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Reproduction of the white grunt, *Haemulon plumieri* (Lacépede, 1802) (Pisces: Haemulidae) from Margarita Island, Venezuela

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SUMMARY: The grunts (Haemulidae) are an important component of the artisan fisheries in eastern Venezuela, but their biology is poorly known. The object of the present work was to supply basic information about the reproductive biology of *H. plumieri* in relation to sex ratio, size at maturity, spawning season and fecundity. Samples were collected from the northeast coast of Margarita Island between September 1994 and August 1995. A total of 469 specimens (232 females and 237 males) were examined. Sex ratio did not differ from 1:1 except in February 1995. Minimum size at maturity was 213 mm total length for females and 271 mm total length for males. Size at maturity (L_{50}) was 309 mm total length for females and 357 mm for males. The spawning season extends throughout the year, with peaks in February-April and August-October. Fecundity ranged from 19873 to 535039 eggs, and was related to body length and weight. White grunt was characterised by asynchronous oocyte development and multiple spawning. The weight-length relationship for the sexes differed and showed negative allometry. Condition factor was over 95% during the sampling period, showing minimum values prior to the reproductive peak, which can be interpreted as the result of mobilisation of somatic energy reserves for reproductive development.

Keywords: reproduction, Haemulidae, white grunt, *Haemulon plumieri*, Venezuela.

RESUMEN: REPRODUCCIÓN DEL COROCORO MARGARITEÑO, *HAEMULON PLUMIERI* (LACÉPEDE, 1802) (PISCES: HAEMULIDAE) EN LA ISLA DE MARGARITA, VENEZUELA. – Los corocoros (Haemulidae) representan un componente importante de las pescas artesanales en el oriente de Venezuela. A pesar de esto, su biología es poco conocida. El objetivo de la presente investigación fue aportar información básica sobre la biología reproductiva (proporción sexual, talla de madurez, época de reproducción y fecundidad) de *H. plumieri*. Fueron examinados 469 ejemplares (232 hembras y 237 machos), obtenidos en muestreos mensuales entre septiembre de 1994 y agosto de 1995. La proporción sexual no se alejó estadísticamente de la unidad excepto en febrero de 1995. La talla mínima de madurez sexual fue de 213 mm de longitud total para las hembras y 271 mm de longitud total para los machos. La talla de maduración (L_{50}) fue de 309 mm de longitud total para las hembras y 357 mm para los machos. La especie se reproduce durante todo el año, con picos de máxima intensidad en febrero-abril y agosto-octubre. La fecundidad osciló entre 19873 y 535039 huevos, y estuvo relacionada con la longitud y peso corporal. La especie se caracteriza por presentar un desarrollo asincrónico de los ovocitos y desoves múltiples. La relación peso-longitud difirió entre los sexos y mostró una alometría negativa. El factor de condición se mantuvo por encima del 95% durante el periodo de muestreo y mostró valores mínimos en los meses previos a los picos reproductivos, lo cual es interpretado como el resultado de la movilización de la energía somática para el desarrollo gonadal.

Palabras clave: reproducción, Haemulidae, corocoro margariteño, *Haemulon plumieri*, Venezuela.

INTRODUCTION

Grunts (Haemulidae) are among the most abundant fishes on reefs and live-bottoms, in shelf areas, in muddy and sandy areas, and in a variety of inshore habitats in the Caribbean Sea and the Gulf of Mexico (Darcy, 1983). They are important energy importers to reef communities and are a major prey of many larger species such as snappers and groupers. Grunts are one of the most frequently

caught fishes by recreational and subsistence fishermen in the western-central Atlantic. They are quality food fish, and the most abundant species are commercially important (Courtenay and Sahlman, 1978; Darcy, 1983).

In Venezuelan waters, 14 species of the genus *Haemulon* have been identified. Most of them are commercially important and represent a significant component of commercial catches (Cervigón, 1993). In eastern Venezuela, *Haemulon plumieri* is known as "corocoro margariteño". This species can be found in waters of both the continental shelf and oceanic (off-shore) islands with extended coral reefs. It is distributed from Chesapeake Bay (USA) to Natal (Brazil), including Bermuda, the Bahamas and the Gulf of Mexico, and occurs over grass beds and rocky and coralline bottoms up to 40 m, where it is caught primarily by hook and line, seines and fish traps. It can attain a total length of over 55 cm and a weight of nearly 1000 g (Manooch, 1976; Courtenay and Sahlman, 1978; Cervigón, 1993).

Investigations regarding the reproduction of *H. plumieri* in the Caribbean Sea are restricted to the Northern Islands and the Gulf of Mexico, especially Puerto Rico (Erdman, 1977), Florida (Moe, 1966; Murie and Parkyn, 1999), Jamaica (Munro *et al.,* 1973) and Cuba (García-Cagide, 1987), but there is a lack of data concerning the species along the South Caribbean coasts, including Venezuela. The aim of this study was to investigate some reproductive traits (sex ratio, gonad development, size at sexual maturity, fecundity, spawning period, weight-length relationship and condition factor) of *H. plumieri* at Margarita Island, southeastern Caribbean.

MATERIALS AND METHODS

Samples of *H. plumieri* were obtained monthly from commercial catches of small-scale vessels using fish traps off the northeast coast of Margarita Island, Venezuela (Lat. 11º00' to 11º15'N, Long. 63º45' to 63º50'W), from September 1994 to August 1995. All specimens were measured to the nearest mm in total length (TL) and fork length (FL), and weighed to the nearest 0.1 g in body weight (W_T) and eviscerated weight (W_E), and to the nearest 0.01 g in gonad weight (W_G) and liver weight (W_L). Sex and maturity stages (I, undeveloped; II, ripening or recovering; III ripe, gamete running; and IV, spent) were determined according to macroscopic and microscopic examination of the gonads (Table 1). A chi-square test with Yates's correction for continuity was used to assess sex ratios. Mean length for the sexes was compared by a Student's t-test (Steel and Torrie, 1985).

For the histological description of maturity stages, the gonads were fixed in 10% formalin or in Bouin's solution, dehydrated in ethanol and embedded in paraffin. Sections of 5-10 μm were stained with haematoxylin-eosin and haematoxylin-VOF (Gutiérrez, 1967). Oocyte diameter was measured

TABLE 1. – Macroscopic and histologic characteristics of each stage of development in the white grunt, *Haemulon plumieri*.

Stage	Characteristics
I. Immature	Ovary and testes are very thin structures, with no evidence of previous spawnings. Previtellogenic oocytes at all stages present below the epithelium lining the lamellae. Oocytes are not visible with naked eyes. Sex not readily distinguishable macroscopically. GSI ranged between 0.02 and 0.12 ($\bar{x}$ = 0.06) in males and between 0.03 and 0.10 ($\bar{x}$ = 0.07) in females.
II. Maturing virgin or recovered spent	Ovaries rounded, increased in size compared with the previous stage, light yellow or reddish in colour and poorly supplied with blood vessels. Ovary wall translucent and the oocytes are visible through it when viewed under a stereomicroscope at low magnification. The oocytes of larger size belonged to cortical alveoli and lipid droplet stages. Those in earlier stages of development were similar in structure and distribution to those mentioned in stage I. Testes are whitish or pale cream in colour, opaque, flattened with a few lobulations over the surface. GSI varied between 0.04 and 0.65 ($\bar{x}$ = 0.17) in males and between 0.06 and 1.17 ($\bar{x}$ = 0.40) in females.
III. Ripe	Ovaries are further enlarged and occupy almost the entire body cavity. They are orange-yellow in colour and well supplied with blood vessels. Oocytes become visible to the naked eye. Oocytes in all development stages can be observed histo logically. Those in the yolk granules stage are very abundant. Testes are opaque, milky white, smooth in texture and angular in cross-section. Pressure applied to the abdomen of the female and male fish resulted in extrusion of eggs and milt, respectively. GSI varied between 0.27 and 0.83 ($\bar{x}$ = 0.48) in males and between 0.81 and 4.77 ($\bar{x}$ = 2.32) in females
IV. Spent	Ovaries and testes flaccid, empty. Posterior portion of oviduct reddish in colour. Testes brown-red in colour, bloodshot in appearance. Ovigerous lamellae are disorganised. A great proportion of remaining vitellogenic oocytes show different stages of atresia. Only a few ovaries with empty follicles were observed. GSI varied between 0.18 and 0.87 ($\bar{x}$ = 0.38) in males and between 0.56 and 2.60 ($\bar{x}$ = 1.55) in females. Partially spent ovaries are slightly flaccid and contain postovulatory follicles alongside vitellogenic and early maturation stage oocytes.

using the ocular micrometer of a microscope. The average oocyte diameter at each developmental oocyte stage was based on 100 randomly chosen oocyte measurements per oocyte stage. To estimate the mean total length at maturity (L_{50}) for males and females, the fraction of mature fish in each 10 mm interval was fitted to a logistic function (Gaertner and Laloe, 1986) using the Marquardt method (Draper and Smith, 1981). The spawning season was inferred from the study of the monthly variation in gonadosomatic index (GSI) and hepatosomatic index (HSI), and the relative frequencies of gonad maturity stages during the study period. GSI and HSI were calculated as: GSI= $100(W_G.W_E^{-1})$; HSI= $100(W_L.W_E^{-1})$.

Fecundity was estimated gravimetrically (Holden and Raitt, 1975) using 50 ripe ovaries preserved in Gilson's fluid. Relative fecundity (RFTL: fecundity related to total length; RFW_T: fecundity related to total weight; RFW_E: fecundity related to eviscerated weight; RFW_G: fecundity related to gonad weight) for each fish was calculated as: $RFTL= F. TL^{-1}$, $RFW_T= F. W_T^{-1}$, $RFW_E = F. W_E^{-1}$ and $RFW_G= F. W_G^{-1}$ (Palazón-Fernández *et al.,* 2001). Fecundity was regressed against body length, body weight, and ovary weight using model II regression on $\log_{10}$ transformed data (Ricker, 1973).

Weight-length relationship was modelled using linear model II regression analysis on the log-transformed variables (Ricker, 1973). Allometry was assessed by a Student's t-test. Relative Condition Factor (Kr) was calculated as the percentage ratio of the observed weight of a fish to the weight expected from the calculated weight-length relationship (Le Cren, 1951). Monthly changes in the mean Kr, GSI, and HSI were assessed using one-way analysis of variance (ANOVA). Significant ANOVAs ($p \leq 0.05$) were followed by Duncan's multiple range test (Steel and Torrie, 1985). When necessary, data were $\log_{10}$ transformed to satisfy the assumptions of the analysis.

RESULTS

In total, 469 specimens with lengths ranging between 183 and 389 mm TL were examined. Overall, 232 (49.5%) specimens were females (183 - 362 mm TL; 94.0 - 709.3 g W_T) and 237 (50.5%) were males (185 - 389 mm TL; 106.5 - 961.0 g W_T).

Males tended to be longer ($t= 1.72$; $p<0.05$) and heavier ($t= 3.09$; $p<0.01$) than females.

TABLE 2. – Number of male and female *Haemulon plumieri* per month and results of the Chi-square test for a 1:1 ratio.

Month/year	Females	Males	Total	χ^2
September/94	16	16	32	0^{NS}
October	21	19	40	0.03^{NS}
November	16	23	39	0.92^{NS}
December	26	13	39	3.69^{NS}
January/95	14	23	37	1.73^{NS}
February	25	11	36	4.69^{*}
March	14	27	41	3.51^{NS}
April	10	18	28	1.75^{NS}
May	20	21	41	0^{NS}
Jun	27	23	50	0.18^{NS}
July	17	28	45	2.22^{NS}
August	26	15	41	2.44^{NS}
Total	232	237	469	

NS= $p>0.05$; *= $p \leq 0.05$; 1 df

TABLE 3. – Number of male and female *Haemulon plumieri* per length class and results of the Chi-square test for a 1:1 ratio.

Length class	Females	Males	Total	χ^2
180 - 200	6	13	19	1.89^{NS}
200 - 220	23	19	42	0.21^{NS}
220 - 240	33	37	70	0.13^{NS}
240 - 260	36	33	69	0.06^{NS}
260 - 280	24	18	42	0.60^{NS}
280 - 300	23	22	45	0.00^{NS}
300 - 320	37	21	58	3.88^{*}
320 - 340	37	19	56	5.16^{*}
340 - 360	12	21	33	1.94^{NS}
360 - 380	1	27	28	22.32^{*}
380 - 400	0	7	7	5.14^{*}
Total	232	237	469	

NS= $p>0.05$; *= $p \leq 0.05$; 1 df

Sexuality

H. plumieri is gonochoristic. Gonads are paired elongated structures lying ventral to the gas bladder that join caudally forming a common genital duct that exits the body through the genital pore. No sexual dimorphism in body shape or colour was observed. Although 91 percent (n=426) of the individuals were macroscopically sexed, for fish between 180 and 220 mm TL external sexing was difficult, especially in males.

Sex ratio

Over the entire size range sex ratios did not differ significantly ($p>0.05$) from 1:1, except in February 1995 when females were favoured significantly (Table 2). The number of males and females was generally equal at lengths of less than 300 mm

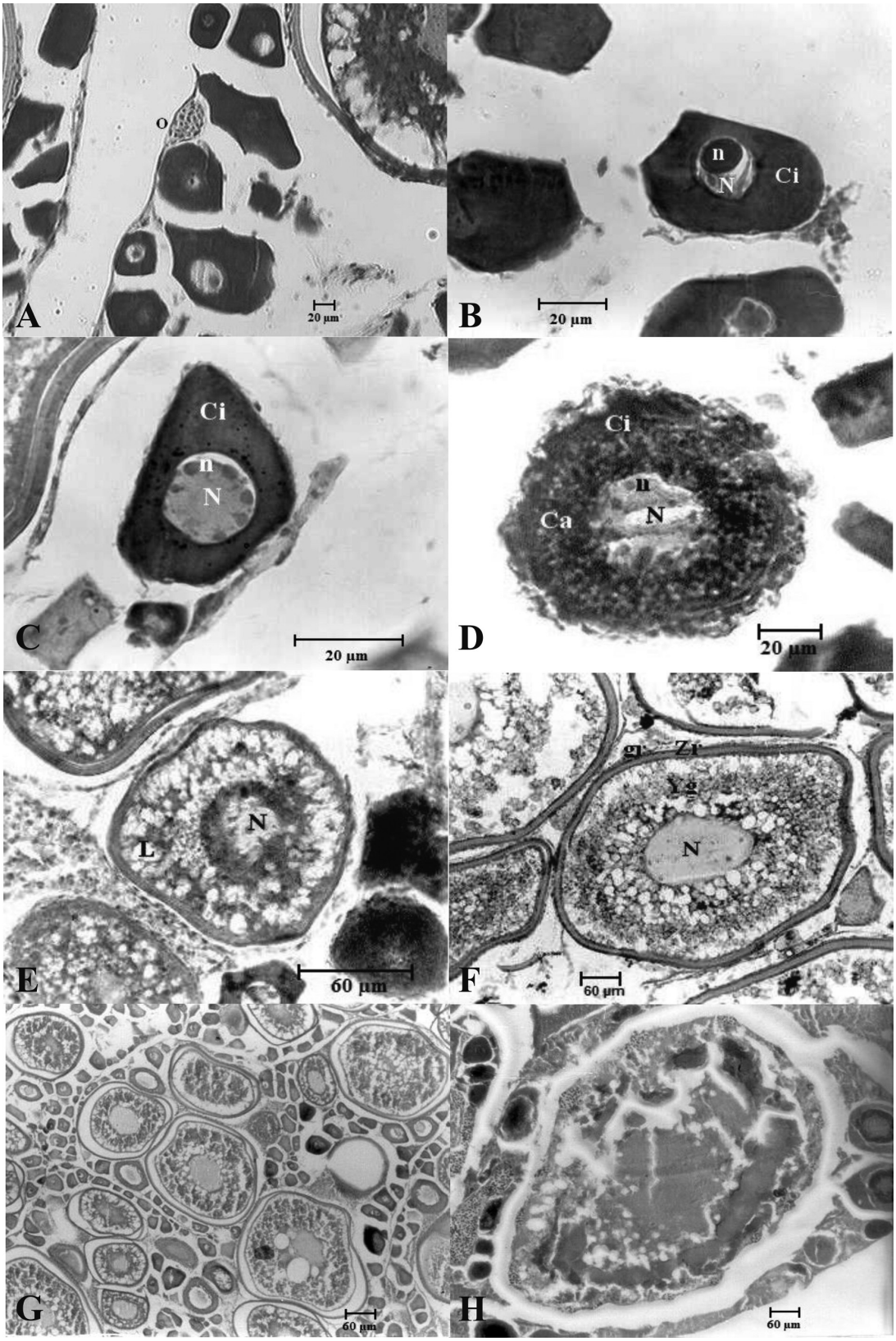

FIG. 1. – Photomicrographs of oocytes at different developmental stages in the white grunt, *H. plumieri*. A) Oogonia, B) Chromatin nucleolus stage, C) perinucleolus stage, D) cortical alveoli stage, E) Lipid vesicle stage, F) Yolk granules stage, G) transverse section through a ripe ovary showing oocytes at different maturity stages, H) Atretic oocyte. Ca: Cortical alveoli., Ci: cytoplasm, gr: granulose, L: lipid droplets, N: nucleus, n: nucleolus, O: oogonia, Yg: yolk granules, Zr: zona radiata.

TABLE 4. – Microscopic characteristics for the determination of the stages of oogenesis in *Haemulon plumieri* ovaries

Stage	Histological features
A. PREVITELLOGENESIS	
0. Oogonia (Fig. 1A)	Small cells, less than 8 μ in diameter, often found in nests in the germinal tissue. These oocytes have a translucent cytoplasm and a large central nucleus. Oocytes ranged from 4 to 8 μ ($\bar{x}$ = 6.12 ± 0.16) in diameter. Nucleus 2-3 μ ($\bar{x}$ = 2.24 ± 0.09 μ)
1. Chromatin nucleolus (Fig. 1B)	Highly basophilic cells, irregular in shape. Nucleus enlarged with a single large and basophilic nucleolus. Oocyte diameter varied between 20 and 72.5 μ ($\bar{x}$ = 44.70 ± 1.97 μ). Nucleus 10 to 37.5 μ ($\bar{x}$ = 17.20 ± 0.86 μ).
2. Perinucleolus (Fig. 1C)	Oocytes in this stage measured 37.5 to 105 μ ($\bar{x}$ = 62.5 ± 1.89 μ). Concomitant with oocyte growth, the nucleus increases in size, becomes translucent and numerous small nucleoli and sometimes one large one appear at its periphery close to the nuclear membrane. The cytoplasm acquires a granular structure and gradually loses its good affinity to haematoxylin and tends to be stained only faintly therewith. In the more advanced oocytes, the cytoplasm was differentiated into two layers, showing a faintly stained outer layer and a deeply stained inner layer. Nucleus measured 15.00-42.50 μ ($\bar{x}$ = 24.95 ± 0.97 μ)
B. VITELLOGENESIS	
3. Cortical alveoli (Fig. 1D)	These oocytes measured 57.5-130.0 μ ($\bar{x}$ = 85.15 ± 2.25). This stage is characterised by the appearance of cortical alveoli in the cytoplasm close to the nuclear membrane. The basophilic character of the cytoplasm decreases. Some oocytes still demonstrate a zoned cytoplasm. Nucleus still translucent with the nucleoli close to the nuclear membrane. Nucleus: 15-60 μ ($\bar{x}$ = 30.94 ± 1.34 μ). Developing follicular layer becomes visible.
4. Lipid vesicle (Fig. 1E)	Small lipid droplets appear around the nucleus and by the end of this stage occur randomly distributed throughout the cytoplasm. Lipid droplets increase in number and fuse forming larger vesicles. The zona radiata starts to develop. Concomitant with oocyte growth the follicular layer becomes much more developed. The nucleus is still centrally located, with the nucleoli at its periphery. Oocyte diameter varied between 77.5-245 μ ($\bar{x}$ = 128.1 ± 5.38 μ). Nucleus: 30-92.5 μ ($\bar{x}$ = 51.16 ± 2.47 μ)
5. Yolk granules (Fig. 1F)	The oocytes in this stage measured 185 to 560 μ ($\bar{x}$ = 395.5 ± 11.06 μ). The appearance of small yolk granules at oocyte periphery characterises the beginning of this stage. The nucleus is still centrally located with the nucleoli aligned at the periphery. The yolk granules increase in number and fuse forming large yolk globules that stain orange-yellow. Fat vacuoles are scattered thorough the cytoplasm. The zona radiata increases in thickness, the radial striations become clearly visible, and exhibit a bipartite structure. Oocyte membranes are 5-20 μ ($\bar{x}$ = 12.19 ± 0.57 μ) in width. In the more advanced oocytes, the nucleus is not seen, possibly owing to its migration towards the animal pole and/or the dissolution of its membrane. Yolk vesicles fuse to form a homogeneous yolk mass that fills most of the cytoplasm. Lipid droplets coalesce forming an oil globule. Nucleus diameter was 42.5-155.0 μ ($\bar{x}$ = 91.39 ± 4.15 μ).
6. Atretic (Fig. 1G)	Some postvitellogenic oocytes fail to undergo maturation and degenerate. In these oocytes yolk loses its structural integrity. The cytoplasmic inclusions lose their organisation. The zona radiata forms a number of folds and breaks at several points, and the oocyte is invaded by phagocytic cells.

TL, but females outnumbered males between 300 and 340 mm TL. Males dominated in specimens larger than 360 mm and all individuals over 380 mm were males (Table 3).

Gonad development

The size (length and weight) and colour of the gonads varied during sexual development. Based on external characteristics, gonads could be classified into four stages of development (Table 1). Histological examination of the gonads showed that immature ovaries contained previtellogenic oocytes; developing ovaries had previtellogenic as well as early vitellogenic (cortical alveoli and lipid vesicle) oocytes; and mature ovaries contained oocytes at all stages. Oocyte development was divided into five stages (Table 4, Fig. 1). In ripe ovaries, oocyte diameter was highly variable and ranged from 20 to 560 μm for the various stages of development.

During oogenesis in *H. plumieri* atretic oocytes were seen (Fig. 1H), mainly in spent ovaries, in which unshed ripe oocytes degenerate forming acidophilic spots. At first, lipid droplets, cortical alveoli and yolk globules disrupt. Then, the chorion breaks at several points and degenerates. At this point, the content of the oocyte is surrounded and invaded by phagocytic granulosa cells; finally resorption of the different inclusions of the oocyte occurs. Eventually, only an empty follicle remains.

Size at sexual maturity

The smallest mature fish were a 213 mm TL (190 mm FL) female and a 271 mm TL (241 mm FL) male. Fifty percent maturity occurred at 309 mm TL (275 mm FL) for females, and at 357 mm TL (317 mm FL) for males (Fig. 2). Based on these results, adults were defined as those individuals at or exceeding the minimal size at sexual maturity and at least stage II.

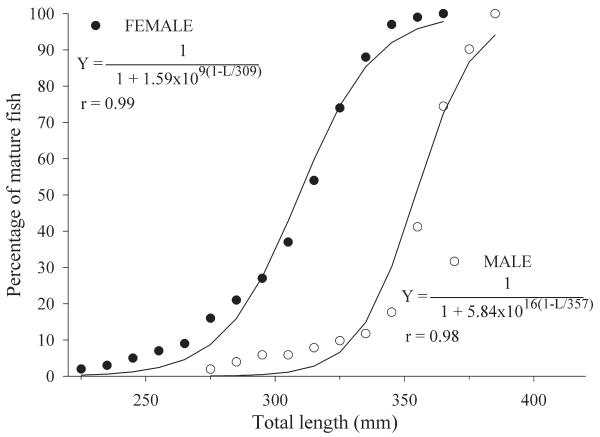

FIG. 2. – Sexual maturity ogives of male (open circles) and female (full circles) white grunts and corresponding size-at-maturity, L_{50}.

Spawning season

GSI increased with stage of development. For stage I and II females it remained below 1.17; for ripe females, it was 0.81-4.77; for immature males it was only 0.03-0.65, while for ripe males it was 0.27-0.83. GSI was significantly higher in females (F= 170.1, p<0.01), and showed a high variability throughout the year for both sexes.

GSI of adult females varied between months (F= 5.39; p<0.01). Higher GSI values occurred in January-March and August and declined sharply thereafter, indicating that oocytes were released. Low values occurred in July and October-December, while the rest of the year a moderate activity was noted (Fig. 3A). The low value in July is due to the absence of ripe fishes in the sample from that month.

Male GSI values showed significant monthly differences (F= 4.78; p<0.01), decreasing in November, April and July. Mean GSI for males remained high and variable in February, March, September, October, and December and low in April, May, July and August (Fig. 3B).

HSI showed strong variations during the sampling period for both sexes (Fig. 4). Differences between months were statistically significant (F = 5.12; p<0.01) in females. Mean HSI values were significantly higher in July, and October-December, and were minimal in January-June, August and September. Males also showed monthly differences in HSI (F= 4.86; p<0.01). Higher values were found in April, July, August and October, and lower ones in January, February, May, June, September and December. The HSI values for females and males

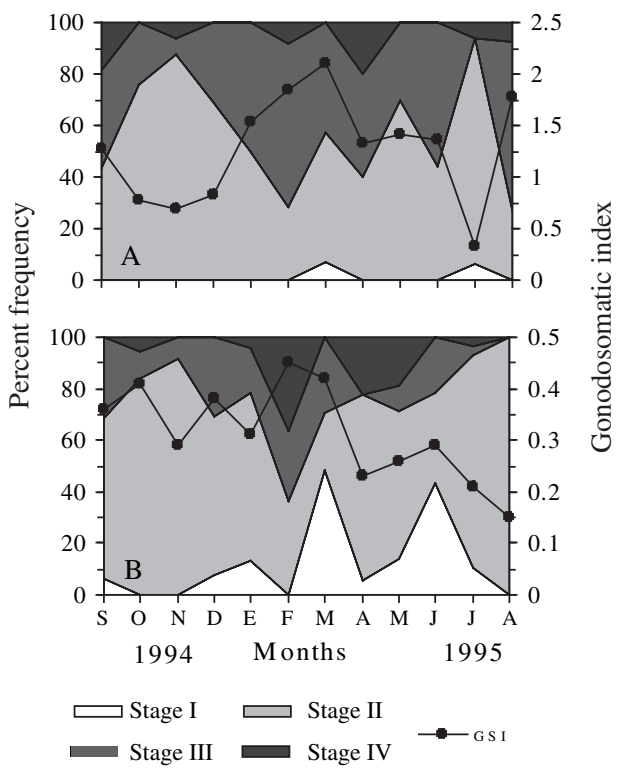

FIG. 3. – Monthly changes in GSI and in the frequency of occurrence of the various maturity stages of gonads for female (A) and male (B) *H. plumieri*.

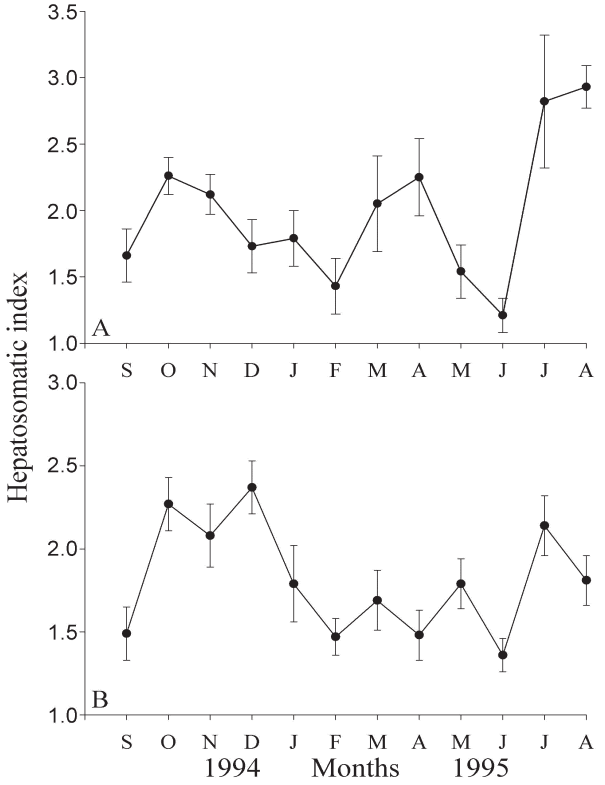

FIG. 4. – Monthly variation in the mean HSI for adult male (A), and female (B) *H. plumieri*.

were inversely related to the GSI ones (r= -0.50, p<0.01; r= -0.46, p<0.01, respectively).

Both ripe males and females were collected all year round, except in July 1995 when no mature females were caught, and April and August 1995 when no ripe males were caught (Fig. 3). The percentage of ripe females was higher in January (50%), February (64%), March (43%), April (40%), June (56%) and August (65%). In October-December 1994 and July 1995, almost all fishes were at stage II. Spent females were observed in low percentages in September, November, February, April, July and August. (Fig. 3A). The greatest proportions of ripe males were found in September (31%), December (31%), February (27%) and March (30%). Developing males were found in high proportions throughout the year, except in February 1995 when ripe and spent individuals dominated, and in March when juveniles were present in higher proportion. Spent males were collected in October, January, February, April, May and June. The highest percentages were observed in February and April-May (Fig. 3B).

The presence of ripe individuals in all months provides strong evidence that the species spawns throughout the year. However, peaks in GSI, along with the changes in percent frequency of ripe and

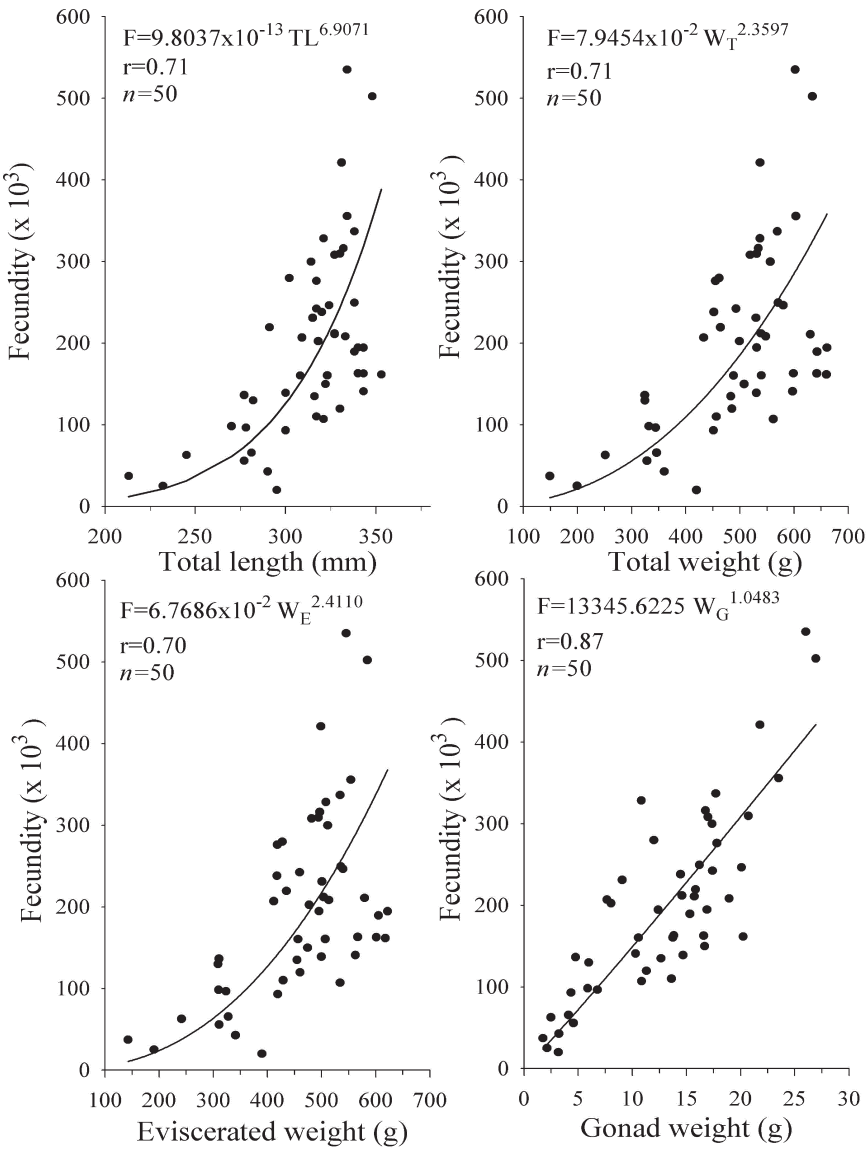

FIG. 5. – Relationship between fecundity and body length, body weight, eviscerated weight and gonad weight in *H. plumieri*.

TABLE 5. – Absolute and relative fecundity statistics in the white grunt, *Haemulon plumieri*, N = 50. N: number of specimens, SE: standard error, CV: coefficient of variation, RF-TL: relative fecundity in relation to total length, RF-W_T: relative fecundity in relation to weight, RF-W_E: relative fecundity in relation to eviscerated weight, RF-W_G: relative fecundity in relation to gonad weight.

Characteristic	Mean	S.E.	Range	CV
Fecundity	197704	16145	19873-535039	57.74
RF-TL	616.01	47.10	67.37-1601.91	54.06
RF-W_T	388.41	26.01	47.35-889.36	47.36
RF-W_E	415.65	28.39	50.99-981.83	48.30
RF-W_G	15917.89	802.61	6249.37-30345.84	35.65

spent individuals, indicates that *H. plumieri* has two reproductive peaks, one in February-April and one in August-October.

Fecundity

Estimates of fecundity (F) ranged from 19873 to 535039 eggs. Mean fecundity was 197704 ± 16145 eggs. Individual relative fecundities are shown in Table 5. Fecundity increased allometrically with body length, total weight, eviscerated weight and ovary weight (Fig. 5). With the exception of gonad weight, there is considerable variation in fecundity in relation to body length and weight. The coefficients of determination (r^2) for the different relationships were about 50%, indicating that only about 50% of the variation in fecundity was explained by these variables.

Weight-length relationship

Weight-length relationships were derived from 469 specimens ranging in size from 183 to 389 mm TL and 94.0 to 961.0 g W_T (Fig. 6). Weight-length relationships differed between juveniles and adult males ($F= 4.21$; $p<0.01$) and females ($F= 4.40$; $p<0.01$). Although the slope of the relationship did not differ ($t = -0.51$; $p>0.05$) between the sexes, the opposite was true for the intercept ($t = 2.96$; $p<0.01$). The exponents of the three regressions were significantly different from 3. Juveniles showed a positive allometry ($t= 2.81$; $p<0.01$), while adults exhibited negative allometry ($t= -5.24$; $p<0.01$).

Condition factor (Kr)

Mean Kr for males and females showed a similar seasonal pattern (Fig. 7). In adult males, Kr showed monthly differences ($F= 4.95$; $p<0.01$). It was higher in March-April and July-December and lower in

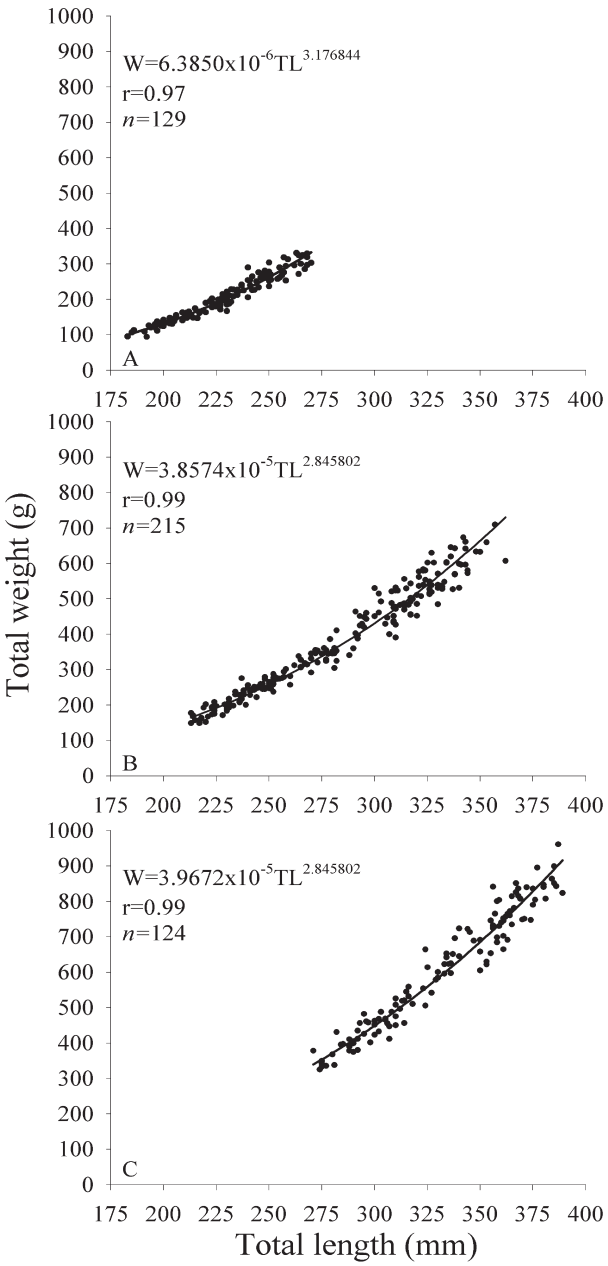

FIG. 6. – Weight-length relationship in *H. plumieri*. A, juveniles; B, females; C, males.

January-February and May-June. Kr for adult females also varied significantly between samples ($F= 2.40$; $p<0.01$). Higher condition was attained in July-December. The lower values occurred in January-June. Kr was not correlated significantly with GSI in either males ($r= -0.08$; $p>0.05$) or females ($r= -0.09$; $p>0.05$), even though lower Kr values were seen prior to the higher reproductive peak and coincident with a decline in GSI. Kr was positively related to HSI both in males ($r = 0.43$; $p<0.01$) and females ($r= 0.40$; $p<0.01$).

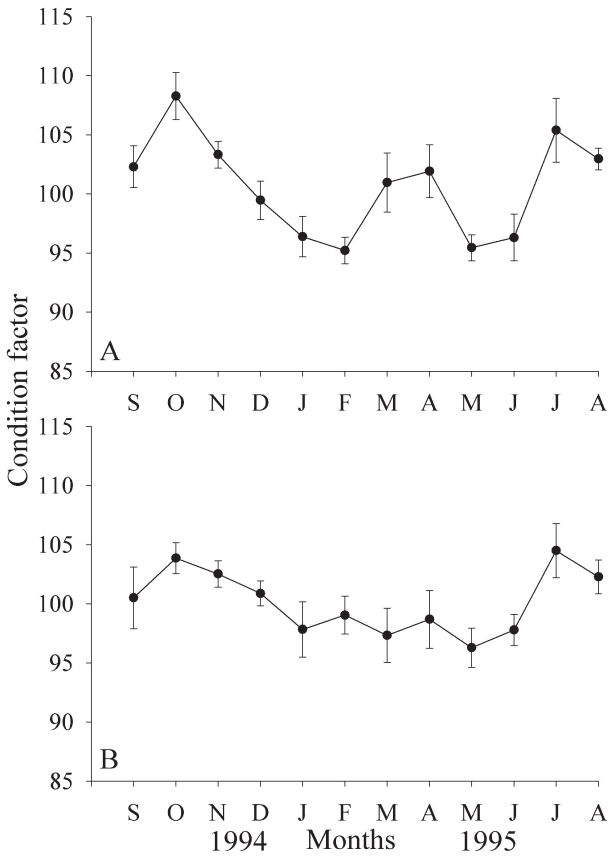

FIG. 7. – Mean monthly variation in Condition Factor for adult male (A) and female (B) *H. plumieri*.

DISCUSSION

Although no sexual dimorphism in body shape or colour was observed in *H. plumieri* in the present work, males were longer and heavier than females, which agrees with observations of Gaut and Munro (1983) in Jamaica. The observed differences are attributed to different growth rates between sexes. Female fish normally have higher energy requirements for reproduction than males, causing them to have a slower growth rate. Bowering (1976) pointed out that differences in growth between sexes are the result of genetics that determines the physiology and behaviour of the fish.

Sex ratios did not differ significantly from 1:1 over the entire size range, except in February 1995 when females were favoured significantly. Gaut and Munro (1983) and García-Cagide (1987) indicated a significantly higher proportion of females than males in the catches from Jamaican and Cuban waters, respectively. Other haemulids showed a clear dominance of females, *H. bonariense* in Jamaican waters (Gaut and Munro, 1983), *H. sciurus* and *H. album* in Cuban waters (García-Arteaga, 1983, and García-Cagide, 1986a,b), although the proportion varied during the year. Gaut and Munro (1983) stated that the greater abundance of females in some haemulid species can be explained by a higher female survival rate. Our results agree well with those described by Kossowski (1985), Rodriguez (1985) and Granado (1989) for *H. aurolineatum*, *H. steindachneri* and *H. melanurum*, respectively, in eastern Venezuelan waters.

Sex ratios were generally equal at lengths of less than 300 mm TL, females outnumbered males between 300 and 340 mm TL, males outnumber females in specimens larger than 360 mm, and all individuals over 380 mm were males. Sauskan and Olaechea (1974, in Darcy, 1983) observed the same tendency for *H. aurolineatum* at Campeche Bank. Differences in size-specific sex ratio have been related to sexual differences in growth, mortality, energetic cost of reproduction, and differential migration or spatial segregation by sex (Sadovy and Shapiro, 1987; Stergiou *et al*., 1996).

The pattern of oocyte development in *H. plumieri* follows the basic progression as described for other haemulids (Kossowski, 1985; García-Cagide, 1986a,b; Granado, 1989). No hydrated oocytes were observed. It is known that oocyte hydration takes place a few hours before ovulation in some species (García-Cagide, 1986a, b; Clarke, 1987). In haemulids, ovaries in spawning condition are rarely observed (Gaut and Munro, 1983), and it is likely that ovulation takes place shortly before spawning, as reported by García-Cagide (1986b) for *H. album* and Clarke (1987) for *Encrasicholina purpurea*. I observed few ovaries with empty follicles. If follicles quickly undergo resorption, as reported for other tropical species by Clarke (1987) and West (1990), and *H. plumieri* spawns at night, it would be difficult to observe hydrated oocytes histologically in fish caught during the day. Some white grunt females with the external appearance of recent spawning had numerous vitellogenic atretic oocytes. This feature, and others such as the presence of marked blood vessels, deorganised ovigerous lamellae, presence of ovulated eggs in the lumen of the ovaries, and necrotic zones in the ovaries, have been used as evidence of spawning condition (García-Cagide, 1986b, 1987; Maddock and Burton, 1999).

In ripe ovaries, oocyte diameter was highly variable, ranging from 20 to 560 μm and showing three to four size groups. This is characteristic of an asyn-

chronous ovary (Marza, 1938, in Wallace and Selman, 1981) and was taken as evidence that the species is a multiple spawner, though the frequency and intervals of spawning remain unclear. Asynchronous oocyte development associated with multiple spawning seems to be generalised in *Haemulon* species, and has been observed in *H. sciurus* and *H. album* (García-Cagide, 1986a, b), *H. steindachneri* (Rodriguez, 1985), *H. aurolineatum* (Kossowski, 1985) and *H. melanurum* (Granado, 1989). Gaut and Munro (1983) stated that ripe ovaries of most haemulid species are frequently found to contain eggs of two distinct size ranges: large ripe ova ready for ovulation, and minute resting stages, which would probably develop into ova in a subsequent breeding season. This suggests that two or more spawning seasons may occur each year for some species, while others spawn more or less continuously throughout the year.

In *H. plumieri* atretic oocytes were seen (Fig. 1H), mainly in spent ovaries in which unshed oocytes degenerate forming acidophilic spots. Similar results were reported by Mota and Pessoa (1973) for the species in Brazilian waters. The progress of atresia in *H. plumieri* ovaries follows the same general pattern described by Granado (1989) for *H. melanurum*, and by Miranda *et al*. (1999) and Micale *et al*. (1999) for other teleosts. Yamamoto and Yamazaki (1961) pointed out that the presence of many atretic oocytes in the spent ovary is characteristic of fish with asynchronous spawning. In fishes, atresia appears as a consequence of a variety of factors such as stress, nutrition, age, biocidal agents, light, temperature, confinement, crowding, inadequate hormone levels, imbalance in sex ratio and cessation of spawning (Mester *et al*., 1974; Guraya, 1986; Trippel and Harvey, 1990; Dickerson *et al*., 1992). Falieva (1975, in García-Cagide, 1986a) argued that rising water temperature and the lack of conditions favouring spawning are the main causes of atresia in ripe ovaries. The mechanisms which initiate and regulate oocyte atresia in teleost fish are poorly known, especially at the molecular level (Miranda *et al*., 1999). Some authors (Hsueh *et al*., 1994; Wood and Van Der Kraak, 2000) have suggested that the cell death mechanism known as apoptosis may be the "in vivo" mechanism of atresia in teleosts.

Size at sexual maturity for *H. plumieri* in this study was larger than those previously reported from the western Atlantic. On Campeche Bank, Dubovitsky and Hondares (1970, in García-Cagide, 1987) reported that most white grunt were in reproductive condition between 175 and 274 mm standard length (about 225 - 344 mm TL, respectively), and Lyubimova and Kapote (1971, in Darcy, 1983) mentioned that *H. plumieri* matures at a length of <180 mm (length type unspecified). In Brazilian waters, Mota and Pessoa (1973) found individuals in maturing condition from 120 mm FL for males and 110 mm FL for females based on external and microscopic features of the gonads. The smallest ripe individuals caught in Jamaican waters by Gaut and Munro (1983) were 143 mm FL, and the mean size at sexual maturity was about 200 mm FL for males and 220 mm FL for females. García-Cagide (1987) reported that the modal size for fishes in reproductive condition caught in Cuban waters was 150 - 170 mm FL for females and 170 - 190 mm FL for males. Size at sexual maturity between populations of the same species can vary due to growth rates, fishing removals, food availability, and hydrologic conditions (Chapman *et al*., 1996; Hood and Johnson, 2000; Potts and Manooch, 2001).

The spawning season for *H. plumieri* observed in the present work (year-round with peaks in February-April and August-October) is similar to that reported by Erdman (1977), Mota and Pessoa (1973), Munro *et al*. (1973), Gaut and Munro (1983), García-Cagide *et al*. (1983) and García-Cagide (1987), and similar to that of congeneric species (*H. aurolineatum* and *H. melanurum* by Kossowski, 1985 and Granado, 1989, respectively) in northeastern Venezuela. Spawning of haemulids in Jamaica (Munro *et al*., 1973) is related to water temperature, with maximum spawning during the lowest temperatures (February-April), though some spawning occurs in all months. The main spawning peak for *H. plumieri* in northeastern Venezuela also occurs in February-April, when water temperatures reach a minimum and the net primary production reaches a maximum associated with coastal upwelling (Gómez and Chanut, 1993). The small number of spent *H. plumieri* collected during the sampling period may suggest that a rapid recovery occurs after spawning.

The inverse relationship between the HSI and GSI values can be related to the use of liver reserves during gonad growth and maturation (Wallace and Selman, 1981). Weight of the liver in fish increases prior to reproduction (Bustamante, 1983), and is associated with the synthesis of lipids and proteins necessary for gonad development.

Estimates of fecundity for *H. plumieri* in the present work ranged from 19873 to 535039 eggs (mean 197704 ± 16145 eggs). A total fecundity of 33477 to 223500 eggs was estimated by García-Cagide (1987) for the white grunt in Cuban waters. Although relative fecundity reported by this author (385 eggs/g) is very close to the present estimates, the small number of specimens used by this author (n=5) does not allow a good comparison. The greatest fecundity observed by Gaut and Munro (1983) for *H. plumieri* was 179000 eggs for a 273 mm FL, 388 g individual.

With the exception of gonad weight, there is a considerable variation in fecundity in relation to body length and weight. The relatively low r^2 values indicated that other factors not considered in the present study, such as age, batch spawning, and the number of previous spawnings also affect fecundity. González *et al*. (1993) has suggested that after fish attain a critical age, a reduction in relative fecundity and sometimes in absolute fecundity may occur. This effect can also induce a progressive lag in the reproductive cycles and, in multiple spawners, a reduction in the number of batches laid in a spawning season. García-Cagide (1986a,b) observed wide variations in fecundity in *H. sciurus* and *H. album* individuals of similar size and weight and stated that the differences were related to the fact that these species were multiple spawners.

Weight-length relationship in *H. plumieri* in the present study showed a positive allometry in juveniles, while adults exhibited negative allometry. The weight-length relationships for *H. plumieri* have been reported by Manooch (1976) for North Carolina and South Carolina waters (males: $W= 1.201\ 10^{-5}\ TL^{3.0503}$; females: $W= 1.452\ 10^{-5}\ TL^{3.0214}$), by Gaut and Munro (1983) for Jamaica ($W=0.0238\ FL^{2.93}$) and by Potts and Manooch (2001) for The Carolinas ($W= 1.12\ 10^{-5}\ L^{3.05}$) and southeast Florida ($W= 6.33\ 10^{-5}\ L^{2.73}$). The differences may reflect interpopulation variations or be related to the seasonality of collections.

Lower Kr values were seen prior to the higher reproductive peak. This has been related to the mobilisation of somatic energy reserves needed for reproductive development, and/or to a reduction in feeding activity during the spawning period (Maddock and Burton, 1999). García-Cagide (1986a) reported marked seasonal differences in condition factor for *H. sciurus* and suggested that they were related to water temperature, food supply, growth and reproductive activity.

Kr was not correlated significantly with GSI even though a decline in GSI coincident with a decrease in Kr was seen. Similar results were reported for *H. melanurum* (Granado, 1989); however, Kossowski (1985) observed a negative relationship between these two indices in females of *H. aurolineatum*, but not in males. In tropical fish, condition factor can decrease during the spawning season due to a loss in body weight of approximately 10% (García-Cagide, *et al*., 1983). Kr was positively related to hepatosomatic index in both males ($r = 0.43$; $p<0.01$) and females ($r= 0.40$; $p<0.01$).

As in the present study, a good general condition has been observed during much of the year in other haemulid species (Kossowski, 1985; Rodriguez, 1985; Granado, 1989) from eastern Venezuela. This is attributed to the fact that upwelling processes are locally important and support a high primary production, guaranteeing an abundant food supply during much of the year.

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