42	0.92 – 33.39	2,463	23.7
CL	263	16.0	16.0	7.9 – 26.0	–	–
Summer						
Female: (38.6%)						
WW	453	8.74	5.74	0.46 – 40.67	3,960	38.1
CL	453	15.2	14.5	7.5 – 28.4	–	–
Male: (39.1%)						
WW	459	8.65	7.81	0.58 – 41.09	3,970	38.2
CL	459	15.2	15.4	7.3 – 28.4	–	–
Totals: (77.6%)						
WW	912	8.70	6.53	0.46 – 41.09	7,930	76.3
CL	912	15.2	14.9	7.3 – 28.4	–	–
Overall Totals						
Female: (50.9%)						
WW	598	8.87	6.36	0.46 – 40.67	5,306	51.1
CL	598	15.3	14.9	7.5 – 28.4	–	–
Male: (49.1%)						
WW	577	8.82	7.96	0.58 – 41.09	5,087	48.9
CL	577	15.4	15.6	7.3 – 28.4	–	–
Totals: (100%)						
WW	**1,175**	**8.85**	**6.98**	**0.46 – 41.09**	**10,393**	**100**
CL	**1,175**	**15.4**	**14.8**	**7.3 – 28.4**	**--**	**--**

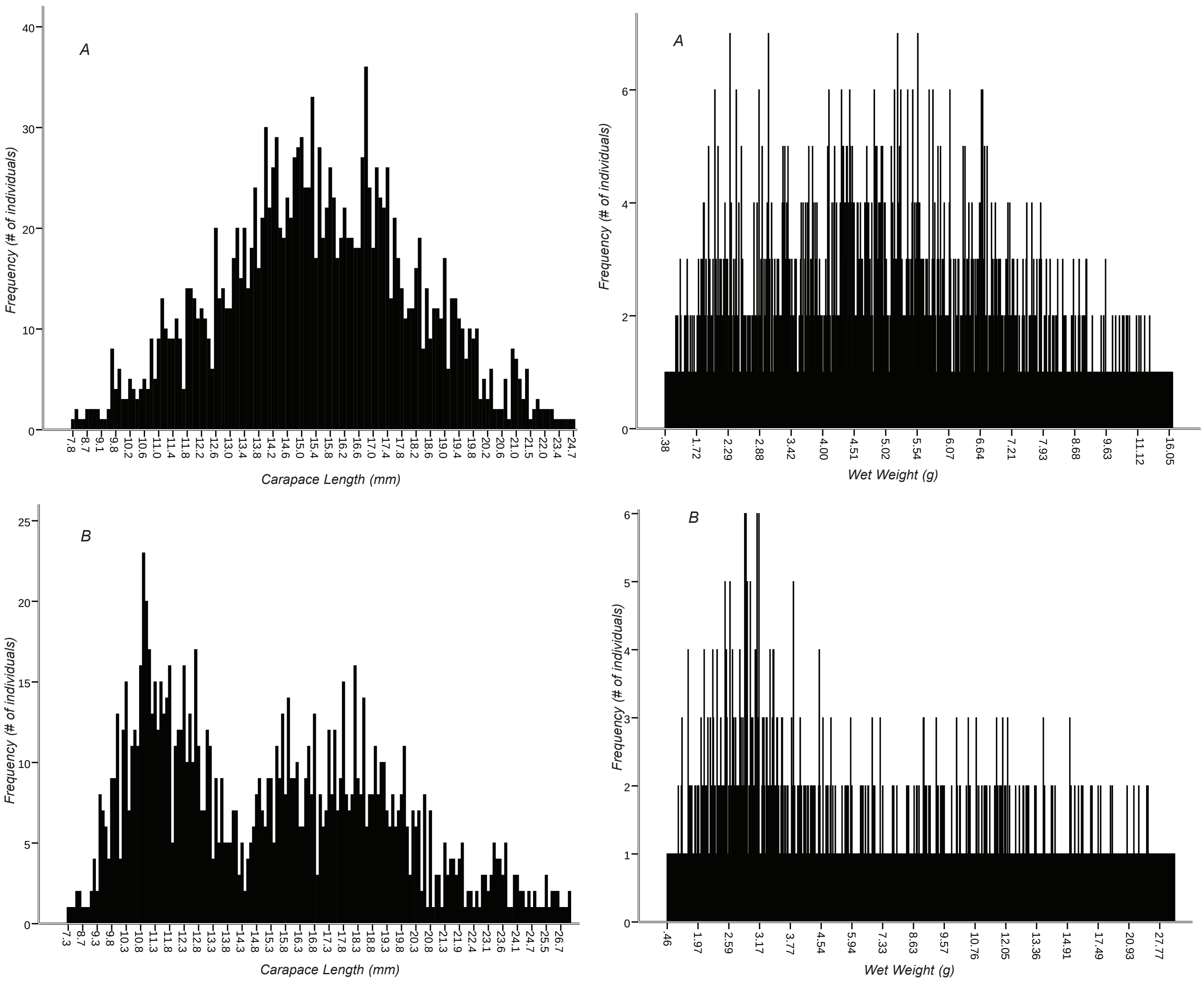

Figure 2.
Carapace length (mm) and wet weight (g) distributions for all Squilla chydaea *(A) and* Squilla empusa *(B).*

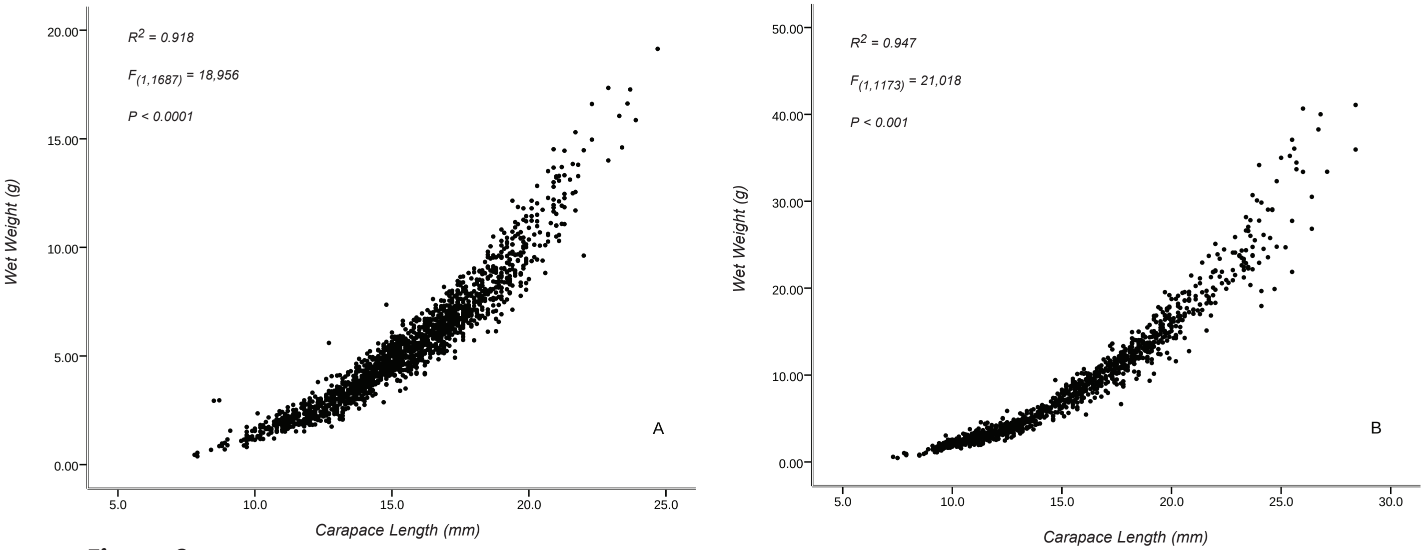

Figure 3.
Regression analyses for predicting wet weight (g) from carapace length (mm) pooled by gender for Squilla chydaea *(A) and* Squilla empusa *(B). Note different axis values for each species.*

Squilla chydaea was collected in significantly higher salinity waters than *S. empusa* and larger individuals were collected in higher salinity waters (Mann Whitney U = -21.5, $p < 0.0001$) (*S. chydaea*: Spearman's *rho* = 0.255, $p < 0.0001$; *S. empusa*: Spearman's *rho* = 0.435, $p < 0.0001$). The range, mean, and most common salinities between the two stomatopods were *S. chydaea*: 31–40 ppt, 36.5 ppt for both males and females, and 35-37 ppt, respectively; *S. empusa*: 32–40 ppt, 36.0 for both males and females, and 35–36 ppt, respectively. Individuals were collected at significantly different salinity between the summer and winter seasons for both species (Tables 3C and 3H). Males and females were collected from waters of similar salinity year round (Table 5B).

Squilla chydaea was collected at a rate of 73.6 individuals/station in the summer compared to 45.7 individuals/station in the winter (Table 2; $\chi_1^2 = 6.47$, $p < 0.02$). Likewise, *S. empusa* was also collected at a higher rate in the summer of 41.9 individuals/station compared to the winter of 6.68 individuals/station (Table 2; $\chi_1^2 = 25.5$, $p < 0.0005$). Trawls in the summer yielded more productive harvests for both species; the per trawl WW of *S. empusa* and *S. chydaea* in the summer was 364.5 g and 390.1 g, respectively, and 62.5 g and 261.4 g, respectively, in winter. For the 2 species combined, a mean trawl in the summer would harvest 754 g whereas a trawl in the winter would harvest 324 g (Table 2). Overall, both species had genders that were equally distributed by all environmental parameters, were collected in higher frequencies in the summer and had summer trawls that yielder larger total WW, and had larger individuals that were collected at deeper, colder, higher salinity waters. *S. chydaea* was found in colder, deeper, higher salinity waters than *S. empusa*.

Discussion

The present study represents the first detailed study and data on *S. chydaea* as well as an analysis of important biological similarities and differences of the two most abundant mantis shrimp in the GOM. Both *Squilla* species were collected in high frequencies in the GOM, often together, with more individuals of *S. chydaea* being collected. Overall, compared to *S. empusa*, *S. chydaea* had more females than males, a smaller WW, and lived in deeper, colder, higher salinity waters. Both species were collected in higher abundances in the summer, were larger in the winter and in deeper, colder, and higher salinity waters, and had genders that were equally distributed by environmental parameters.

Similar to research on other spearer mantis shrimp, the sex ratio of *S. empusa* also differs between winter and sum-

TABLE 3. *Seasonal abiotic and size data for collections of* Squilla empusa *(A-E) and* Squilla chydaea *(F-J) with sexes pooled. U = Mann-Whitney Test.; * indicates a significant difference; IQR is the interquartile range.*

Measurement	Median (IQR)	Statistic *U*	p
Squilla empusa			
(A) Carapace length (mm)	Summer: 14.1 (6.3) Winter:17.7 (6.5)	-3.64	<0.0001*
(B) Body mass (g)	Summer:5.64 (8.34) Winter:10.6 (10.5)	-3.50	<0.0001*
(C) Salinities (ppt)	Summer: 35.5 (1) Winter:34.7 (4)	-12.4	<0.0001*
(D) Water temperature (°C)	Summer:23.2 (3.2) Winter:24.4 (1.6)	-5.91	<0.0001*
(E) Depth (m)	Summer:21.0 (7.0) Winter:13.0 (19.0)	-15.0	<0.0001*
Squilla chydaea			
(F) Carapace length (mm)	Summer:15.2 (3.4) Winter:16.3 (4.1)	-6.27	<0.0001*
(G) Body mass (g)	Summer:4.96 (3.29) Winter:5.47 (3.74)	-3.35	0.001*
(H) Salinities (ppt)	Summer: 36.1 (1.0) Winter:37.0 (0.0)	-7.55	<0.0001*
(I) Water temperature (°C)	Summer:21.1 (2.4) Winter:16.8 (2.2)	-29.4	<0.0001*
(J) Depth (m)	Summer:47.0 (24.0) Winter:66.0 (18.0)	-17.7	<0.0001*

TABLE 4. *Wet weight (WW, g) and carapace length (CL, mm) of* Squilla chydaea *and* S. empusa. *"Largest trawl" refers to the station in which the largest biomass of a species of mantis shrimp was collected.*

Measurement	***Squilla chydaea***	***Squilla empusa***
Number of individuals in analyses	1,689	1,175
Total WW of all stations	9,163	10,393
Mean (± se) individual WW	5.42 ± 0.065	8.85 ± 0.204
Median individual WW	5.13	6.98
Mean (± se) individual CL	15.5 ± 0.066	15.4 ± 0.121
Median individual CL	15.4	14.8
Number of individuals collected in 30-min largest trawl	329	125
Largest biomass (g) collected/ 30-min (i.e. largest trawl)	2,341	1,476
Mean (± se) individual WW in largest trawl	7.11 ± 0.150	11.80 ± 0.335
Median individual WW in largest trawl	6.60	11.35
CL mean (± se) in largest trawl	17.0 ± 0.120	17.9 ± 0.178
CL median in largest trawl	16.8	17.8

mer. For the entire year, the sex ratio was 1:1.04, but it was 1:1.01 in the summer and 1:1.23 in the winter. Sex ratios of spearer stomatopods, including *S. empusa* (Rockett et al. 1984), vary during the spawning season (usually in the summer months) because females remain in their burrows to care for egg masses and are less likely to be captured, leading to a more equal sex ratio. However, males actively search for a new cavity after giving this resource to the female in the breeding season, thus allowing males to be collected (Ohtomi et al.1989, Torisawa et al. 1998, Maynou et al. 2005). For example, *O. oratoria* and *Hemisquilla californiensis* Stephenson 1967 (Basch and Engle 1988) have a sex ratio of more males compared to females during the breeding months when the females are in the burrows and males may be actively searching for a burrow, but a biased sex ratio towards more females (1:5.24) in the non-breeding months when females are more likely to be out of their burrow (Hamano and Matsuura 1987).

While abiotic factors such as salinity, temperature, and depth influenced what *Squilla* species were collected (Abello and Martin 1993, Jesse 1996, Perry and Larsen 2004), interspecific competition for resources may also influence *Squilla* distributions (Dingle and Caldwell 1975). Both *Squilla* in this study likely live in similar burrow types (both spearers living in muddy bottoms and collected in same trawls) and eat similar prey (both have similar raptorial appendages; Manning 1969), suggesting that they may compete for resources and live in different environmental niches.

In this study, larger *S. chydaea* were more likely to be females than males. However, in *S. empusa*, there were no differences between male and female CL, which is similar to the findings of Rockett et al. (1984). No difference between CL of pooled males and females were found in the spearers *O. oratoria* (Torisawa et al. 1998), *O. neap* (Sukumaran 1987), *S. mantis* (Abello and Sarda 1989, Abello and Martin 1993), and *K. mikado* (Hamano et al. 1996). In contrast, males were larger than females in *S. parva* and *S. aculeata* (Dittel 1991), and body sizes of both species were smaller during the winter months compared to summer months. However, in my study where individuals were larger (CL and WW) in the winter, the size difference between seasons may be biased due to females residing in burrows in summer and not being collected as frequently.

Two main species of stomatopods are harvested commercially worldwide, *O. oratoria* in Japan and *S. mantis* in Europe, and both are comparable to the mantis shrimp in this study. For example, like *Squilla* in the GOM, *Oratosquilla* has differences between the seasons in total landings and individual size (Ohtomi et al. 1989, Ohtomi and Shimizu 1996). *Squilla mantis* is very similar to the two species of stomatopods in this study by being collected mostly in night trawls (Froglia and Giannini 1989) and having seasonality in total landings (Abello and Martin 1993). Other similarities between *S. mantis* and *S. empusa* include males and females with similar CL (Maynou et al. 2005), smaller individuals located in shallower waters (Abello and Martin 1993), and

TABLE 5. *Characteristics of female and male related to size and abiotic factors for* Squilla empusa *and* Squilla chydaea. *U = Mann-Whitney Test.; * indicates a significant difference; IQR is the interquartile range.*

Measurement	Species	Median (IQR)		Statistic *U*	p
		Males	Females		
(A) Carapace length (mm)[A]	*S. empusa*	15.2 (7.3)	14.1 (6.7)	-0.60	0.55
	S. chydaea	15.2 (3.2)	15.7 (4.0)	-4.33	<0.0001*
(B) Salinity (ppt)[B]	*S. empusa*	35.5 (1.0)	35.0 (1.0)	-1.75	0.08
	S. chydaea	37.0 (1.0)	36.3 (1.0)	-0.011	0.99
(C) Water temperature (°C)[C]	*S. empusa*	23.2 (2.3)	24.0 (2.3)	-2.17	0.03*
	S. chydaea	19.6 (1.8)	20.1 (2.3)	-0.96	0.34
(D) Depth (m)[D]	*S. empusa*	21.0 (7.0)	21.0 (7.0)	-0.64	0.52
	S. chydaea	56.0 (21.0)	47.0 (21.0)	-1.34	0.18

[A] The range of carapace length for male and female in *S. empusa* was 7.3–28.4 mm and 7.5–26.8 mm, respectively; *S. chydaea* was 7.8–24.7 mm and 7.9–23.3 mm, respectively. The range of body mass for male and female in *S. empusa* was 0.58–41.09 g and 0.46–40.67 g, respectively; *S. chydaea* was 0.45 19.14 g and 0.38–16.6 g, respectively. [B] The range of salinity for both males and females of *S. empusa* was 32.0–40.0 ppt; *S. chydaea* was 35.0–40.0 ppt. [C] The range of temperatures for both male and female of *S. empusa* was 20.8–25.5 °C; *S. chydaea* was 16.8–23.5 °C. [D] The range of depths for both males and females of *S. empusa* was 1–57 m; *S. chydaea* was 21–96 m.

TABLE 6. *Depth (m) and temperature (°C) distributions of* Squilla chydaea *and* Squilla empusa.

Measurement	*Squilla chydaea*	*Squilla empusa*
DEPTH:		
Depth range of species	21-96	1-57
Mean (± se) depth of species	48 ± 0.341	26 ± 0.298
Median depth of species	48	21
Mean (± se) depth of males	49 ± 0.492	26 ± 0.420
Mean (± se) depth of females	47 ± 0.472	26 ± 0.423
Median depth of males	56	21
Median depth of females	47	21
Most common catch range (m)	30-60	10-40
Median depth caught in summe	47	21
Median depth caught in winter	66	13
TEMPERATURE:		
Temperature range of species	16.8–23.5	21.0–25.0
Mean (± se) temperature of species	20.2 ± 0.049	23.1 ± 0.039
Median temperature of species	20.1	23.5
Mean (± se) temperature of males	20.1 ± 0.067	23 ± 0.055
Mean (± se) temperature of females	20.1 ± 0.070	23 ± 0.054
Median temperature of males	19.6	23.2
Median temperature of females	20.1	24.0
Most common catch range (°C)	18–22	21-24
Median temperature caught in summer	21.1	23.2
Median temperature caught in winter	16.8	24.4

high abundance in collections <60 m (Froglia and Giannini 1989, Maynou et al. 2005; Table 7). *Squilla mantis* is similar to *S. chydaea* in that there not being a relationship between individual size and depth (Maynou et al. 2005), they are collected at depths up to176 m (Abello and Sarda 1989), and the sex ratio is variable between seasons (Froglia and Giannini 1989, Maynou et al. 2005).

While there is no current fishery or management in the United States for stomatopods, some predictions about a mantis shrimp fishery in the GOM may be made using data from current mantis shrimp fisheries in other countries. For example, the type of net used and vessel size has been reported to influence the catch of *O. oratoria* (Ohtomi et al. 1992, Tokai et al. 1997). Several population dynamics studies have

TABLE 7. *Review of depth range where* Squilla empusa *has been most abundantly collected.*

Reference	**Depth (m)**	**Location of Collections**
Hildebrand (1954)	35-42	Gulf of Mexico—Louisiana coast
Camp (1973)	18	Gulf of Mexico—Florida coast
Rockett et al.[A]	9-16	Gulf of Mexico—Texas coast
Wenner and Wenner (1988)[B]	< 20	Atlantic Ocean—Southeast
Wortham (present study)[C]	15-60	Gulf of Mexico—Northern coast

[A] Total depth range 5-86 m with minimum collections at 64-86 m, [B] Collections made only in the daytime, [C] Off the coasts of Texas, Louisiana, Alabama, Mississippi, and Florida

been conducted on *S. mantis* (Badia et al. 1976, Abello and Martin 1993) and determined that gravid females are more valuable at market than males and non-gravid females (Abello and Martin 1993). In *S. empusa*, gravid females were collected only in the summer months (Wortham-Neal 2002b) and stomatopods may therefore be more marketable in the summer in the United States.

The GOM shrimp trawl fishery has an estimated 20,000 licensed boats and generates more than $500 million annually just by focusing on three species of penaeid shrimps: brown shrimp (*Farfantepenaeus aztecus*), white shrimp (*Litopenaeus setiferus*), and pink shrimp (*Farfantepenaeus duorarum* Burkenroad 1939) (Diamond 2004). Harvesting stomatopods by trawling in conjunction with other fisheries is likely to be the only method of utilizing them because aquaculture is not feasible for several reasons. First, *Squilla* may be carriers of deadly viruses (Chakraborty et al. 2002), which would prevent developing a multi-species aquaculture system with *Squilla*. Life history characteristics such as larval development stages requiring fluctuating diets and having high mortality rates after hatching (Rudloe 1971, Wortham-Neal 2002b), as well as adult cannibalism of *Squilla*, are additional limitations to aquaculture development.

In summary, *S. chydaea* and *S. empusa* are abundant in the GOM and are collected together roughly half the time. *Squilla chydaea* was collected in higher abundance but S. *empusa* was found in more trawls and had larger total biomass and larger individual biomass than S. *chydaea*. *Squilla empusa* reaches larger sizes than *S. chydaea*; however, because greater abundance of *S. chydaea* was collected, *S. chydaea* had a higher maximum catch rate year round/trawl. *Squilla chydaea* and *S. empusa* live at different depths but trawling year-round in high salinity waters at depths <60 m with maximum catch rates around 20 m would likely yield large biomass of stomatopods. *Squilla chydaea* and *S. empusa* are similar to *S. mantis* in their biology and behaviors and thus many aspects of the fishery for *S. mantis* could likely be used in the GOM. Mantis shrimp are currently harvested in abundance as bycatch in the penaeid fishery, and harvesting both penaeid shrimp and mantis shrimp at the same time might yield optimal economic and ecological efficiency.

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