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FECUNDITY OF *LITOPENAEUS SETIFERUS, FARFANTEPENAEUS AZTECUS AND F. DUORARUM*, IN THE SOUTHWESTERN GULF OF MEXICO

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ABSTRACT Fecundity of white shrimp, *Litopenaeus setiferus*, brown shrimp, *Farfantepenaeus aztecus*, and pink shrimp *F. duorarum* and relationships to gonad weights and total and carapace length were estimated. Ovigerous females were collected in the southern Gulf of Mexico in February, May, August and November 1993. Fecundity was estimated by means of a gravimetric method. The equations relating fecundity to total weight and fecundity to gonad weight were linear in the 3 species. However, an exponential relationship was found between fecundity and carapace length in *L. setiferus* and *F. aztecus*. Of the relationships examined, gonad weight was considered a more precise indicator of fecundity. Fecundity estimates ranged from 70,647 to 558,270 eggs for 0.203 and 5.639 g gonad weight of *L. setiferus*, from 23,298 to 494,292 eggs for 0.061 to 2.561 g gonad weight in *F. aztecus* and from 138,618 to 225,543 eggs for 0.120 to 0.998 g gonad weight in *F. duorarum.*

Introduction

Penaeid shrimps are a valuable fishing resource and are in high demand throughout the world. In the Gulf of Mexico, 3 species are of commercial importance: brown shrimp *Farfantepenaeus aztecus*, pink shrimp *F. duorarum* and white shrimp *Litopenaeus setiferus*. These species support an important industry both in the USA and in México. The US shrimp annual harvest from the Gulf of Mexico has fluctuated between 64,000 and 121,000 metric tons (Klima 1989) and is now about 100,000 metric tons (Anonynomous 1997). In eastern Mexico penaeid shrimps also support a large industry which yields about 20,000–24,000 metric tons annually and represents an important source of employment and foreign currency received through exports (Gracia and Vázquez-Bader in press).

The exploitation of penaeid shrimp takes place inside coastal lagoons by artisanal fisheries and offshore by industrial fishing techniques. The offshore fishing effort has decreased in the past 2 decades (from 1400 to around 660 boats), whereas, the inshore fishery landings based solely on small shrimp increased substantially. The steady increase in artisanal fishing effort has led to growth overfishing of shrimp stocks and resulted in a net decrease of total volume of shrimp landings (from 39,000 to 24,000 metric tons) in the Mexican fishery (Gracia 1995, Gracia 1997, Gracia et al. in press, Gracia and Vázquez-Bader in press). However, the continuous demand for shrimp and its high value encourages an increase in fishing effort which poses a risk for shrimp resource sustainability.

Management of the penaeid shrimp fishery requires detailed information about reproduction and factors affecting production (i.e. total weight and value). Understanding the dynamics of the reproductive process is a key factor for management regulations. Fecundity estimates related to size, combined with abundance of spawners, may give a more precise picture of potential productivity.

Different aspects of the general reproductive biology of shrimp have been examined in the Gulf of Mexico including spawning periods, spawning areas and size of first reproduction (Soto and Gracia 1987, Gracia 1989). However, studies of the fecundity of these organisms are scarce. Fecundity of a single white shrimp specimen was estimated by Anderson et al. (1949). Martosubroto (1974) carried out a detailed study on fecundity of pink shrimp and provided equations that related fecundity to total weight (TW, g), gonad weight (GW, g) and total length (TL, mm). To our knowledge, no fecundity estimates are available for brown shrimp. The aim of the present study is to estimate fecundity of white shrimp, brown shrimp, and pink shrimp in the southern Gulf of Mexico and to relate fecundity to TW, GW, TL and carapace length (CL).

Materials and Methods

Ovigerous females of the 3 species were collected between 18°–20° N and 91°–94° W in Campeche Bay between the southern Gulf of Mexico during February, May, August and November 1993 on board R/V *Justo Sierra* from the Universidad Nacional Autónoma de

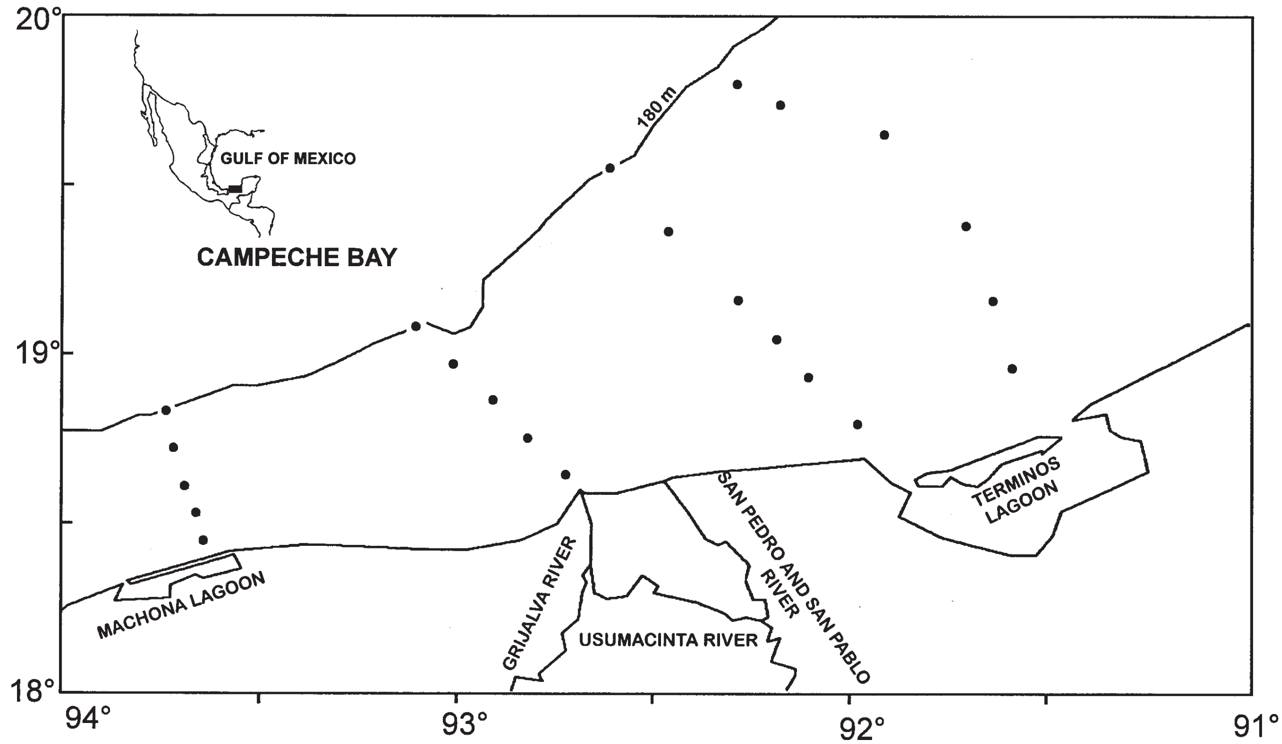

Figure 1. Study area and sampling locations.

México. During each cruise replicate samples were collected at 22 stations along 4 transects (Figure 1) using a commercial trawl net of 18 m opening and 2.5 cm stretch mesh size. Trawl duration was 30 min. and was done in a depth range of 12–120 m. Ripeness of the ovaries was scored according to Cummings (1961) and Sandoval and Gracia (1998). Total length (tip of rostrum to tip of telson) and CL of shrimp (orbital depression of carapace to dorsoposterior end of carapace) were measured to the nearest millimeter and TW was measured to the nearest 0.1 g. Total gonad and gonad tissue sample weight were recorded to an accuracy of 0.1 mg. Ripe and nearly ripe females were separated from the catch and preserved in Bouin's picroformaldehyde solution (Gaviño de la Torre 1972).

After the cruise, ovaries were removed in the laboratory and samples were taken from the first section of the abdominal lobes, as done in previous fecundity studies (Caillouet 1972, Cummings 1961, Martosubroto 1974). Other penaeid studies in different species have shown that there were no significant differences between the number of ripe eggs in different parts of the gonad (Crocos and Kerr 1983).

Eggs were counted only after being separated from connective tissue by consecutively transferring them to 30%, 50% and 70% ethanol solutions for 24 hours each. The ovarian tissue was then transferred to Gilson's solution (nitric acid concentrated 15 ml, glacial acetic acid 4 ml, mercuric chloride crystals 20 g, 60% ethyl alcohol 100 ml, distilled water 888 ml; Simpson 1951), and stored for 2 weeks to loosen even more of the eggs. Ovarian tissue samples were transferred to Bouin's solution which stains eggs with a yellowish color and simplifies counting. Egg diameter units were measured using a light microscope fitted with a calibrated micrometer eyepiece, and eggs were counted gravimetrically. Preliminary analysis showed that the mean number of eggs/sample (A) calculated from three 0.001 g gonad sampling units was enough to estimate the number of eggs for each female. Fecundity (F), defined as the total number of ripe and nearly ripe eggs in the ovary (Bagenal 1978), was calculated as $F = A (W_O/0.001)$; where W_O is the total gonad weight (g) and 0.001 g is the individual sample weight.

Least squares regression (Zar 1974) was employed to calculate the relationship of F to TW, GW, TL, and CL. Regression lines between body weight and GW and between body weight and relative fecundity (number of eggs/gram of shrimp) were also computed. Log_{10} transformations were used to estimate the best curve fitting to the data. Comparison of fecundity among species was accomplished by analysis of covariance (ANCOVA; Zar 1974) with GW as the covariate. Condition factor (CF) was calculated as the ratio of individual weight

TABLE 1

Female shrimp caught during 4 seasonal cruises in 1993.

Season	*Litopenaeus setiferus*			*Farfantepenaeus aztecus*			*Farfantepenaeus duorarum*		
	Total	gravid	%	Total	gravid	%	Total	gravid	%
February	580	22	3.8	385	23	6	17	17	100
May	297	2	0.7	195	0	0	3	3	100
August	198	13	0.7	35	21	60	38	7	18
November	486	3	0.7	217	0	0	0	0	0

(W) to the mean weight (W_a) for each length. CF = W/ W_a where W_a was obtained from the weight-length relationship of shrimp ($W = aL^n$).

RESULTS

The number of ripe (stage IV) and nearly ripe (stage III) females caught was 40 white shrimp, 44 brown shrimp, and 27 pink shrimp (Table 1). Regression equations and correlation coefficients (Table 2) indicate that the relationship between F and GW was the best estimation of fecundity among those examined.

White shrimp

Egg diameters ranged from 200 to 340 μm, which were the highest values for the 3 species. Relative fecundity values varied between 1,436 and 13,079 eggs/g TW. The relationship between GW and F was linear (Figure 2A), with a correlation coefficient ($r = 0.77$, $P < 0.01$, $n = 40$) significantly different from zero. The lowest and highest F estimates were 70,647 and 558,270 eggs, corresponding to 0.208 g and 5.639 g GW, respectively.

The relationship between F and TW was also linear with a lower coefficient relationship compared to GW (Figure 2B). The relationships between F and TL and CL were exponential and significant with even lower correlation coefficients (Table 2). There was a significant correlation between TW and GW ($r = 0.54$, $P < 0.001$, $n = 40$), but not between TW and relative fecundity ($r = 0.04$, $P > 0.50$, $n = 40$). Multiple linear regression of TLand CF vs. F (Table 3) increased the correlation coefficient ($r = 0.79$, $P < 0.01$, $n = 40$) compared to those simple correlations obtained using TW and CL and TL (Table 2). The multiple correlation coefficient was not very different from that obtained with GW.

Brown shrimp

Egg diameter was 180 to 280 μm and relative fecundity varied within the range 1,013 to 10,330 eggs/ g TW. The relationship between GW and F was linear (Figure 3A) ($r = 0.76$, $P < 0.01$, $n = 44$). The number of eggs counted was 23,298 for 0.031 g of GW and 494,292 eggs were counted for 2.561 g GW.

Table 2

Regression and correlation coefficients for fecundity relationships of white, brown and pink shrimp. F = fecundity; GW = gonad weight;TW = total weight; TL = total length; CL = carapace length.

Variables	*Litopenaeus setiferus* (*n* = 40) Equation	r	*Farfantepenaeus aztecus* (n = 44) Equation	r	*Farfantepenaeus duorarum* (*n* = 27) Equation	r
Gonad weight and fecundity	F=94,709(GW)+138,644	0.77	F=163,107(GW)+107,821.4	0.76	F=124,356.47(GW)+73,743.35	0.46
Total weight and fecundity	F=7,328(TW)-139,471	0.67	F=4,537(TW)+13,533.97	0.54	F=4,856.1(TW)-33,295.87	0.44
Total length and fecundity	$F=2.06\ (CL)^{3.13}$	0.42	$F=0.05(CL)^{4.05}$	0.49	non significant	0.22
Total weight and gonad weight	GW=0.036509(TW)-0.7431	0.54	non significant	0.25	non significant	0.24
Total weight and relative fecundity	non significant	0.04	non significant	0.07	non significant	0.04

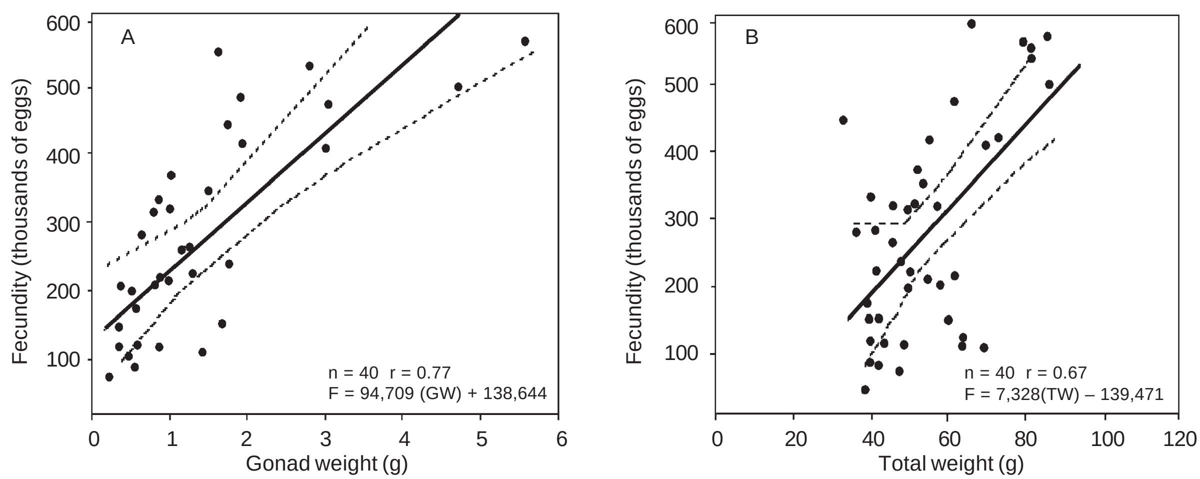

Figure 2. Relationship between gonad weight (GW) and fecundity (A), and total weight (TW) and fecundity (B) of *L. setiferus.* Regression lines are plotted with 95% confidence limits.

The regression relationship for TW on F was also linear (Figure 3B), with a significant correlation coefficient (r = 0.50, $P < 0.01$, n = 44). Significant relationships of F on TL and CL were also found, but the correlation coefficients were relatively low (Table 2). Correlation coefficients for the relationship between TW on GW and TW on relative fecundity were not significant. Multiple regressions with TL and CF vs. F were also significant (r = 0.54, $P < 0.001$, n = 44), but the correlation coefficient was lower than the one calculated for GW vs. F and similar to that of TW vs. F (Tables 2 and 3).

Pink shrimp

Egg diameter ranged from 230 to 320 μm and the values for relative fecundity varied from 1,497 to 7,978 eggs/g TW. The relationship between GW and F was linear (Figure 4A), even though the correlation coefficient was low (r = 0.46, $P < 0.02$, n = 27). Fecundity values varied within the range 138,618 to 225,543 eggs for 0.119 g to 0.998 g TW, respectively. The relationship between TW and F fitted into a linear model (Figure 4B) with a low correlation coefficient (r = 0.44, $P < 0.02$, n = 27) significantly different from zero. Correlation coefficients for the regressions TL on F, CL on F, TW on GW, and TW on relative fecundity were not significantly different from zero (Table 2). A multiple regression (Table 3) among TL and CF vs. F increased substantially the correlation coefficient (r = 0.87; $P < 0.01$, n = 27) in comparison to all simple correlations calculated (Table 2).

Fecundity among the 3 species was compared (Figure 5), since the GW vs. F relationship had the highest correlation coefficient. Significant differences were found among the slopes of the 3 species (ANCOVA; F = 3.70, $P < 0.05$, n = 102). The regression line corre-

TABLE 3

Multiple regressions for fecundity of white, brown and pink shrimp. F = fecundity; TL = total length; CF = condition factor; CL = carapace length; TL = total length.

	equation	r
Litopenaeus setiferus		
Total length, condition factor and fecundity	F= 0.390 (TL)+5,195 (CF)-1,234,491	0.79
Carapace length, condition factor and fecundity	F= 0.607 (CL)+471,893 (CF)-922,263	0.76
Farfantepenaeus aztecus		
Total length, condition factor and fecundity	F= 0.436 (TL)+4,204 (CF)-690,675	0.54
Carapace length, condition factor and fecundity	F= 0.196 (CL)+169,971 (CF)-484,664	0.51
Farfantepenaeus duorarum		
Total length, condition factor and fecundity	F= 0.237 (TL)+1,563 (CF)-581,660	0.87
Carapace length, condition factor and fecundity	F= 0.813 (CL)+408,641 (CF)-523,680	0.86

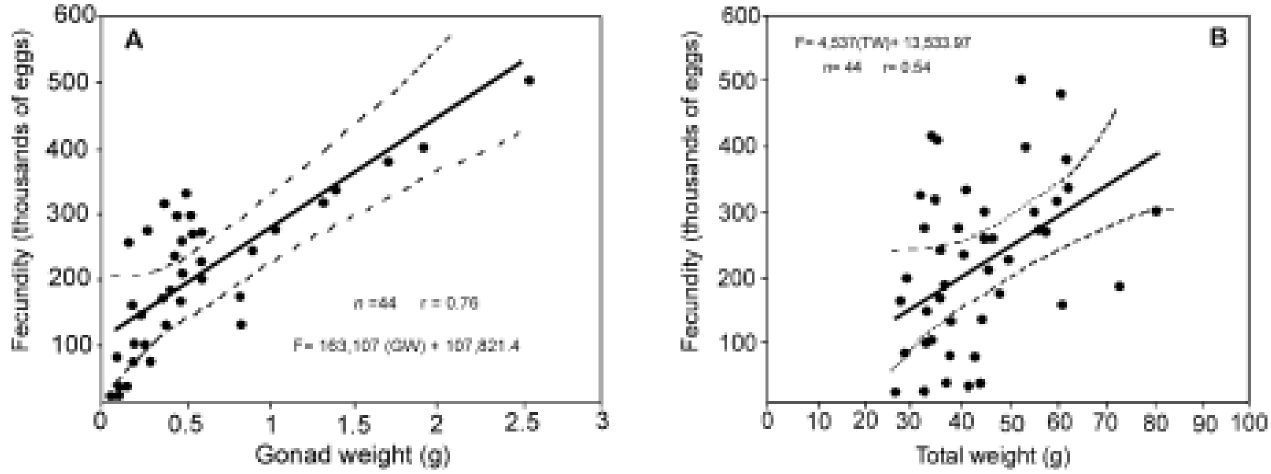

Figure 3. Relationship between gonad weight (GW) and fecundity (A), and total weight (TW) and fecundity (B) of *F. aztecus*. Regression lines are plotted with 95% confidence limits.

sponding to brown shrimp indicated a faster growth of eggs/unit of GW, except within the interval between 0.2 to 0.5 g GW where white shrimp seem to have a higher egg production/GW unit (Figure 5). White shrimp, in turn, showed higher fecundity than pink shrimp over the range 0.2 to 2.2 g GW, but at higher GW values the pink shrimp had a greater fecundity. Because GW varied among species, we also ran an ANCOVA of the common GW range of the 3 species which also demonstrated a significant difference among slopes ($F = 4.88$, $P < 0.01$, $n = 77$).

DISCUSSION

Fecundity in brown shrimp, white shrimp, and pink shrimp is linearly related to GW and TW and exponentially related to TL and CL. These results are in agreement with previous fecundity studies in a number of species, including crustaceans and fishes (Bagenal and Braun 1968, Bagenal 1978, Phillips 1980, Rodriguez 1985).

The most precise estimation of F appears to be the relationship of GW and F. Decreasing accuracy is observed in the 3 other comparisons, which supports previous data reported for several penaeid species (Rao 1968, Martosubroto 1974, Rodríguez 1985). All fecundity estimates in this study fall within the range calculated for penaeid species around the world (Martosubroto 1974, Crocos and Kerr 1983, Penn 1980, Crocos 1987a,b). This relationship is logical since the number of eggs contained within the gonad is dependent on its volume. In these species the extensively used relationship between female weight and fecundity could give biased estimates. Although removing the gonad and measuring

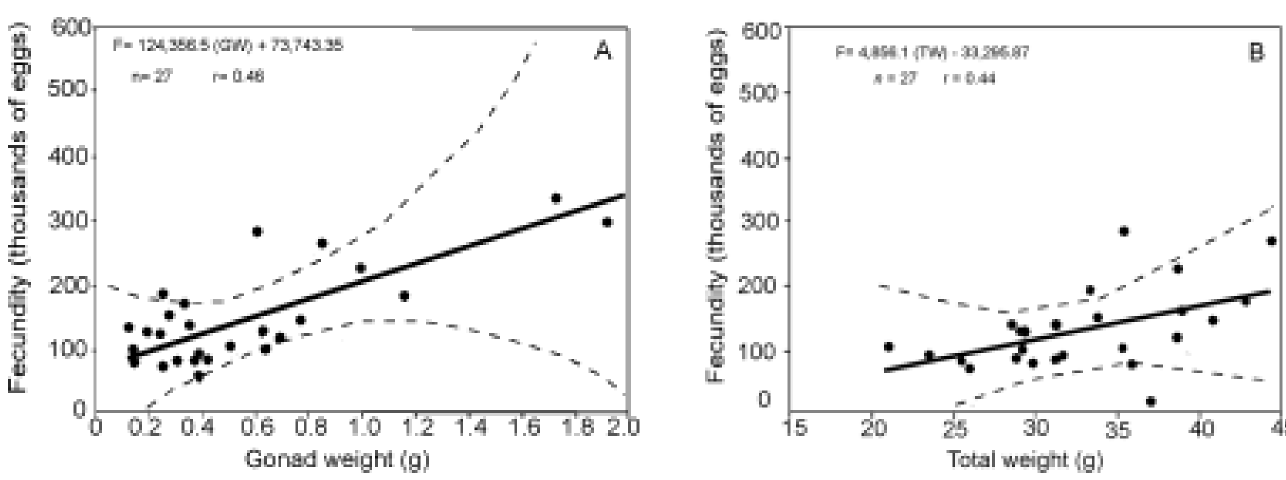

Figure 4. Relationship between gonad weight (GW) and fecundity (A) and total weight (TW) and fecundity (B) of *F. duorarum*. Regression lines are plotted with 95% confidence limits.

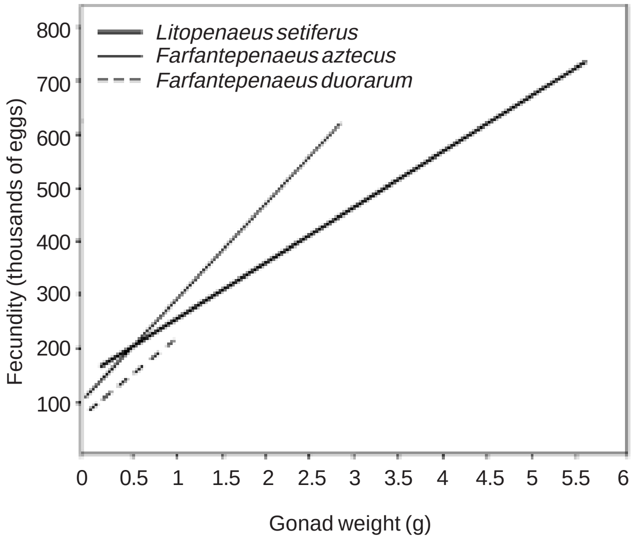

Figure 5. Comparison of regressions of gonad weight-fecundity of *L. setiferus, F. aztecus* and *F. duorarum*.

its weight is a more difficult task than recording the length or weight of the animals, a more precise result can be obtained by following this procedure.

Variability of fecundity estimates based on weight can be related to the fact that shrimp are partial and multiple spawners. Precise data of the number of spawns produced by a female in nature is unavailable (Bray and Lawrence 1992); however, evidence of repeated spawning has been presented for a number of penaeid species. Multiple spawning in wild penaeid shrimp has been reported in the Gulf of Mexico (Lindner and Anderson 1956, Cummings 1961, Eldred et al. 1961, Martosubroto 1974). Crocos and Kerr (1983) found for *Fenneropenaeus merguiensis* that there is only one spawning per molt cycle; however in captivity, multiple spawnings per molt cycle had been noted for *Fenneropenaeus indicus* and *Penaeus semisulcatus* (Emmerson 1980, Browdy and Samocha 1985). Anderson et al. (1985) found in the sicyoniid *Sicyonia ingentis* that multiple spawning can occur without molting and estimated a spawning frequency from field and laboratory data. Although no data exist about spawning frequency from the Gulf of Mexico, a preliminary estimate can be calculated from the percentage of mature females (Table 1) that are ripe in the sample (100% of ripe females). This suggests a spawning frequency of once every 26 days for white shrimp and once every 17 days for brown shrimp during the main reproductive season. This estimate is one of the first, so there is no possibility for comparison. Emmerson (1980) reported that wild caught females of *P. indicus* could spawn up to 3 times without a molt. Based on this spawning frequency, the duration of the main reproductive season (Gracia 1989, Gracia 1997, Gracia et al. in press) and the molt period (~22 days) (Browdy and Samocha 1985, Dall et al. 1990), these Gulf of Mexico species could have up to 3 spawns per season. It is not know precisely how often species of the Gulf of Mexico molt in the wild, although field data suggests they molt every lunar month. The molt period and the possibility of multiple spawning without molting, support the statement that shrimp could spawn up to 3 times per season. This also coincides with available information that white and pink shrimp could have at least 2 spawns per season (Lindner and Anderson 1956, Cummings 1961, Eldred et al. 1961). Given its importance, more field studies are needed to obtain accurate data of spawning frequency.

White shrimp females are able to spawn several times during their life and spawning females can be found throughout the year (Gracia 1989). A peak in reproductive output is reflected in the seasonal distribution of the catches of ripe/nearly ripe females (Table 1) and the abundance of postlarvae entering the nursery areas peaking around May-June and a less abundant one in October-November (Gracia 1989). Anderson et al. (1949) estimated that a 172 mm TL female white shrimp carried 860,000 eggs. In the present study, a female of the same length was estimated to have 365,156 eggs. These data indicate that Anderson et al. (1949) may have over-estimated maximum fecundity, as our results show that 196 mm TL females were estimated to carry only 558,270 eggs.

Although the catch of ovigerous brown shrimp was restricted to the spring and autumn cruises in the present study, this species has been shown to spawn throughout the year. The largest spawning peak occurs from February to April (Gracia et al. in press) with a secondary spawning peak occurring in fall. This secondary spawning is responsible for a less important second recruitment pulse that can be found in some years in brown shrimp (Gracia 1997). Renfro and Brusher (1982) reported that brown shrimp spawn year-round in depths of 46 to 110 m; however, in shallow depths peak spawnings occur in spring and fall.

Pink shrimp have also been reported to have a protracted reproductive season, with the greatest reproductive output occurring from summer to autumn (Gracia 1989). The large proportion of ovigerous pink shrimp females in the spring in the present study could be due to a shift in the timing of the spawning peak in this year. Seasonal changes in spawning events have been observed previously in this species (Gracia and Soto 1990) with the late spring-summer spawning period being more important than the autumn period. However, in this study the relative abundance of females in autumn was higher than spring (Table 1). Cummings (1961), Eldred et al. (1961) and Martosubroto (1974) suggested that female pink shrimp spawn more than once during their lives. This is supported by the fact that part of the shrimp catch in this study consisted of small individuals whose ovaries were already ripe or nearly ripe and would have the opportunity to produce more batches of eggs later in theirs lives. Pink shrimp fecundity data reported by Martosubroto (1974) in southern Florida shows a lower egg production/unit of GW than in our study. This difference may be due to differences in developmental stage and therefore egg diameter found in the females in each area. The egg diameter range in Campeche Bay was 230 to 320 μm, whereas in Florida it was between 274 and 343 μm. If the number of eggs contained in the ovary is inversely proportional to egg size, then a greater fecundity for the pink shrimp of Campeche Bay at any given GW would be expected. Another difference can be attributed to the developmental stage of ovaries which in this study comprised stages III and IV with different egg mean size. Studies with *F. brasiliensis* have shown that these stages have different mean egg size, but these sizes were not significant differently (Sandoval and Gracia 1988). These 2 stages were considered in the study because a clear differentiation between them can only be attained by histological analysis (Sandoval and Gracia 1998), which is not practical for field studies. Besides the gonad characteristics, Martosubroto (1974) determined cytological differences of the ova, which probably excluded small size eggs from fecundity estimates and also led to higher egg diameter values. Another reason is that they may belong to different genetic stocks.

Gonad weight is a more reliable parameter for estimating shrimp fecundity in this part of the Gulf of Mexico. It reflects directly the number of eggs that can be produced, and it represents a good predictor for assessing fecundity variation due to multiple spawnings or environmental influence. Fecundity indices based only on weight or any length parameter can give biased results because there is no way of knowing if shrimp have spawned and previous spawnings can affect the number of eggs produced/spawn. Fecundity estimate precision can be enhanced by using other practical indices like shrimp CF with a length parameter. Our multiple regression analysis showed that the correlation coefficient was increased for white shrimp and pink shrimp by adding the CF of shrimp in the equation. Using a multiple regression could be more practical than removing shrimp gonads to estimate fecundity.

There were significant differences among the slopes of the GW vs. F relationships for all 3 species. Brown shrimp demonstrated higher fecundity than the others. Since the egg diameter of these species shows an inverse order (brown shrimp have smallest eggs), it is reasonable to expect a higher number of eggs for brown shrimp as a result of proportional increases of the GW for each species.

Relative fecundity varied greatly when compared with TW. This suggests that increases of somatic weight are not necessarily accompanied by proportional increases in GW, which could depend on gonad ripeness and previous shrimp spawnings. This is supported by the fact that regression of TW on GW was only significant for white shrimp. This could be related to seasonal variations in fecundity with multiple spawnings or temporal changes in the CF of the shrimp.

The large number of eggs that can be spawned by penaeid shrimp produces a great abundance of planktonic larvae, enhancing the probability of some reaching inshore waters. The major spawning peaks of white, pink and brown shrimps in the southern Gulf of Mexico are related to an increase in primary production and a peak in planktonic biomass abundance (Licea et al. 1982, Flores-Coto et al. 1988, Espinosa-Villagran 1989). The increased availability of food for shrimp larvae favors survival at this developmental stage. The large number of eggs spawned by a single female, together with continuous reproduction throughout the year, confers a high reproductive potential for penaeid shrimp which enhances possibilities for larvae to reach estuaries. However, the success of spawning and subsequent recruitment to the adult stock is highly dependent on survival of juveniles in the estuaries and during emigrations from these areas (Gracia 1989). A large proportion of the stock is removed by inshore and offshore fisheries leaving a small stock for spawning. Gracia (1996) suggests that penaeid shrimp stocks can support exploitation levels of about 20% without affecting the recruitment.

Fecundity estimates for the commercially important species of shrimp of the Gulf of Mexico presented here are basic data which were not previously available in the literature, except in pink shrimp. Future research needs are: 1) an estimate of egg production in different seasons; and 2) detailed histological assessments relative to spawning frequency estimates. These data would allow a more accurate estimate of fecundity variation and better estimates of population fecundity during the reproductive season. Data obtained here can be used for developing population models that can serve to assess the impact of the fishery on reproductive output. Management strategies could then be focused to achieve optimal exploitation of healthy brown shrimp stock (Gracia 1997, Gracia and Vázquez-Bader 1999) or to rebuild overexploited white and pink shrimp stocks in the southwestern Gulf of Mexico (Gracia 1995, Gracia 1996, Gracia and Vázquez-Bader 1999).

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