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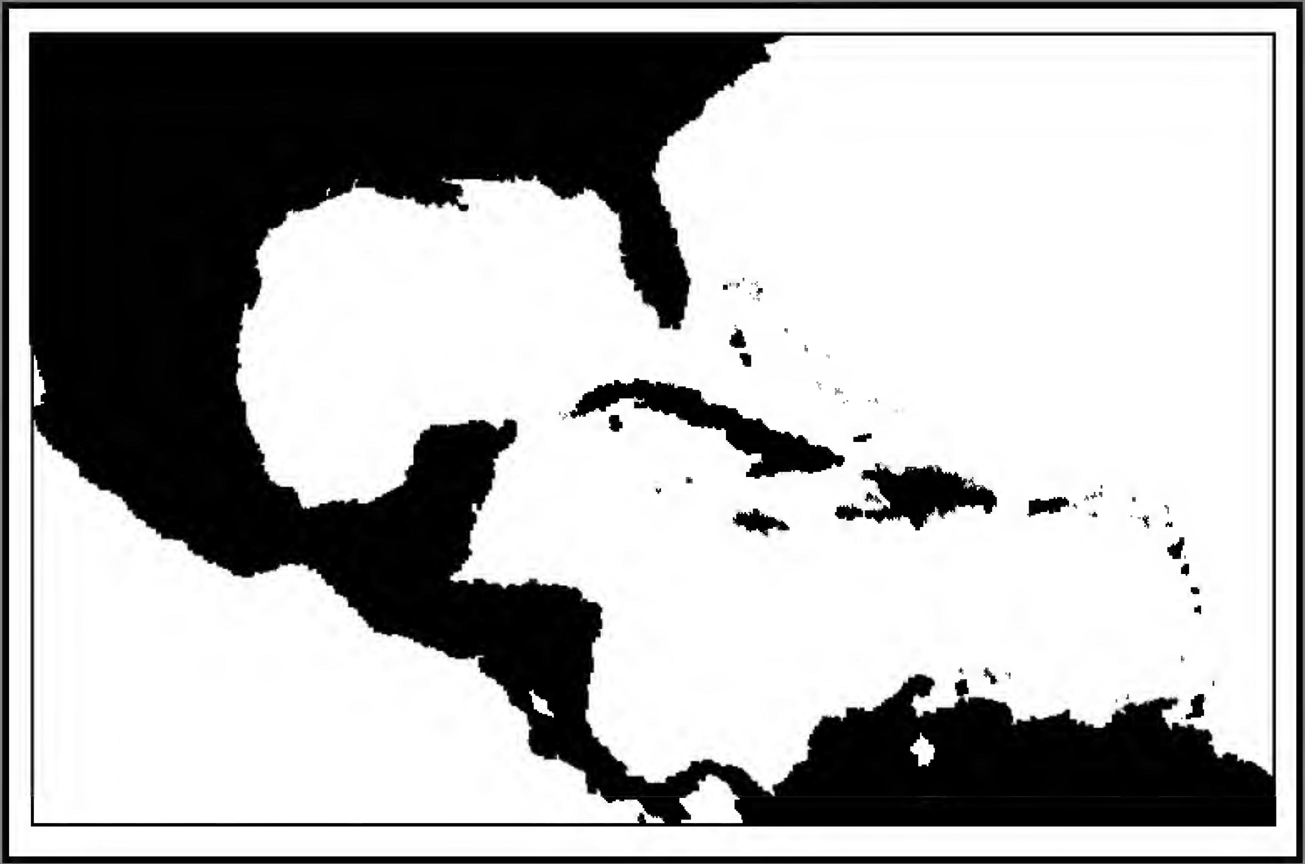

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FECUNDITY OF *LITOPENAEUS SETIFERUS, FARFANTEPENAEUS AZTECUS AND F. DUORARUM*, IN THE SOUTHWESTERN GULF OF MEXICO

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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

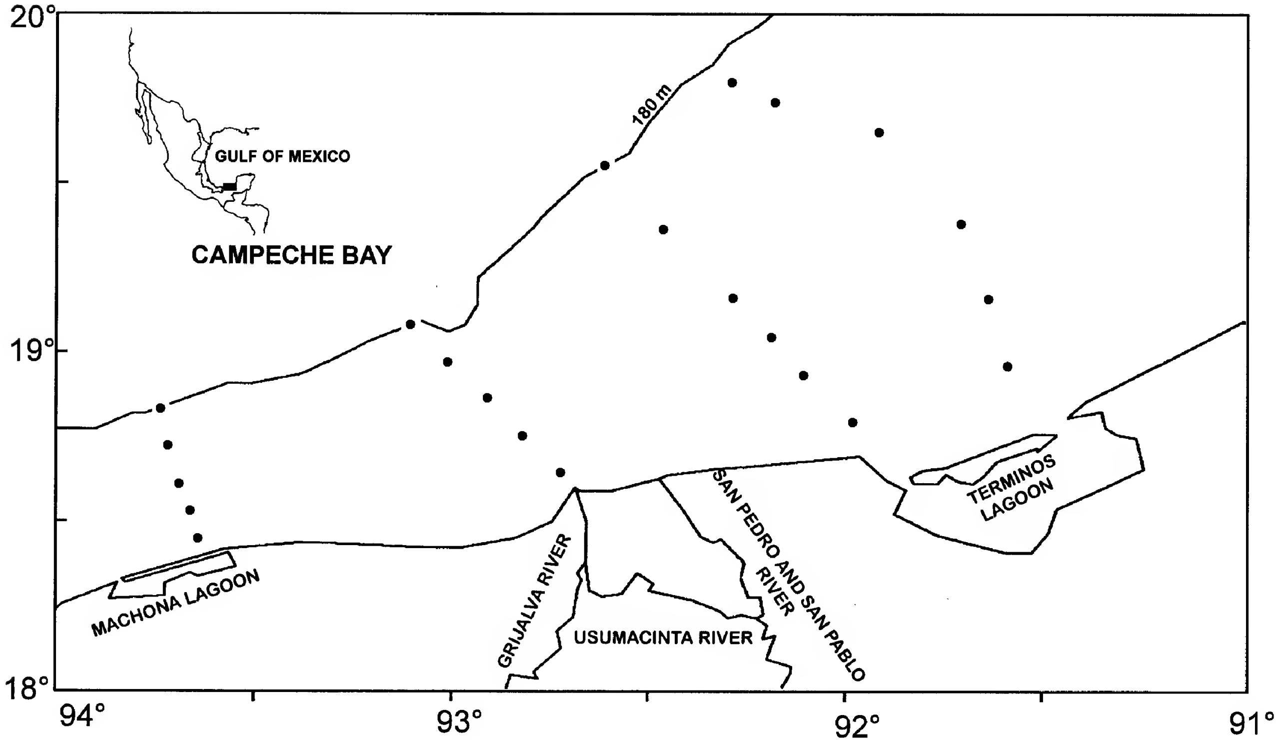

Figure 1. Study area and sampling locations.

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.

	Litopenaeus setiferus ($n = 40$)		*Farfantepenaeus aztecus* (n = 44)		*Farfantepenaeus duorarum* ($n = 27$)	
Variables	Equation	r	Equation	r	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

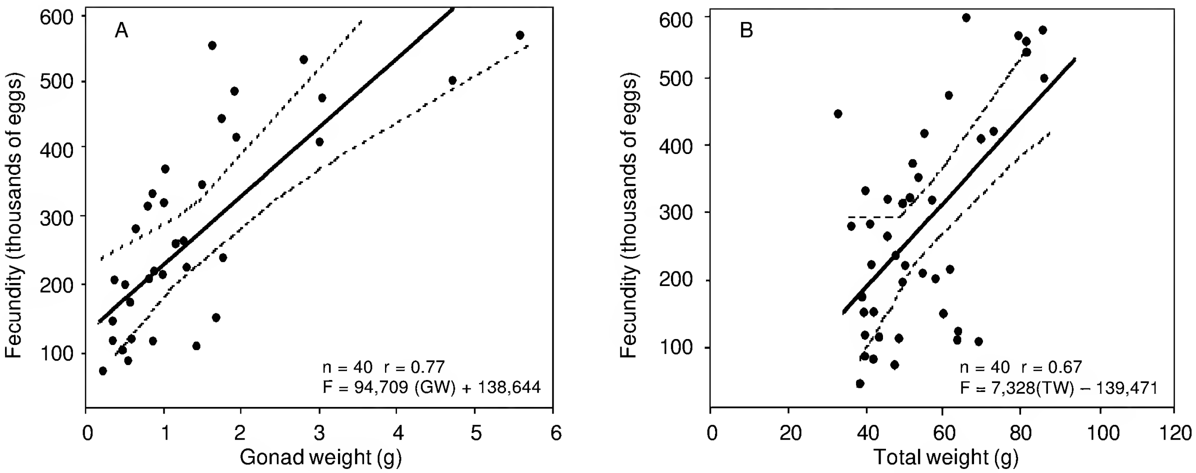

Figure 2. Relationship between gonad weight (GW) and fecundity (A), and total weight (TW) and fecundity (B) of *L. setiferus*. Regression lines are plotted with 95% confidence limits.

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

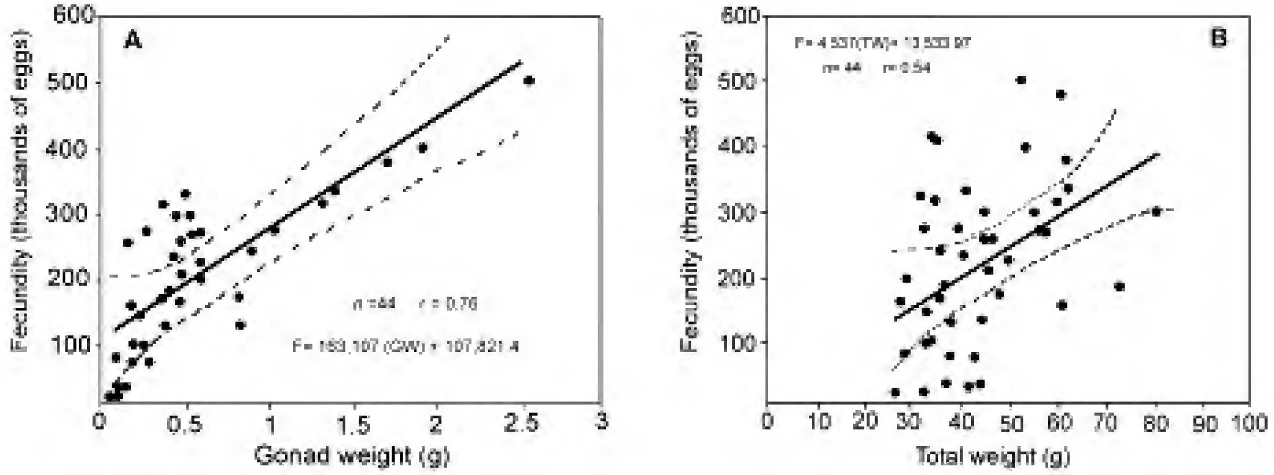

Figure 3. Relationship between gonad weight (GW) and fecundity (A), and total weight (TW) and fecundity (B) of *F.* aztecus. Regression lines are plotted with 95% confidence limits.

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

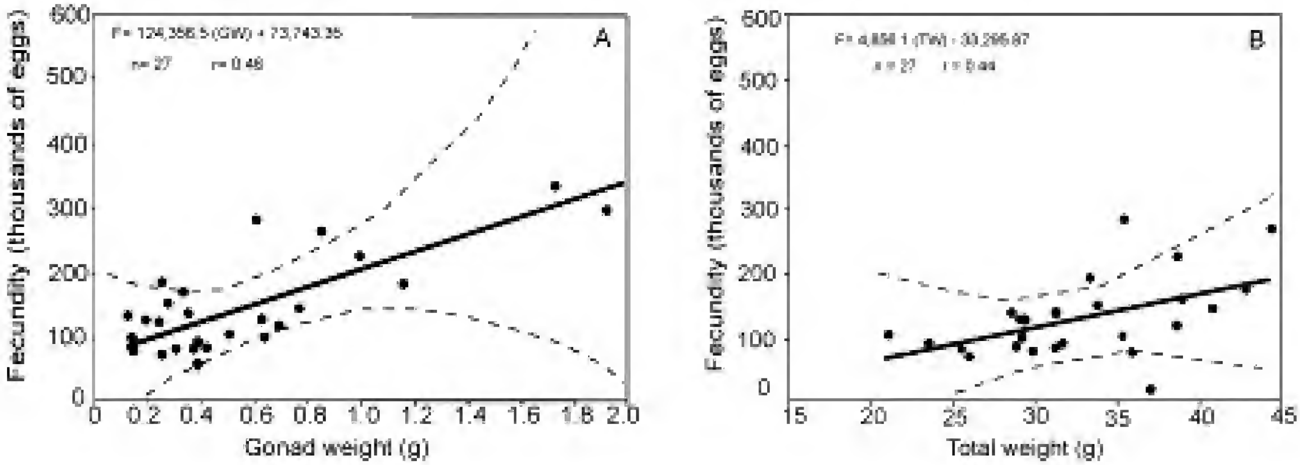

Figure 4. Relationship between gonad weight (GW) and fecundity (A) and total weight (TW) and fecundity (B) of *F. duorarum*. Regression lines are plotted with 95% confidence limits.

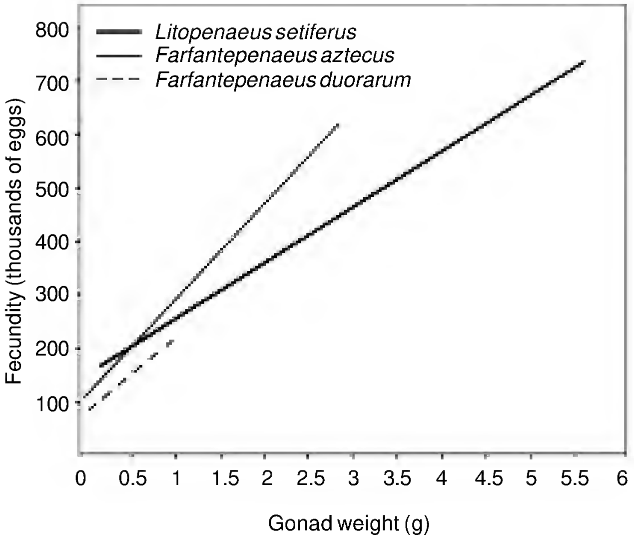

Figure 5. Comparison of regressions of gonad weight-fecundity of *L. setiferus*, *F. aztecus* and *F. duorarum*.

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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Feeding Habits of Juvenile Lane Snapper *Lutjanus synagris* from Mississippi Coastal Waters, with Comments on the Diet of Gray Snapper *Lutjanus griseus*

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FEEDING HABITS OF JUVENILE LANE SNAPPER *LUTJANUS SYNAGRIS* FROM MISSISSIPPI COASTAL WATERS, WITH COMMENTS ON THE DIET OF GRAY SNAPPER *LUTJANUS GRISEUS*

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ABSTRACT Stomach contents analysis was used to quantitatively describe the diets of juvenile lane snapper, *Lutjanus synagris,* and juvenile gray snapper, *Lutjanus griseus*, from the northern Gulf of Mexico. Juvenile snapper were collected by trawling at two estuarine, deep channel sites in Mississippi coastal waters from September 1996 to January 1997. Lane snapper (n = 53) and gray snapper (n = 12) both consumed a variety of prey organisms, but primary prey were amphipods, decapods (shrimp and crabs), and fishes. The most important prey items for lane snapper based on percent Index of Relative Importance (%IRI) were shrimp remains (44%IRI), the shrimp *Latreutes parvulus* (23%IRI) and fish remains (13%IRI). Fishes of the genus *Anchoa* (43%IRI), shrimp remains (21%IRI) and the amphipod *Corophium* sp. (13%IRI) dominated the gray snapper diet. Intraspecific comparisons of lane snapper diet revealed significant overlap between collection sites, seasons and fish sizes.

INTRODUCTION

Lane snapper (*Lutjanus synagris*) and gray snapper (*Lutjanus griseus*) occur in the western Atlantic from the mid-eastern coast of the United States and Bermuda southward to Brazil, including the Caribbean and the Gulf of Mexico (Gulf) (Hoese and Moore 1998). Although widespread throughout the northern Gulf, these 2 lutjanid species are generally less abundant than in the southern Gulf (Benson 1982, Pattillo et al. 1997). Adults of both species generally inhabit offshore reefs and other hard bottom features, whereas juveniles typically occur inshore and are often found in seagrass beds and over mud bottom (Randall 1967, Acosta and Appledoorn 1992, GMFMC 1981). In the northern Gulf, juveniles of both species consistently occur within the Mississippi Sound estuary (Wieland 1994, Warren and Perry 1996, Pattillo et al. 1997).

Temperature ranges for lane and gray snapper are similar; however, gray snapper are apparently more tolerant of low salinity waters. Lane snapper are found at temperatures between 15.0 and 27.5°C and salinities between19.0 and 35.0‰ (Springer and Woodburn 1960), whereas gray snapper are found between13.0 and 32.5°C (Springer and Woodburn 1960) and between 1.0 and 35.0‰ (Starck 1970). Juvenile lane (15–104 mm standard length, SL) and gray (11–113 mm SL) snapper have been reported from Mississippi coastal waters ranging from 11.5 to 31.5°C and 7 to 33‰ for lane and from 14.8 to 34°C and 5 to 33‰ for gray[a].

Both species support important commercial and recreational fisheries in the northern Gulf (GMFMC 1981). The combined annual commercial (1990–1997[b]) and recreational (1990–1998[c]) landings for lane and gray snapper from the Gulf averaged 225,000 kg and over 636,000 kg, respectively. Despite the commercial and recreational importance of lane and gray snapper in the Gulf, their life history and ecological roles in the northern Gulf require further study. Biological and ecological aspects of lane and gray snapper from southern Florida were studied by Springer and Woodburn (1960), Starck (1970), Manooch and Mason (1984), Bortone and Williams (1986), Rutherford et al. (1989a, b) and Chester and Thayer (1990). Dietary studies of gray snapper in south Florida were conducted by Croker (1962), Starck (1970), Rutherford et al. (1983), Hettler (1989) and Harrigan et al. (1989). In the northern Gulf, Shipp (1991) and Johnson et al. (1995) examined age and growth of lane snapper. There are no published life-history studies on gray snapper from the northern Gulf; however, the feeding habits of juvenile gray snapper from northwest Florida were examined by Koenig[d]. Information on feeding habits of lane and gray snapper in the northern Gulf is important for understanding the life history of these 2 species whose juveniles occupy estuarine habitat. Thus, the purpose of our study was to quantitatively describe the diet of juvenile lane and gray snapper from Mississippi coastal waters.

MATERIALS AND METHODS

Juvenile lane and gray snapper were collected from the eastern Mississippi Sound with a 5 m otter trawl with 35 mm codend mesh. Lane snapper were collected between November 1996 and March 1997, and gray snapper were collected between September 1996 and January

1997. Trawling was conducted between 0700 and 1500 h, and upon removal from the net, snappers were placed on ice to minimize digestive activity. At the dock, specimens were placed in labeled plastic bags and frozen, then later provided to us for examination.

Specimens were collected at 2 sites: Site 1 was located at the mouth of the East Pascagoula River (30°21′N, 88°34′W) with depth ranging from 10 to12 m; Site 2 was located at the mouth of Bayou Casotte (30°0′N, 88°31′W), a large bayou located about 3 km east of Site 1, with depth ranging from 13 to14 m. Both collection sites were located within industrial shipping channels near their confluence with the Mississippi Sound. The dominant substratum at both sites was a mud and shell rubble mixture. Bottom temperatures ranged from 15 to 18°C at the East Pascagoula River site and from 16 to 20° C at the Bayou Casotte site, and salinities ranged from 25 to 30‰ at both sites.

In the laboratory, specimens were thawed, measured to the nearest 0.1 mm SL, blotted dry, and weighed to the nearest 0.01 g. Stomachs were removed and placed in labeled vials containing 95% ethanol. Stomachs were later opened, and the contents were sorted, identified to the lowest possible taxonomic level and counted. In each stomach, all remnants identified as the same taxa were scored as a single prey item unless items obviously came from multiple individuals. Prey which were finely digested were assigned to a higher taxonomic level as "remains" and were included in the contributions of those higher taxa to the diet. Prey items were sorted into pre-weighed aluminum pans, placed in a 55°C drying oven for 18 h, cooled in a desiccator, and weighed to the nearest 0.001 mg using a Cahn electronic microbalance. Parasitic isopods, nematodes and plant material found in stomachs were considered non-food items ingested incidentally in normal feeding and were not used in our description of the diets.

Prey were pooled for all stomachs of each species and were represented as percent numeric abundance (%N), percent of total weight (%W), and percent frequency of occurrence (%F). The above values were used to calculate an index of relative importance (IRI): IRI = (%N + %W) × %F (Pinkas et al. 1971). Percent IRI (%IRI) was also calculated by dividing the IRI value of each prey taxon by the sum of IRI values (Cortés 1997). Empty stomachs were excluded from the above calculations.

Both the simplified Morisita index of overlap (C_H, Horn 1966) and Horn's index of overlap (R_o, Horn 1966) were used to determine dietary overlap. These indices exhibit less bias than other overlap measures when sample size (n) and resources (number of prey types in diet) are not constant (Krebs 1989, Cortés 1997). Both indices range from 0.0 (no overlap) to 1.0 (complete overlap), and a value of 0.60 indicates a high degree of overlap (Krebs 1989). Juvenile lane snapper were separated into 3 groups to determine intraspecific diet overlap: collection site (Pascagoula River vs. Bayou Casotte); season (early winter vs. late winter); and fish size (< 75 mm SL vs. ≥75 mm SL).

RESULTS

A total of 94 juvenile lane snapper were collected at Site 1 ($n = 61$) and Site 2 ($n = 33$), whereas16 juvenile gray snapper were collected from Site 1. Lane ($n = 53$) and gray ($n = 12$) snapper with prey in their stomachs ranged from 63.7 to 86.5 mm SL and 71.2 to 151.1 mm SL, respectively. The percentage of empty stomachs was 44% for lane snapper ($n = 41$) and 25% for gray snapper ($n = 4$). Although prey varied between snapper species, most prey taxa in both diets could be grouped into 3 main prey groups: amphipods, decapods and fish.

Diet composition of lane snapper

The diet of juvenile lane snapper was predominately decapods (shrimp and crabs) which comprised 48% of the diet numerically and 78% of the diet by weight (Figure 1, Table 1). Furthermore, decapods occurred with the greatest frequency (70%F) among the main prey groups and exhibited a 69%IRI. Decapod prey consisted of 9 prey taxa; however, the Sargassum shrimp, *Latreutes parvulus* and unidentified shrimp remains together accounted for 88%N and 68%W of the entire decapod prey group (Table 1). Other decapod prey, e.g., palaemonid shrimp and portunid crabs, were of less importance in the diet (Table 1).

Fish and amphipods exhibited similar %IRI values (fish 13%; amphipods 18%), but varied substantially in weight and numeric contribution to the diet (Figure 1). While the total number of amphipods consumed was about 5 times greater than the number of fish consumed, the %W of amphipods (4%) was about 4 times less than that of fish (17%) (Table 1). The amphipod prey group consisted of 6 prey taxa. The combination of *Batea catharinensis* and amphipod remains accounted for 85%N and 88%W, respectively, for the group (Table 1). The %F of amphipods (40%) was nearly twice that of fish (22%), identified only as remains.

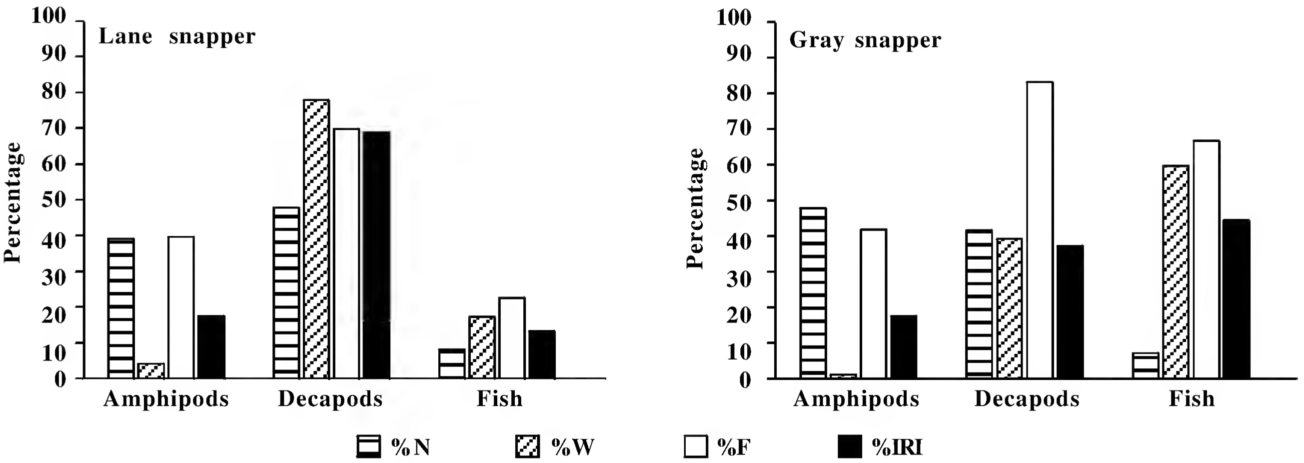

Figure 1. Percent numerical abundance (%N), percent total weight (%W), percent frequency of occurrence (%F), and percent index of relative importance (%IRI) for primary prey categories in the diet of juvenile lane snapper, *Lutjanus synagris*, and juvenile gray snapper, *Lutjanus griseus*, from Mississippi coastal waters.

Diet composition of gray snapper

The diet of juvenile gray snapper was primarily comprised of decapods (37%IRI) and fish (44%IRI) (Figure 1, Table 2). *Anchoa* sp. was the major component of the fish group in both numeric and weight contribution to the diet (Table 2). The decapod prey group (shrimp and crabs) included 11 taxa with shrimp remains the most dominant component (Table 2). Whereas amphipods were numerically abundant (48%N), with *Corophium* sp. and unidentified caprellids the most abundant members, their contribution to the diet by weight was only 1%W. Although *Corophium* sp. exhibited a 13%IRI, amphipods contributed moderately to the overall diet.

Diet Overlap

All 3 intraspecific comparisons of lane snapper showed high degrees of diet overlap (Table 3). Among these comparisons, the greatest dietary overlap occurred between size classes ($C_H = 0.94$; $R_o = 0.91$).

DISCUSSION

Our study provides fundamental information on the diet and food habits of juvenile lane and gray snapper from Mississippi coastal waters. The IRI showed decapods were important foods for both species (lane, 69%IRI; gray, 37%IRI); amphipods were of equal importance in both diets (17%IRI). Fish, comprised mostly of anchovies, were substantially more important in the diet of gray (44%IRI) than lane (13%IRI) snapper, primarily because of their high %W contribution (60%W) and %F (50%F) to the gray snapper's diet.

Many of the prey from snapper stomachs are organisms which comprise the macrobenthic and demersal communities within Mississippi Sound (Christmas and Langley 1973). The occurrence of small anchovies in the stomachs of gray snapper suggests some feeding occurred in the water column.

Among published studies from the Gulf, Springer and Woodburn (1960), Croker (1962), Starck (1970) and Hettler (1989) present the most detailed accounts of the diet of juvenile gray snapper. We found no published studies on the diet of lane snapper from the northern Gulf, and to the best of our knowledge, the only published information on the diet of lane snapper from US Gulf waters is that of Springer and Woodburn (1960). Therefore, our findings apparently represent the first account of diet and food habits of lane and gray snapper from the northern Gulf.

We report palaemonid shrimp (*Palaemonetes*), miscellaneous decapod crustaceans and fishes as being prey of lane snapper, prey that were also recorded for a similar size of juvenile lane snapper from Tampa Bay (Springer and Woodburn 1960). Among studies on lane snapper outside the US Gulf region, Rodriguez-Pino (1962), Randall (1967), Claro (1981) and Rivera-Arriaga et al. (1993) also reported diets primarily of crustaceans and fish for specimens examined from Cuba, the West Indies, Caribbean and Campeche, Mexico, respectively.

We found copepods, amphipods, palaemonid shrimp, mysids, portunid crabs and fishes in juvenile gray snapper stomachs, prey that were also reported by Starck (1970) and Hettler (1989) for juvenile gray snapper from south Florida. Our findings that juvenile gray snapper from 75–150 mm SL preyed heavily upon shrimp and fish are consistent with Starck (1970), Hettler

TABLE 1

Prey items found in stomachs of juvenile lane snapper, *Lutjanus synagris,* from Mississippi coastal waters. Percent frequency of occurrence is based on stomachs containing prey (*n* = 53). Unid. = unidentified.

Prey Items	Number of prey	% Number of prey	Prey weight (mg)	% Prey weight	% Frequency occurrence	Index of Relative Importance	% Index of Relative Importance
Arthropoda							
Copepoda	4	2.51	0.15	0.05	5.66	14.54	0.33
Amphipoda							
Bateacatha rinensis	28	17.61	6.03	2.02	18.87	370.82	8.56
Corophium sp.	4	2.51	0.25	0.08	7.55	19.35	0.45
Erichthonius brasiliensis	2	1.26	0.67	0.22	1.89	2.70	0.06
Unid. Caprellidae	1	0.63	0.06	0.02	1.89	1.18	0.03
Paracaprella tenuis	2	1.26	0.36	0.12	3.77	5.02	0.12
Amphipod remains	25	15.72	4.88	1.63	20.75	360.46	8.32
Mysidacea							
Americamysis sp.	3	1.89	1.53	0.51	3.77	9.16	0.21
Unid. Mysidae	1	0.63	0.74	0.25	1.89	1.62	0.04
Decapoda							
Palaemonetes sp.	1	0.63	3.26	1.09	1.89	3.21	0.07
Palaemonetes vulgaris	1	0.63	41.50	13.90	1.89	27.55	0.64
Latreutes parvulus	33	20.75	94.70	31.72	18.87	992.44	22.90
Alpheus sp.	1	0.63	4.10	1.37	1.89	3.74	0.09
Shrimp remains	33	20.75	63.15	21.15	45.28	1,900.34	43.85
Unid. Portunidae	1	0.63	3.95	1.32	1.89	3.65	0.08
Callinectes sapidus	2	1.26	15.92	5.33	3.77	24.81	0.57
Crab remains	3	1.89	2.95	0.99	5.66	16.47	0.38
Decapoda remains	1	0.63	3.17	1.06	1.89	3.15	0.07
Chordata							
Osteichthyes							
Fish remains	13	8.18	51.23	17.16	22.64	573.14	13.23
Totals	159		298.60			4,333.35	
Stomachs analyzed = 94		Stomachs (%) with prey = 53 (56%)			Stomachs (%) empty = 41 (44%)		

(1989) and Koenig[d]. In agreement with Springer and Woodburn (1960), we found juvenile gray snapper stomachs to contain copepods, annelids and small fishes. Croker (1962) and Rutherford et al. (1983) reported that gray snapper consumed shrimp, crabs and fish, including anchovies which were prevalent in the stomachs of our specimens.

Various studies on the feeding habits of juvenile gray snapper suggest an association with and feeding in seagrasses (Randall 1967, Starck 1970, Odum and Heald 1972, Koenig[d]). Although several prey reported here may occur in seagrasses, no submerged vegetation currently occurs or has occurred previously at our study sites (Christmas and Eleuterius 1973). The bryozoan *Amathia alternata* was occasionally collected in large mats or found attached to shell fragments in trawls at Site 2 (Bayou Casotte). *Amathia alternata* possibly served as habitat for juvenile lane snapper and provided refuge for potential prey organisms.

High levels of dietary overlap were found between lane snapper compared by catch location (Site 1 and Site 2), season (early winter and late winter), and size (4.1–6.0 and 6.1–8.6 mm SL). The 2 study sites were located only 5 km apart, and water temperatures, salinities and depths were similar during collecting. Christmas and Eleuterius (1973) reported the persistence of a "wedge" of high saline, eastern Mississippi Sound water along the bottom in both areas. The similarity between sites might account for the high dietary overlap for specimens of lane snapper from both sites. The limited collection months and the narrow size range of specimens probably account for the high dietary overlap

TABLE 2

Prey items found in stomachs of juvenile gray snapper, *Lutjanus griseus,* from Mississippi coastal waters. Percent frequency of occurrence is based on stomachs containing prey (*n* = 12). Unid. = unidentified; T = trace amount (< 0.01).

Prey Item	Number of prey	% Number of prey	Prey weight (mg)	% Prey weight	% Frequency occurrence	Index of Relative Importance	% Index of Relative Importance
ANNELIDA							
Polychaeta							
Unid. Nereidae	1	0.89	0.04	T	8.33	7.46	0.12
MOLLUSCA							
Bivalvia							
Unid. Bivalvia	1	0.89	0.02	T	8.33	7.44	0.12
ARTHROPODA							
Amphipoda							
Batea catharinensis	4	3.54	1.43	0.19	16.67	62.18	1.00
Corophium sp.	37	32.74	5.54	0.73	25.00	836.75	13.41
Unid. Caprellidae	10	8.84	0.90	0.12	16.67	149.36	2.39
Amphipod remains	3	2.65	0.29	0.04	16.67	44.84	0.72
Mysidacea							
Americamysis sp.	2	1.77	0.24	0.03	16.67	30.01	0.48
Decapoda							
Palaemonetes sp.	6	5.31	15.16	2.00	25.00	182.75	2.93
Latreutes parvulus	7	6.19	13.90	1.84	16.67	133.86	2.15
Alpheus sp.	1	0.89	5.11	0.68	8.83	13.08	0.21
Shrimp remains	14	12.39	74.56	9.86	58.33	1,297.84	20.81
Callinectes sapidus	3	2.65	48.18	6.37	25.00	225.56	3.62
Callinectes sp.	1	0.89	10.53	1.39	8.33	18.99	0.30
Eurypanopeus depressus	5	4.42	74.83	9.90	8.33	119.28	1.91
Mennipe adina	1	0.89	5.72	0.76	8.33	13.74	0.22
Unid. Xanthidae	5	4.42	35.66	4.72	25.00	228.50	3.66
Crab remains	3	2.65	2.56	0.34	25.00	74.75	1.20
Decapoda remains	1	0.89	9.97	1.32	8.33	18.41	0.30
CHORDATA							
Osteichthyes							
Anchoa sp.	6	5.31	361.95	47.88	50.00	2,659.50	42.64
Unid. Triglidae	1	0.89	84.04	11.12	8.33	100.04	1.60
Fish remains	1	0.89	5.30	0.70	8.33	13.24	0.21
TOTALS	115		755.93			6,237.52	
Total stomachs analyzed = 16		No. (%) containing food = 12 (75%)			No. (%) empty = 4 (25%)		

of lane snapper between seasons and size groups, respectively.

Information on age, growth, term of residency and patterns of movement of juvenile lane and gray snapper within the Mississippi Sound estuary is lacking. Additionally, there is no information on the size and age of lane and gray snapper at the time of their emigration from the Mississippi Sound estuary to open Gulf waters. Both of our study sites were located within shipping channels which were substantially deeper than adjacent waters. The channels may serve as "conduits" for the movement of sub-adult lane and gray snapper out of the estuary into offshore waters.

Our findings show that some juvenile lane and gray snapper utilized Mississippi's estuarine habitat as nursery area. Documentation of juvenile habitat and monitoring the juvenile snapper population along the northern Gulf coast will enhance the ability to assess relationships between habitat and early life history stages of these important fishes, and ultimately may provide indicators useful in assessing recruitment and status of the stocks. Identification of the food habits of juvenile

TABLE 3

Dietary overlap among juvenile lane snapper, *Lutjanus synagris*, from Mississippi coastal waters. Site 1 (Pascagoula River, *n* = 25), Site 2 (Bayou Casotte, *n* = 28). Early winter (Nov./Dec., *n* = 26), Late winter (Jan./Feb./Mar., *n* = 27). Size class A (< 75 mm SL, *n* = 24), Size class B (> 75 mm SL, *n* = 29). The simplified Morisita (C_H) and Horn's (R_o) indices range from 0 = no overlap to 1.0 = complete overlap.

Comparison Group	C_H	R_o
Site 1 vs. Site 2	0.77	0.82
Early winter vs. Late winter	0.71	0.73
Size class A vs. Size class B	0.94	0.91

lane and gray snapper is an important step in developing a better understanding of the life history requirements, estuarine ecology and trophic role of these 2 species within the Mississippi Sound estuarine ecosystem.

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Possible Sustained Effects of Hurricanes Opal and Erin on the Macrobenthos of Nearshore Habitats Within the Gulf Islands National Seashore

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POSSIBLE SUSTAINED EFFECTS OF HURRICANES OPAL AND ERIN ON THE MACROBENTHOS OF NEARSHORE HABITATS WITHIN THE GULF ISLANDS NATIONAL SEASHORE

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ABSTRACT Possible sustained effects of hurricanes Opal and Erin on the macrobenthos of nearshore habitats of the Florida district of Gulf Islands National Seashore were assessed. Pre-hurricane macrobenthic data originating mainly from a large-scale faunal inventory conducted during 1993 were compared with post-hurricane data collected one year after the 1995 disturbances. Nearshore habitats examined included both exposed and protected sand beaches, as well as grassbed and lagoon sites. Within one year after the hurricanes, few faunal effects could be discerned at exposed beach sites, whereas possible faunal effects were apparent in protected nearshore habitats. Abundances of 4 major epifaunal crustacean taxa were notably lower one year after the hurricane disturbances. Assemblages of relatively stable nearshore habitats appeared to be more diverse but less resilient than assemblages of unstable nearshore habitats, possibly reflecting the extent of disturbance normally experienced by assemblages within those habitats.

INTRODUCTION

Although catastrophic disturbances such as hurricanes exert potentially large impacts on nearshore biotic communities, relatively few studies document the effects of severe storms on macrobenthos. Several notable exceptions include studies by Tabb and Jones (1962), Boesch et al. (1976), and Posey et al. (1996). These studies document several detrimental storm-related impacts on benthic organisms, due to reduced salinity, depletion of dissolved oxygen, and direct physical disturbance of the substrate. Additional ecosystem effects of Hurricane Bob on Cape Cod included changes in nutrient dynamics, ecosystem metabolism, and hydrography (Valiela et al. 1996). Moreover, hurricane induced impacts on macrobenthos may be further exacerbated by anthropogenic practices (Mallin et al. 1999).

Depending on the environmental context, the nature and severity of hurricanes can have very different consequences for the benthic community. Posey et al. (1996) noted moderate selective effects of storm-induced sediment disturbance on an offshore benthic community at 13 m depth, wherein abundances of surface-dwelling species declined while deep burrowing species remained unchanged. Boesch et al. (1976) found many species declined from drastic storm-induced decreases in salinity and dissolved oxygen in some areas, followed by irruptive increases in several opportunistic species within one year. The deep and relatively stable mud-bottom community in the lower York estuary had still not recovered after 2.5 years, suggesting relatively low resilience for diverse equilibrium communities.

During late summer and autumn 1995, two consecutive hurricanes, Erin and Opal, severely impacted the western coast of the Florida panhandle. One year later, as part of a resource damage assessment by the National Park Service, a macrobenthic study of the nearshore habitats of the Florida district of Gulf Islands National Seashore (GUIS) was conducted. A large baseline data set was available for comparison from several previous macrobenthic assessments that were conducted within GUIS, including an early survey of sand beaches in 1986/1987 (Rakocinski et al. 1991) and a comprehensive baseline inventory of nearshore habitats in 1993 (Rakocinski et al. 1995, 1998a).

The objective of this study was to compare baseline macrobenthic data with post-hurricane data obtained one year after the storm impacts to ascertain possible sustained effects on the nearshore resources of the Florida district of GUIS. To accomplish this objective, we considered: 1) pre- and post-hurricane variation in species richness, diversity, and total abundance; 2) assemblage-level variation in 23 selected sand-beach taxa previously used to develop a historical baseline; 3) abundance patterns expressed by dominant sand-beach taxa; and 4) differences in faunal metrics and abundances of dominant taxa from grassbed and lagoon habitats.

METHODS

Hurricane Impacts

During late summer and autumn 1995, two consecutive hurricanes, Erin and Opal, severely impacted the western panhandle coast of Florida. The Category 1 Erin made landfall first along Santa Rosa Island on 3

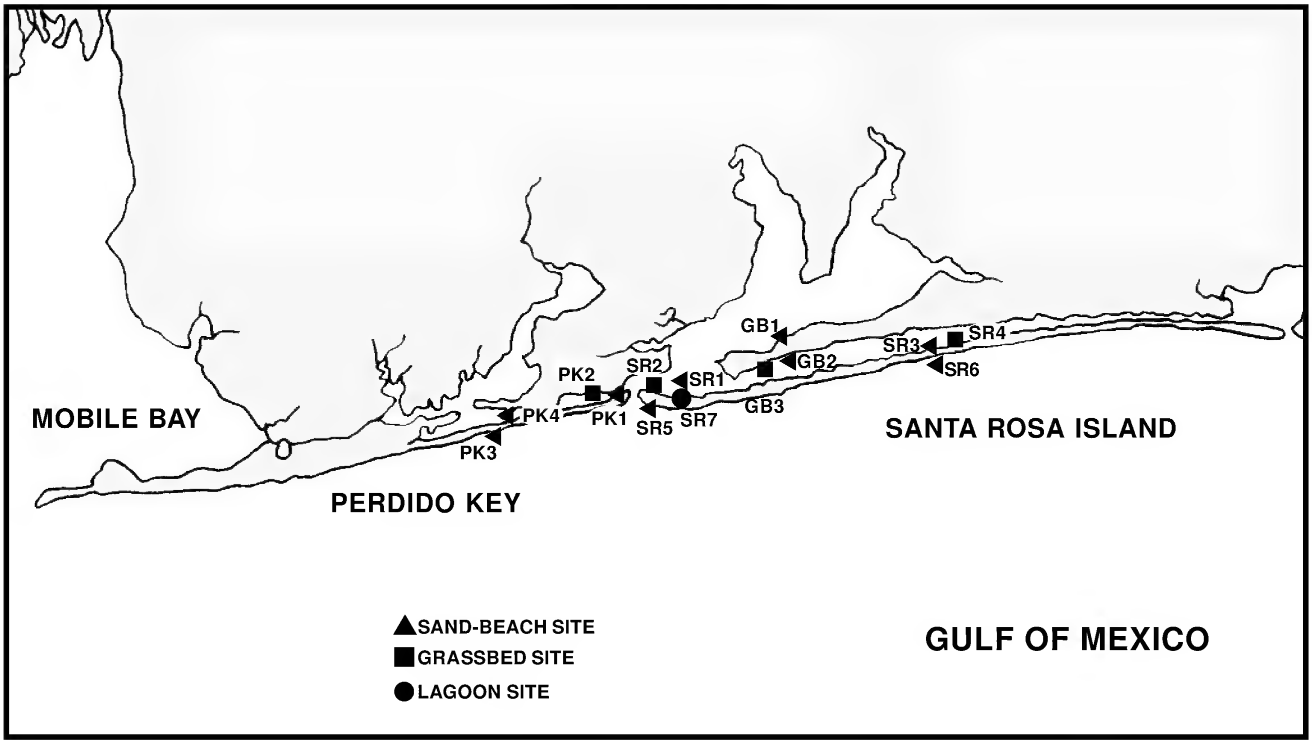

Figure 1. Map of the Florida district of the Gulf Islands National Seashore showing study sites used for the 1993 faunal inventory and for the 1996 post-hurricane survey. Western sites fall right at the border between the Florida panhandle and Alabama. See Table 1 for site codes.

August 1995, where it displaced the upper foreshore berm gulfward over a wide area and displaced considerable sediment towards the island interior (Stone 1996). Some beach erosion also occurred and substantial sediment was displaced from the beach to the dune system.

A much harsher Hurricane Opal devastated the same coastal region exactly 2 months later on 4 October 1995, when it made landfall just east of Pensacola, Florida (Stone et al. 1996). Opal was the most severe storm of the century to affect this area. It neared Category 5 strength with sustained wind speeds of over 65 m s^{-1}, 12 hours before landing. Estimated storm surge levels reached 5 m, overwashing most of Santa Rosa Island. Opal caused major erosion and sediment displacement within the GUIS portion of Santa Rosa Island. Vegetated stable foredunes reaching 5 m in height were removed entirely by Opal along Santa Rosa Island and Destin. Between 95–99% of the sediment eroded from the beach-dune system was redeposited to the island interior and along the northern bay shoreline, with overwash fans extending bayward by almost 100 m. Along the south shoreline of the island a notable coarsening of the quartz sand-beach sediments occurred. Considering the magnitude of the disturbances associated with the 1995 hurricanes, it is likely that the macrobenthic biota in the Florida district of GUIS was everely impacted.

Study Design

The design of this impact assessment closely followed that for the comprehensive 1993 macrobenthic inventory (Rakocinski et al. 1995, 1998a), for which sites were distributed among the GUIS barrier islands both to allow historical comparisons and to provide a balanced baseline study. To achieve a balanced study design, at least one exposed beach site and one protected beach site were located on each GUIS barrier island (Figure 1). Three stations were placed at each beach site, including a mid-swash intertidal station, as well as 5-m and 15-m subtidal stations. Grassbed and lagoon sites also were established throughout the study region. Each grassbed site included 2 stations, while lagoon sites encompassed 3 or 4 stations.

The GUIS Florida district locations sampled for the 1993 inventory included 2 sand-beach sites (PK1, PK3), one grassbed site (PK2), and one lagoon site (PK4) at Perdido Key; 2 sand-beach sites (GB1, GB2), and one grassbed site (GB3) at Gulf Breeze; and 4 sand-beach sites (SR1, SR3, SR5, SR6), two grassbed sites (SR2, SR4), and one lagoon site (SR7) at Santa Rosa Island

(Figure 1, Table 1). The 1996 post-hurricane survey utilized the same configuration of study sites in the Florida district, but owing to the lack of seagrass at one station, only one of the 2 stations was sampled at site SR4 in 1996.

Field Sampling

The 1996 macrobenthic survey was completed over a 4-day period between 28 and 31 October 1996. At beach sites, samples were taken from the upper 20–25 cm of sediment using a 0.016 m^2 stainless steel boxcorer (12.5 cm on a side) covered with 0.5 mm screen tops (Saloman and Naughton 1977). Stations at sand-beach sites were located at 0 m, 5 m, and 15 m from shore. From each station, 8 evenly spaced boxcores were taken every 1 m in a line parallel to the shore. Stations at the 2 Florida district lagoon sites were sampled with one epibenthic kicknet sweep each. A 0.45 m wide rectangular 0.5 mm mesh kicknet was swept along the bottom sediment surface for 20 m (9.0 m^2). Stations at the 4 Florida district grassbed sites were sampled with duplicate 5 m epibenthic 0.5 mm mesh kicknet sweeps (4.5 m^2) through submerged vegetation.

Small and/or light-bodied organisms were removed in the field by elutriating samples 5 times with a dilute formalin solution through a 0.5 mm sieve. Remaining material, including sediment, was washed through a 1.0 mm sieve to recover large and heavy organisms. This process has been shown to be effective in removing more than 95% of the organisms (Rakocinski et al 1991). Kicknet samples were first treated with 5% formalin and then passed through a 0.5 mm sieve. All processed samples were labeled, fixed with 5–10% formalin and returned to the laboratory.

LABORATORY METHODS

In the laboratory, macrobenthic invertebrates were sorted into major groups and transferred to 70% ethanol. As quality control, 5% of the samples were resorted to check for at least 90% accuracy. Grassbed and lagoon samples that contained vast numbers of organisms were split into 3 size fractions using nested sieves. The coarsest fraction was completely sorted visually using a lighted magnifying glass and finer fractions were subsampled using a MATODA plankton splitter. Following identification and enumeration of subsamples, abundance estimates were extrapolated by the appropriate split-factor. When superabundant, small snails were enumerated using a gridded petri-dish of 62.2 cm^2 within which organisms in 0.208 of the dish area (9 grid squares) were counted and extrapolated. Specimens were identified to the lowest practical taxonomic level and enumerated. Some organisms in poorly known groups were not identified to species. A voucher collection of all nominal taxa is maintained as part of The University of Southern Mississippi Institute of Marine Sciences Gulf Coast Research Laboratory Invertebrate Zoology collection, and a complete list of taxa occurring from this study is available upon request.

TABLE 1

Fourteen sites sampled during the Hurricane Opal/Erin macrobenthic impact study along with descriptions of locations and their position coordinates. Only one of the 2 grassbed stations from the 1993 inventory at site SR4 had seagrass present in 1996.

Island	Site	Habitat Type	Location	Latitude	Longitude
Perdido Key	PK1	Sand Beach	North Beach—FDNR range marker R63	30°19'08.6"	87°19'38.5"
Perdido Key	PK2	Grassbed	Grassbed adjacent to site PK1	30°19'08.6"	87°19'38.5"
Perdido Key	PK3	Sand Beach	South Beach—FDNR range marker R40	30°18'15.2"	87°23'31.9"
Perdido Key	PK4	Lagoon	Lagoon at Redfish Point—FDNR marker R51	30°18'57.0"	87°21'31.9"
Gulf Breeze	GB1	Sand Beach	North Beach—Naval Live Oaks campground	30°22'12.8"	87°08'36.1"
Gulf Breeze	GB2	Sand Beach	South Beach—east of Naval Live Oaks Visitor Center	30°21'49.5"	87°07'39.3"
Gulf Breeze	GB3	Grassbed	Grassbed adjacent to site GB2	30°21'47.6"	87°07'41.7"
Santa Rosa Island	SR1	Sand Beach	North Beach—Fort Pickens	30°18'49.1"	87°15'07.9"
Santa Rosa Island	SR2	Grassbed	Grassbed adjacent to site SR1	30°19'10.7"	87°15'24.8"
Santa Rosa Island	SR3	Sand Beach	North Beach—Santa Rosa	30°21'56.0"	86°58'05.8"
Santa Rosa Island	SR4	Grassbed	Grassbed adjacent to site SR3	30°22'01.9"	86°58'04.3"
Santa Rosa Island	SR5	Sand Beach	South Beach—Fort Pickens	30°19'06.8"	87°14'45.0"
Santa Rosa Island	SR6	Sand Beach	South Beach—Santa Rosa	30°21'41.9"	86°58'14.7"
Santa Rosa Island	SR7	Lagoon	Lagoon—Fort Pickens	30°19'19.9"	87°13'49.2"

Data Analysis

We used the Matrix Report feature of the Community Analysis System 4.0 (CAS) (Bloom 1992) to calculate organism abundances and summary community metrics for individual collections. Only 5-m and 15-m stations at beach sites were considered hereinafter. Summaries for box-core collections reflect combined abundances from all 8 cores per station (0.125 m^2), whereas abundances represent each 20-m kicknet sweep (9.0 m^2) for lagoon collections, or combined abundances for two 5-m kicknet sweeps (4.5 m^2) for grassbed collections.

Species richness (S = number taxa per collection), total density, diversity (H′), evenness (H'/H_{max}), and Simpson's Dominance Index (λ) were calculated (Magurran 1988). For box-core collections, species richness (S) was defined as the number of taxa collected by 8 cores (i.e., number taxa/0.125 m^{-2}). Diversity (H′) was calculated on the $\log_e$ scale. H_{max} is the maximum value H' could take for a given number of taxa and organisms in a collection. The ratio of the 2 metrics then gives a normalized estimate of evenness.

Total density was presented as the total number of organisms per m^2. Geometric mean densities along with 2 standard errors (se) were calculated for individual taxa as well as for total numbers of organisms for each set of 8 cores per station and compared between sites in 1993 and 1996. Based on a sample size (n) of 8, two se gives >95% confidence limits for one-tailed tests of differences between years.

Principal Coordinate Ordination (PCO) provided a frame-of-reference for assessing variation in community structure, which incorporated historical reference samples from 1986/1987 and 1993, in addition to the 1996 post-hurricane samples. Through the use of an association matrix, PCO effectively translates differences in assemblage structure into intersample distances in ordination space. Twenty-three taxa used in former ordinations (Rakocinski et al. 1991, 1995, 1998a) were also used for this analysis. Case entries were geometric mean numbers per core ($\mathrm{Inv}[\sum \ln(N + 1)/$ number cores per case$]$) for each of the 23 taxa. Every collection taken prior to 1996 from the same 1996 sand-beach stations was included, yielding 19 cases representing the 7 swash-zone stations and 20 cases representing the eight 15-m subtidal sand-beach stations.

Separate PCO analyses were performed for the 19 swash-zone cases and the twenty 15-m subtidal cases. The PCO was based on a dissimilarity matrix using Gower's Distance Index, where association values between each pair of samples are calculated for the ith taxa (Gower 1966). Following previous studies, abundance data were transformed by the e_{th} root and were not standardized, resulting in moderate weighting of the ordination according to the relative abundances of the various taxa. Sample coordinates were arrayed throughout PCO space so that possible sustained hurricane impacts on community structure could be assessed.

To detect possible hurricane effects at grassbed and lagoon stations, abundances of dominant taxa and faunal metrics were compared between the 2 groups of stations representing pre-hurricane (October 1993) and post-hurricane (October 1996) periods. Comparisons were based on the premise that changes in the same direction among all the stations likely represented real differences between the 2 periods. Where the normality assumption was met and the statistical power was ample (*i.e.*, b > 0.5), differences in abundances between years were examined using paired-t tests; otherwise, non-parametric Wilcoxin Signed Rank (WSR) tests were used (Siegel 1956). Normality was checked with the Kolmogorov-Smirnov one-sample test and SigmaStat Version 2.0 was employed for all tests (Fox et al. 1995).

RESULTS

Sand-Beach Sites

Species Richness

Among swash-zone stations of both exposed and protected sand-beach sites, S patterns did not reflect sustained hurricane impacts on species composition. S was highly variable and ranged similarly among exposed swash-zone stations during both years (7–8 taxa in 1993 vs. 6–8 taxa in 1996) as well as among protected swash-zone stations (8–25 taxa in 1993 vs. 7–26 taxa in 1996) (Figure 2). Likewise, among 15-m subtidal stations at exposed beach sites, S ranged similarly (9–14 taxa in 1993 vs. 8–16 taxa in 1996), although S was higher at both Santa Rosa Island stations in 1993. In contrast, among the 5 eastern protected beach sites on Santa Rosa Island and Gulf Breeze, where the strongest hurricane impacts occurred, S was consistently and considerably lower in 1996. Indeed, S clearly ranged higher among protected 15-m subtidal beach stations in 1993 (39–55 taxa) compared to 1996 (24–46 taxa).

Faunal Diversity

H′ at exposed beach sites was similar between 1993 and 1996, although values ranged somewhat higher among exposed swash-zone stations in 1993 (1.42–1.56) than in 1996 (0.97–1.39) (Figure 3). However,

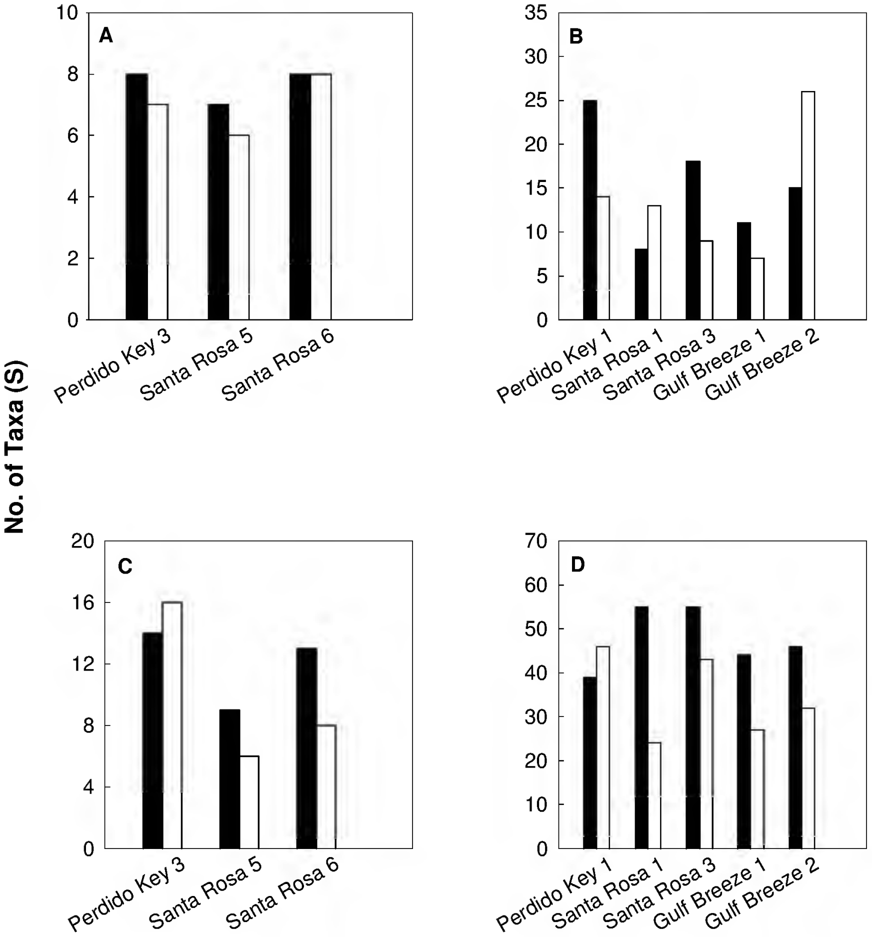

Figure 2. Variability in species richness among sand-beach stations. (A) exposed swash zone; (B) protected swash zone; (C) exposed 15-m subtidal; (D) protected 15-m subtidal. Black bars = October 1993; white bars = October 1996.

among exposed 15-m subtidal stations, H′ ranged similarly between 1993 (1.57–1.83) and 1996 (1.31–1.78).

Among protected swash-zone stations in 1993, H′ ranged somewhat narrower (0.76–1.78) than in 1996 (0.24-1.83). Two protected swash-zone stations with notably low H′ in 1996 included one at Santa Rosa Island site 3 (1.16 in 1993 vs. 0.24 in 1996), and one at Gulf Breeze site 2 (1.68 in 1993 vs. 1.00 in 1996). Among protected 15-m subtidal stations, H′ ranged similarly between 1993 (1.62–3.10) and 1996 (1.48–2.96). However, H′ was notably low in 1996 at 3 protected 15-m subtidal stations within the most severely impacted area, including Santa Rosa site 1 (3.10 in 1993 vs. 1.69 in 1996), Gulf Breeze site 1 (2.72 in 1993 vs. 1.48 in 1996), and Gulf Breeze site 2 (2.78 in 1993 vs. 2.33 in 1996).

Total Density

Among swash-zone stations at both exposed and protected sites, geometric-mean total density varied erratically between 1993 and 1996 (Figure 4). However, among 4 of the 5 protected swash-zone stations, considerably higher densities occurred in 1993 than in 1996. Total densities at exposed swash-zone stations ranged similarly between 1993 (98–1,374 m^2) and 1996 (226-1,116 m^2), but densities ranged narrower among protected swash-zone stations in 1993 (1,197–10,658 m^2) than in 1996 (449–13,320 m^2).

Total densities generally ranged substantially lower in 1996 than in 1993 among 15-m subtidal stations from both exposed (491–1,312 m^2 in 1993 vs. 179–861 in 1996) and protected beaches (5,353–7,757 m^2 in 1993 vs. 3,109–4,857 m^2 in 1996). Subtidal total densities at the 2 exposed Santa Rosa sites were distinctly lower in 1996. Furthermore, total densities among protected subtidal sites were generally substantially lower in 1996 than in 1993 (Figure 4).

Sand-Beach Dominance Patterns

Differences in total densities between 1993 and 1996 subtidal sand-beach stations could not be attributed consistently to responses by particular dominant

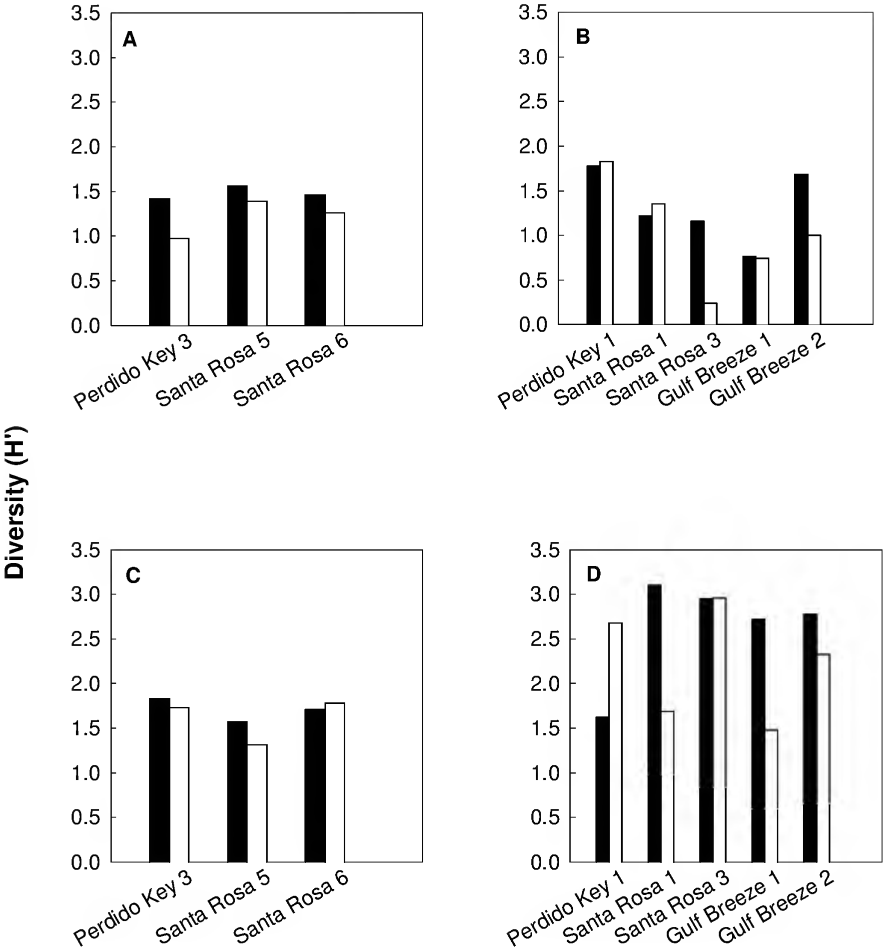

Figure 3. Variability in faunal diversity among sand-beach stations. (A) exposed swash zone; (B) protected swash zone; (C) exposed 15-m subtidal; (D) protected 15-m subtidal. Black bars = October 1993; white bars = October 1996.

taxa. Dominant taxa occurring among the five 15-m subtidal stations from protected beaches in 1993 included oligochaetes, polychaetes (e.g., *Laeonereis culveri*, *Capitella capitata*, *Heteromastus filiformis*, *Paraonis fulgens*, *Streptosyllis pettiboneae*, and *Polygordius* sp. A), Nemerteans, Turbellarians, the lancelet (*Branchiostoma* cf. *floridana*), and several crustaceans (e.g., *Kalliapsuedes* sp. A, and *Acanthohaustorius uncinus*) (Rakocinski et al. 1998b). Several of these dominant taxa were lacking among the same subtidal stations in 1996, including *C. capitata*, *H. filiformis*, *A. uncinus*, *Kalliapsuedes* sp. A., and *B.* cf. *floridana*. Moreover, the haustoriid amphipod, *Lepidactylis* sp A., became a dominant taxon at 2 of the 15-m subtidal stations of protected beaches in 1996, but was lacking at those same stations in autumn 1993 (Rakocinski et al. 1995, 1998a).

PCO Ordination

Most meaningful community variation among the swash-zone stations could be examined within the first 3 PCO dimensions, as implied by a cumulative vector efficiency of 85%. The first 3 PCO axes explained 42% of the variance in macrofaunal dissimilarity among the 19 swash-zone stations: Axis 1 represented 20.37% of the variance, Axis 2 represented 13.83% and Axis 3 represented 8.03%.

Swash-zone sample coordinates from protected beach sites were much more variable than variables from exposed beach sites, reflecting the more diverse macrofauna at protected sites (Figure 5A). Strongly aggregated groups of swash-zone stations representing protected and exposed sites also were evident. However, faunal-dissimilarity patterns among the swash-zone stations could not be attributed to hurricane effects, as PCO coordinates for the 1996 stations did not stand out from those of historical reference stations. Indeed, the most outstanding swash-zone PCO coordinate represented a protected Gulf Breeze site in 1993.

Most meaningful community variation among the twenty 15-m subtidal stations at sand beach sites could be examined within the first three PCO dimensions, as

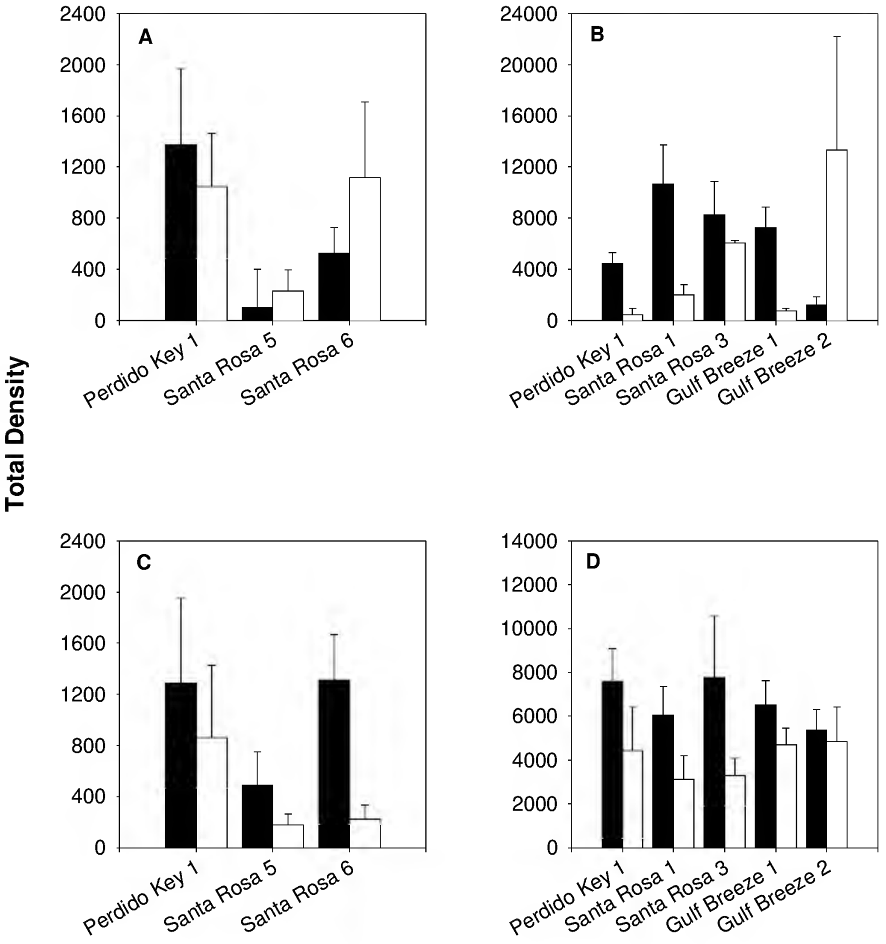

Figure 4. Variability in geometric mean total density (± 2 se) among sand-beach stations. (A) exposed swash zone; (B) protected swash zone; (C) exposed 15-m subtidal; (D) protected 15-m subtidal. Black bars = October 1993; white bars = October 1996.

indicated by a cumulative vector efficiency of 63%. The first 3 PCO axes effectively explained 31% of the variance in macrofaunal dissimilarity among the twenty 15-m subtidal stations: Axis 1 represented 14.64% of the variance, Axis 2 represented 9.46%, and Axis 3 represented 6.82%.

The pattern of 15-m subtidal coordinates in 3-D PCO space revealed more variability in community structure among protected beaches than among exposed beaches. Coordinates representing protected and exposed sites were separated in PCO space, reflecting different faunal complements from protected and exposed beaches (Figure 5B). For exposed beach sites, differences in community structure attributable to hurricane effects were not apparent from the dispersion of 15-m subtidal coordinates. However, 2 of the PCO coordinates representing 15-m subtidal stations from protected beaches in 1996 fell outside the range of previously measured variability in faunal dissimilarity, including one at Gulf Breeze and another at Santa Rosa Island.

Grassbed and Lagoon Sites

Faunal Summary Metrics

WSR tests failed to reveal any overall directional changes in S, H′, H'/H_{max}, λ, or total density ($0.469 > P_{exact} > 0.156$) among grassbed stations between 1993 and 1996. However, the lowest metric values occurred in 1996. S ranged lower among the 7 grassbed stations in 1996 (31–72) than in 1993 (48–84); H′ ranged similarly in 1993 (1.17–2.82) and 1996 (0.58–2.54); H'/H_{max} and λ paralleled H′ in 1993 (H'/H_{max} = 0.27–0.64; λ = 0.48–0.87) and in 1996 (H'/H_{max} = 0.15–0.61; λ = 0.22–0.83); and total densities varied widely and overlapped among stations in 1993 (779–5,865) and 1996 (358–7,126).

WSR tests did not indicate any overall directional changes in S, H′, H'/H_{max}, λ, or total density ($1.0 > P_{exact} > 0.688$ among lagoon stations. Wide ranges for some summary metrics reflected the relatively high habitat heterogeneity among lagoon stations. However, ranges of most metrics overlapped between 1993 and

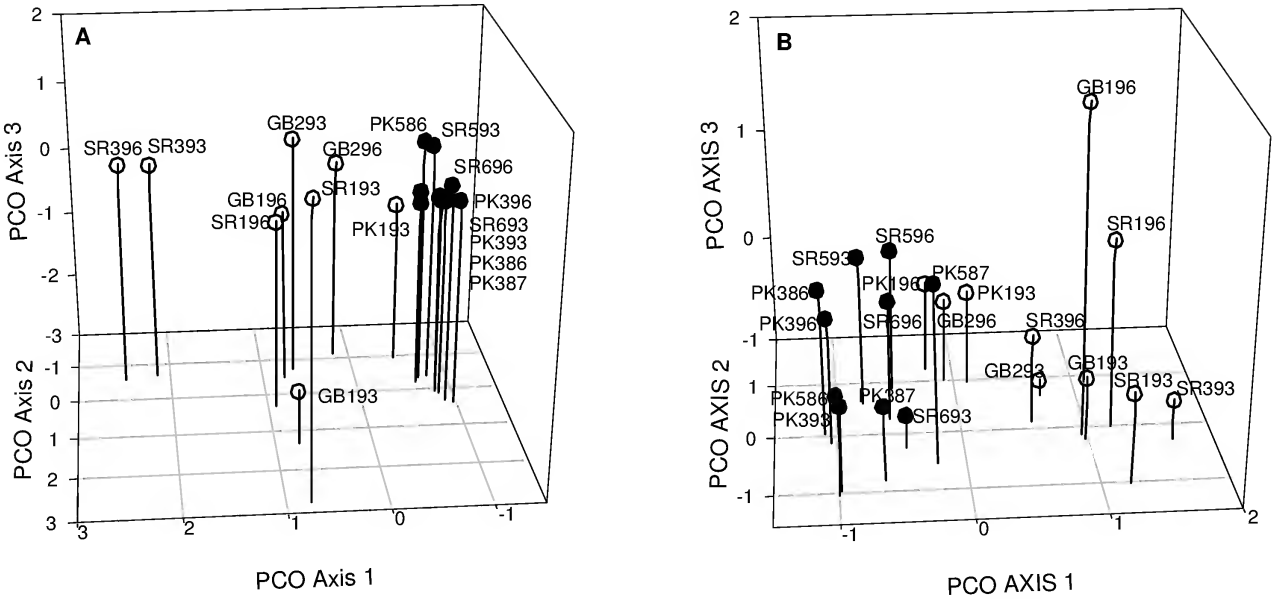

Figure 5. Principal Coordinate Ordinations of sand-beach stations from before hurricanes Opal and Erin, in October 1986/1987 and 1993, and the same stations in October 1996, one year after hurricane impacts occurred. Coordinate labels denote the station numbers and years. (A) Swash-zone ordination; (B) 15-m subtidal ordination. Solid = exposed sites; open = protected sites.

1996. Among the 6 lagoon stations, S ranged similarly in 1993 (17–69) and 1996 (16–81); H' overlapped in 1993 (1.84–2.91) and 1996 (2.11–2.87); H'/H_{max} and λ paralleled diversity in 1993 (H'/H_{max} = 0.50–0.78; λ = 0.66–0.91) and in 1996 (H'/H_{max} = 0.59–0.82; λ = 0.73–0.92). Total density also varied widely among lagoon stations and overlapped broadly in 1993 (10–809) and 1996 (11–274).

Grassbed and Lagoon Dominance Patterns

Comparisons of relative abundances of taxa from grassbed and lagoon stations between years showed that the same taxa were generally dominant during both pre- and post-hurricane periods (Rakocinski et al. 1995, 1998b). Comparisons of infaunal taxa among the grassbed stations for each sampling period did not reveal any overall directional shifts. For example, total abundances of syllids ranged similarly in 1993 (0–52) and 1996 (0–139); and a WSR test showed that these estimates were not different (P_{exact} = 0.84).

Comparisons of epibenthic micrograzer gastropods from grassbed stations also failed to show any overall directional shifts in abundances between sampling periods. Numbers of *B. varium* ranged similarly in 1993 (307–8,618) and 1996 (289–28,345), and numbers of *A. lunata* also ranged similarly in 1993 (109–2,679) and 1996 (83–1,414), and WSR showed no difference between sampling periods (P_{exact} = 0.94 for both taxa).

Remarkably, abundances of several epifaunal crustaceans were lower at grassbed stations between 1993 and 1996 (Figure 6). Total numbers of ampithoids, *Hippolyte* spp., *Pagurus* spp., and palaemonids were reduced in 1996. Numbers of ampithoids in grassbed kicknet samples averaged and ranged higher in 1993 (127.1 ±35.6 se; 5–246) than in 1996 (36.6 ±18.0 se; 0–116) (paired-t test = 2.54, P = 0.04) (Power = 0.50 at α = 0.05). Numbers of *Hippolyte* in grassbed samples also averaged and ranged higher in 1993 (5,224 ±1,292.5 se; 1,266–10,363) than in 1996 (447.9 ±165.8 se; 73–1,125) (paired-t test = 7.57, P < 0.001; ln transformed) (Power = 1.0 at α = 0.05). Again, numbers of *Pagurus* in grassbed samples averaged and ranged higher in 1993 (103.1 1 ±20.9 se; 27–183) than in 1996 (25.0 ±6.0 se; 0–44) (paired-t test = 3.85, P = 0.008) (Power = 0.88 at α = 0.05). Finally, numbers of palaemonids in grassbed samples averaged and ranged higher in 1993 (47.4 ±15.2 se; 6–124) than in 1996 (10.6 ±5.0 se; 0–33) (paired-t test = 2.75, P = 0.03) (Power = 0.57 at α = 0.05).

DISCUSSION

Sustained hurricane effects were evident in some habitats based on comparisons of 1993 and 1996 macrobenthic surveys, notwithstanding insufficient sampling frequency. One year after the hurricane impacts, lower species richness usually occurred at the protected beach stations and lower total densities usually oc-

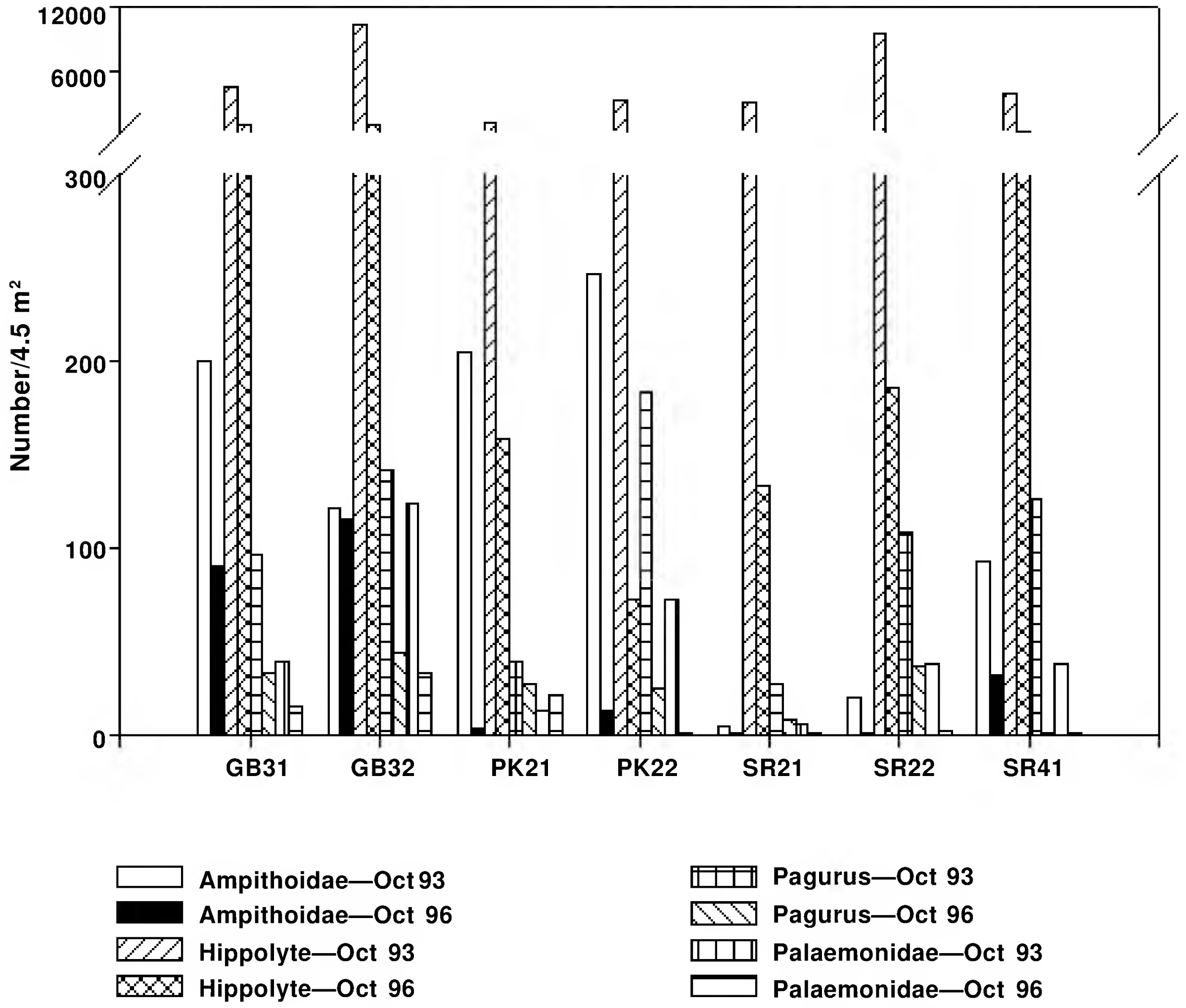

Figure 6. Abundances of important epifaunal crustaceans from grassbed stations in 1993 before hurricanes Opal and Erin and in October 1996 one year after hurricane impacts.

curred at protected swash-zone as well as at both protected and exposed subtidal stations. The lowest faunal metric values in 1996 were generally from the stations hardest hit by the hurricanes. PCO showed that 2 of the most impacted subtidal protected stations in 1996, including one at Gulf Breeze and another at Santa Rosa Island, fell outside the range of previously measured variability in faunal dissimilarity. *Lepidactylis* sp A is usually a dominant subtidal organism in spring. However, this amphipod became dominant at the 2 stations in October 1996, although it was lacking at those same stations in autumn 1993 (Rakocinski et al. 1995).

Differences in total densities between 1993 and 1996 at subtidal sand-beach stations did not reflect consistent responses by the dominant taxa, indicating that density differences reflected individualistic responses by various taxa. For example, several dominant taxa from 1993 were lacking among protected 15-m subtidal stations in 1996, including *C. capitata*, *H. filiformis*, *A. uncinata*, *Kalliapsuedes* sp. A., and *B.* cf. *floridana*. Interestingly, *B.* cf. *floridana* usually is abundant in stable subtidal habitats (Rakocinski et al. 1993, 1996). The lack of *Capitella* and *Heteromastus*, and the increase in *Lepidactylis* sp. A, may reflect relatively low availability of organic matter in the newly disturbed and overwashed sandy sediments of the impacted protected beaches since opportunist capitellids colonize organically rich sediments following a disturbance (Boesch et al.1976). Finally, epibenthic crustacean taxa in seagrass habitats were generally lower in 1996 than in 1993, although abundances of many grassbed taxa were similar for each sampling period. Evidence that grassbed habitats incurred sustained hurricane effects included significant decreases in total ampithoids, *Hippolyte* spp., *Pagurus* spp., and total palaemonids. Thus sustained hurricane effects were apparently selective on certain taxa. The same trends were upheld by data from lagoon stations in which grassbed habitat occurred (Rakocinski et al. 1998b). Posey et al. (1996) noted selective effects of storm disturbance on vulnerable surface sediment-dwelling organisms as opposed to deep sediment-dwelling taxa. The finding that such benthic effects are selective and individualistic supports the currently accepted Gleasonian concept of community organization, which views assemblages as associations of organisms that are individually adapted to live under particular conditions (Ricklefs 1983).

Although effects of severe meteorological events on macrobenthic assemblages are often difficult to ascertain, documented impacts of hurricanes on the biota include burial by sediment deposition, turbidity effects, suffocation from the decomposition of organic matter, scouring, osmotic stress, physical stranding, and thermal shock (Saloman and Naughton 1977). In a thorough study of the effects of Hurricane Eloise on the swash-zone macrofauna of several exposed beach sites at Panama City Beach, Florida, Saloman and Naughton (1977) failed to find any major differences between pre- and post-hurricane periods, despite substantial erosional alteration of the beach. Using the same type of box-corer as this study, the authors found that abundances of swash-zone organisms were inherently variable. They mainly attributed the lack of measurable hurricane effects to the adaptations of organisms inhabiting this high-energy environment as well as to inherent faunal variability. They also cited other studies that found little evidence of hurricane impacts on the biota inhabiting exposed beach sites (Keith and Hulings 1965, Croker 1968). Thus, despite the large extent of the hurricane disturbance in this study, it is not surprising that we found less evidence of sustained effects on the fauna of exposed beaches.

Various factors noted in other studies of hurricane effects on macrobenthos also may have played some role in our study, including hydrography, sediment disturbance, and depletion of dissolved oxygen. In a study of hurricane effects on the aquatic fauna of north Florida Bay, Tabb and Jones (1962) found that both direct disturbance and subsequent oxygen depletion greatly impacted seagrass associated organisms. Moreover, fish and invertebrates remained scarce for several months in the area of greatest oxygen depletion. Similar detrimental impacts may have been responsible for the effects we observed on epifaunal crustacean populations of grassbed habitats. Boesch et al. (1976) found that many species declined from drastic storm-induced decreases in salinity and dissolved oxygen, followed by irruptive increases in several opportunistic species within one year. Moreover, the deep and relatively stable mud-bottom community in the lower York estuary still had not recovered after 2.5 years, suggesting low community resilience. This time frame for recovery is comparable to that inferred from our study, as possible effects on grassbed macrofauna were still apparent one year after the storm impact. The resiliency of estuarine populations is thought to be related both to the spatial extent of impact as well as to the life-history characteristics of impacted species (Dauer 1984). The larger the area impacted and the longer-lived the species, the longer the expected recovery time.

The extent of inferred sustained effects of Hurricanes Erin and Opal corresponded inversely to the degree of disturbance typically experienced by resident assemblages. Exposed swash-zone stations showed the least evidence of faunal effects, followed by progessively greater effects at exposed subtidal, protected swash-zone, protected subtidal, and grassbed stations. Assemblages of relatively stable habitats like protected subtidal sand-beaches and grassbeds are richer and presumably less resilient than simpler assemblages of exposed sand beaches and shorelines. After one year, the post-hurricane assemblages of exposed beaches and swash-zone habitats were indistinguishable from those of pre-hurricane conditions. By contrast, abundances of epifaunal crustaceans of grassbed habitats were still low one year after the hurricanes. Thus, apparent differences in faunal recovery between protected and exposed sites might reflect differences in adaptations of resident taxa to typical disturbance regimes.

In a study of the effects of extensive beach restoration on macrobenthic assemblages across exposed-beach transects, Rakocinski et al. (1993, 1996) hypothesized that diverse offshore subtidal assemblages are less resilient than contiguous nearshore sand-beach assemblages. Faunal recovery near the beach was rapid, with complete colonization in less than one year. Indeed, Grant (1980, 1981) found that small patches of azoic beach sand could be completely colonized within one month. Being adapted to frequent disturbance from high energy conditions confers considerable resilience to macrobenthic assemblages of exposed sand beaches (Nelson 1993). Other studies of the impacts of beach nourishment also usually find rapid and complete macrobenthic recovery within the course of one year (Nelson 1989, 1993; Baca et al. 1991). However, like exposed offshore macrobenthos, assemblages of relatively stable habitats like protected subtidal sand-beaches and grassbeds appear to be less resilient than assemblages of exposed sand beaches (Rakocinski et al. 1991, 1995).

CAVEATS

Despite infrequent sampling, inadequate pre- and post-disturbance sampling, and the lack of an unimpacted reference area, the existence of GUIS baseline information from the 1993 macrobenthic inventory and the faunal survey of sand beaches in 1986/1987 provided a standard frame-of-reference for considering environmental impacts. The scope of the 1993 inventory furnished a preexisting balanced arrangement of study sites throughout GUIS and built-in spatio-temporal redundancies afforded by the inclusion of multiple sites and years. Established standard quantitative and semi-quantitative sampling methods and protocols also ensured comparability. This study demonstrates the utility of building a comprehensive and current database on macrobenthic resources to facilitate sound management decisions.

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Oceanic and Neritic Ichthyoplankton at the Edge of the Continental Shelf in the Southern Gulf of Mexico

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OCEANIC AND NERITIC ICHTHYOPLANKTON AT THE EDGE OF THE CONTINENTAL SHELF IN THE SOUTHERN GULF OF MEXICO

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ABSTRACT Oceanic and neritic ichthyoplankton were examined at a single sampling site at the edge of the continental shelf in the southern Gulf of Mexico. Double oblique tows were made with a 60 cm Bongo net fitted with 505 μm mesh netting. Collections were taken every 2 hours over a 24 h period during spring, summer and fall of 1992. Fish larvae were described as either oceanic or neritic depending upon adult life-stage habitat. The larvae of 59 taxa were collected in spring (50 oceanic, 9 neritic), 53 in summer (26 oceanic, 27 neritic) and 55 in fall (22 oceanic, 33 neritic). Larvae were least abundant during spring and most abundant in fall, for both oceanic and neritic taxa. Highest abundances of larvae were collected at night indicating increased gear avoidance during daylight.

INTRODUCTION

Several areas in the Gulf of Mexico (GOM) exhibit great biological diversity, including frontal areas of the Loop current (Richards et al. 1993), and transitional zones between oceanic and neritic water, in a wide area around the continental shelf-break in the southern GOM (Flores-Coto et al. 1988, Sanvicente-Añorve 1990, Flores-Coto et al. 1993). This paper describes the variation in ichthyoplankton composition and abundance, and the possible causes of this variation at a fixed sampling site at the edge of the continental shelf in the southern GOM.

This transitional area, where oceanic and neritic provenance communities meet, is dynamically complex and exhibits large seasonal variation in the location, extent and composition of ichthyoplankton assemblages (Sanvicente-Añorve et al. 1998). The origin of this variation in composition and abundance has not been well studied but is likely due to the mixing of oceanic, neritic and even estuarine water masses.

MATERIALS AND METHODS

Collections used in this study were obtained at a single site at the edge of the continental shelf (Figure 1) along the 180 m isobath (19^{0}33'5"N, 92^{0}37'5"W). Sampling was conducted every 2 hours during one 24 h period in spring, summer and fall of 1992. Collections were taken with paired 60 cm Bongo nets fitted with 505 μm mesh and calibrated flowmeters. Double oblique tows were made to a maximum depth of 170 m at a speed of 2 knots (1 m s^{-1}).

All fish larvae were sorted and identified to the lowest taxonomic level possible. Each taxon (genus or species) was classified according to the habitat most commonly frequented by the adult life stage. Four habitats were considered: oceanic (O); neritic-pelagic (NP); neritic-demersal (ND); and reef (R). The abundance was standardized as larvae per 100 m^3 and presented as the mean of the 24 h cycle. Larval engraulids and gobiids were not considered in our analysis because larvae in these 2 families cannot be reliably identified to genus or species level.

RESULTS

Larvae of 103 taxa were identified in these collections; 57 were oceanic, 9 neritic-pelagic, 34 neritic-demersal, and 3 reef (Table 1). The oceanic taxa were comprised mainly by members of the mesopelagic families Myctophidae, Gonostomatidae, Paralepididae and Bregmacerotidae. The neritic-pelagic taxa were represented primarily by the Carangidae and Sphy-raenidae. Neritic-demersal forms were represented by species of pleuronectiforms and several perciforms. Mean total abundance of all larvae varied widely among seasons and highest abundances of larvae were collected at night, indicating increased gear avoidance during daylight (Figure 2).

Seasonal Variation

Composition of ichthyoplankton assemblages changed seasonally, but the total taxa number collected remained relatively constant. Of the 17 taxa that occurred in all seasons sampled, 14 were oceanic and 3

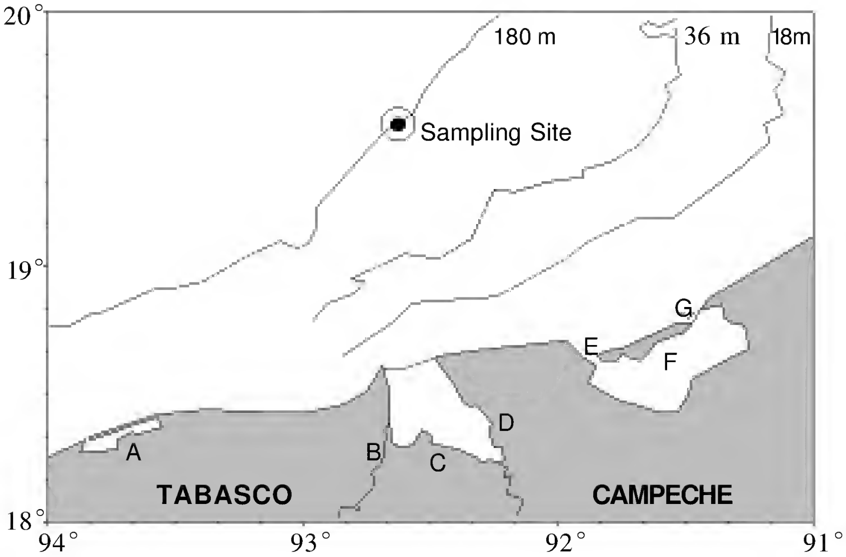

Figure 1. Sampling site location and local bathymetry for ichthyoplankton collections in the southern Gulf of Mexico. A = Carmen and Machona Lagoons; B = Grijalva River; C = Usumacinta River; D = San Pedro y San Pablo River; E = Carmen Inlet; F = Terminos Lagoon; G = Puerto Real Inlet.

were neritic-demersal. In spring, a total of 59 taxa were collected: 50 were oceanic; 9 were neritic-demersal; and 25 taxa occurred only in this season (Table 2). During summer, a total of 53 taxa were collected: 26 were oceanic; 4 were neritic-pelagic; and 23 were neritic-demersal. Fourteen of these taxa occurred only during summer. In fall, a total of 55 taxa were collected: 22 oceanic; 7 neritic-pelagic; 23 neritic-demersal; and 3 reef taxa. Seventeen of these were found only in fall, and most of these latter were neritic forms (Table 2). Of the species collected exclusively in fall only one was oceanic.

Collections from oceanic habitat were most diverse during spring when the number of taxa were about 50% greater than during summer or fall. Taxa occurring exclusively in one of the 3 seasons accounted for 9.7% of the total abundance of fish larvae. These taxa together represented 54% of all taxa identified, and most of them occurred in spring. Mean larvae abundance obtained from each 24 h cycle were 20, 42 and 56 larvae

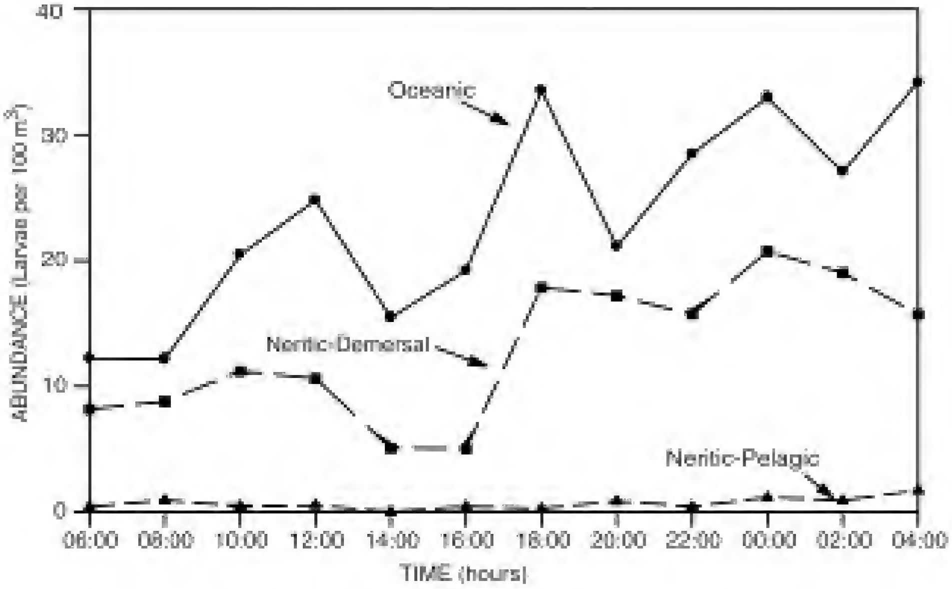

Figure 2. Mean total abundance of fish larvae per 100 m^3 captured every 2 hours over a 24 h cycle during spring, summer, and fall in 1992 in the southern Gulf of Mexico.

TABLE 1

Composition and abundance (larvae per 100 m^3) of ichthyoplankton that could be identified to at least genus during spring, summer, and fall in 1992 at a single site in the southern Gulf of Mexico. Adult habitats are coded as: O = oceanic; ND = neritic-demersal; NP = neritic-pelagic; and R = reefs. Larvae of the families Engraulidae and Gobiidae were not included in this summary.

	Adult habitat	Spring	Summer	Fall
Conger oceanicus	R			1.88
Neoconger mucronatus	R			1.99
Ophichthus spp.	ND	0.23		0.16
Pisodonophis sp.	ND		0.15	0.14
Pisodonophis cruentifer	ND			1.47
Myrophis punctatus	ND			0.83
Etrumeus teres	NP			0.03
Bathylagus spp.	O	0.13	0.07	0.13
Cyclothone spp.	O	0.04		
Cyclothone braueri	O	0.83	1.22	4.65
Maurolicus muelleri	O	1.56	1.35	3.85
Vinciguerria sp.	O	0.04		
Vinciguerria poweriae	O	0.17		
Vinciguerria nimbaria	O	0.04		
Gonostoma elongatum	O	0.22	0.60	
Pollichthys mauli	O	1.46	0.20	5.59
Diplophos taenia	O			0.04
Argyropelecus sp.	O	0.06		
Synodus foetens	ND		4.89	5.64
Trachinocephalus myops	ND		0.06	0.22
Paralepis sp.	O	0.06		
Paralepis atlantica	O	1.52		
Lestidiops jayakari	O	0.73		
Lestidiops affinis	O	0.13		
Lestidium atlanticum	O	0.32		0.17
Lestrolepis intermedia	O	0.54		
Notolepis rissoi	O	0.30	0.10	
Macroparalepis breve	O	0.16		
Scopelarchus analis	O		0.12	
Diaphus spp.	O	0.98	0.55	2.22
Benthosema suborbitale	O	0.28	2.13	0.56
Notolychnus valdiviae	O	0.52	0.24	
Lampanyctus spp.	O	0.11		
Myctophum asperum	O	0.07		0.21
Myctophum nitidulum	O	0.27	0.35	0.13
Myctophum obtusirostre	O	0.07	0.03	0.93
Myctophum punctatum	O	0.55	0.22	0.04
Hygophum taaningi	O	0.59	0.06	0.04
Hygophum macrochir	O	0.20	0.03	
Hygophum hygomii	O	0.91	2.12	
Hygophum reinhardtii	O	0.07		
Hygophum benoiti	O	0.07		
Lobianchia gemellarii	O	0.10		
Diogenichthys atlanticus	O	0.48	0.24	0.03
Lepidophanes gaussi	O	0.07		
Ceratoscopelus maderensis	O	0.96	1.58	0.58
Notoscopelus resplendens	O	0.06		0.04
Lampadena spp.	O	0.03		0.26
Lampadena luminosa	O	0.32		
Loweina rara	O	0.07		
Bregmaceros atlanticus	O	1.44	0.41	0.54
Bregmaceros cantori	O	0.75	10.64	12.34
Bregmaceros maclellandii	O		0.03	
Bregmaceros sp.	O		0.03	
Syngnathus sp.	ND		0.18	
Scorpaena sp.	ND		0.06	
Scorpaenodes sp.	ND	0.16	0.04	
Sebastes sp.	ND			0.03
Serranus spp.	ND		0.45	0.04
Centropristis spp.	ND		0.03	0.03
Diplectrum spp.	ND		0.06	0.10
Gonioplectrus sp.	ND			0.04
Hemanthias sp.	ND			0.04
Anthias sp.	ND			0.04
Caranx sp.	NP			0.04
Chloroscombrus chrysurus	NP		0.70	0.06
Decapterus punctatus	O		0.20	
Selar crumenophthalmus	NP		0.24	0.04
Selene spixii	NP		0.17	
Selene setapinnis	NP		0.13	
Trachurus lathami	NP			0.03
Gerres spp.	ND	0.26	0.13	
Mugil cephalus	ND		0.12	0.04
Mugil curema	ND			0.06
Sphyraena sp.	NP			0.04
Sphyraena barracuda	NP			0.03
Naso sp.	R			0.04
Microdesmus spp	ND	0.24	0.06	
Diplospinus sp.	ND		0.03	0.32
Diplospinus multistriatus	ND	0.28	0.10	0.19
Thunnus spp.	O	0.19		0.06
Thunnus thynnus	O	0.10		
Thunnus alalunga	O	0.04		
Thunnus albacares	O	0.30	0.04	
Acanthocybium solanderi	O	0.03		0.04
Auxis sp.	O	0.03		
Scomber japonicus	O		0.03	
Scomberomorus cavalla	O		0.27	0.07
Xiphias sp.	O	0.04		
Istiophorus americanus	O	0.35		
Cubiceps pauciradiatus	O	0.04		
Bothus ocellatus	ND		1.30	3.50
Citharichthys sp.	ND		0.06	0.04
Citharichthys spilopterus	ND	0.04		0.58
Citharichthys cornutus	ND			0.04
Syacium gunteri	ND	0.07	3.95	3.78
Engyophrys sp.	ND		0.03	
Engyophrys senta	ND	0.04		
Etropus spp.	ND		1.08	
Cyclopsetta fimbriata	ND		0.22	
Symphurus sp.	ND		1.70	
Symphurus plagiusa	ND	0.03	2.83	1.72
Monacanthus hispidus	ND		0.03	
TOTAL		19.75	41.60	55.75

TABLE 2

Number of taxa whose larvae were captured during spring, summer, and fall in 1992 at a single site in the southern Gulf of Mexico. Numbers in parentheses are larvae per 100 m^3. [1]Total unique taxa found related to each habitat, pooled across all seasons.

		OCEANIC	NERITIC PELAGIC	NERITIC DEMERSAL	REEFS	TOTAL TAXA
SPRING	Total	50 (18.40)		9 (1.35)		59 (19.75)
	Spring only	24		1		25
SUMMER	Total	26 (22.86)	4 (1.24)	23 (17.56)		53 (41.66)
	Summer only	5	2	7		14
FALL	Total	22 (32.52)	7 (0.24)	23 (19.08)	3 (3.91)	55 (55.75)
	Fall Only	1	5	8	3	17
TOTAL[1]		57	9	34	3	103

per 100 m^3 in spring, summer and fall, respectively (Table 1). Larvae were 3 times more abundant in fall than in spring, and the abundance of oceanic fish larvae was always higher than those of neritic habitat regardless of season. Oceanic fish larvae abundance and taxa number varied inversely, while the neritic group varied directly (Figure 3).

DISCUSSION

Most oceanic and neritic species of fishes in the southern GOM reproduce all year long with spawning peaks in spring and summer (Flores-Coto et al. 1988, Flores-Coto and Ordoñez-López 1991, González-Felix 1994). However, at our study site larvae of oceanic and neritic fishes were most abundant in fall and not in spring and summer as expected based on times of reproductive peaks. Larvae of neritic fishes were particularly scarce in spring, and although the abundance of larval oceanic fishes was also relatively low in spring, the highest larval richness of oceanic fishes was found at this time. These results indicate that our study site is not a major spawning area for either group of fishes.

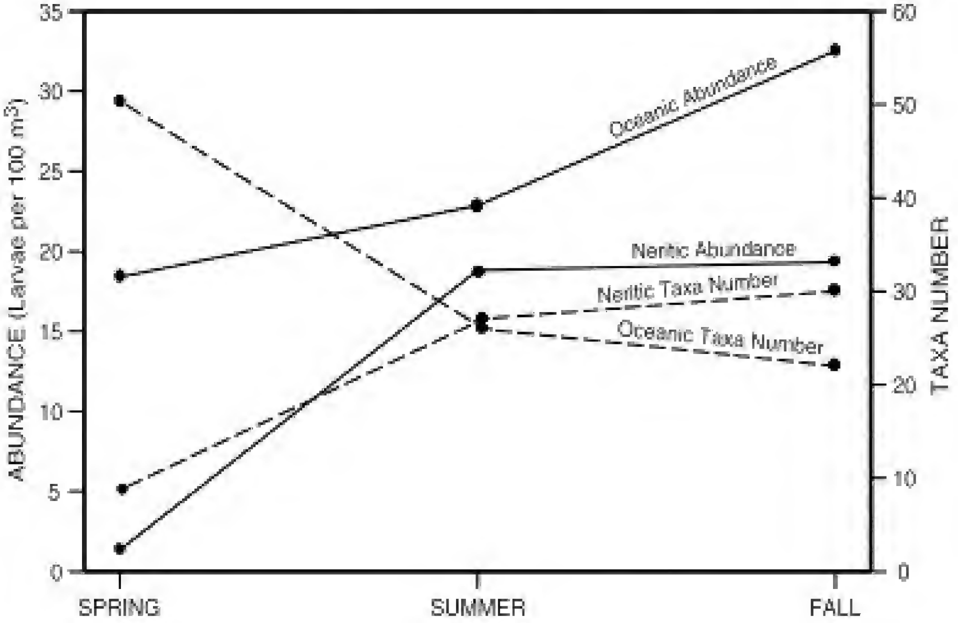

Figure 3. Total taxa number (dashed line) and mean abundance pooled by time (solid line, per 100 m^3) of oceanic and neritic fish larvae during spring, summer, and fall in 1992 at one site in the southern Gulf of Mexico.

Seasonal variations in larval abundance and taxa richness may be caused in part by seasonal currents. The Campeche Bay is dominated by the presence of a large cyclonic eddy, which varies in size and duration (Salas de León and Monreal-Gómez 1986, Velasco-Mendoza 1989, Monreal-Gómez and Salas de León 1990, Vázquez de la Cerda 1993). The effects of this cyclonic eddy, in conjuntion with cold winter winds (northerns) and the discharge from several rivers, combine to play an important role in the hydrodynamics of this area. These undoubtedly influence the variation of the ichthyoplankton composition and abundance at our study site. Salas de León et al. (1998) found that the cyclonic eddy modified the position of the principal axis of the Grijalva-Usumacinta front moving it westward in spring, and eastward in winter. These authors showed that strong westward mesoscale currents in spring displace the haline front to the west of the Grijalva-Usumacinta embrouchure, allowing the penetration of oceanic taxa. In summer, the eddy currents are less intense and the coastal front shows its maximum penetration in the GOM establishing a balance between the oceanic and neritic taxa. During fall, the front moves to the east of the Grijalva-Usumacinta axis and the resulting currents move northeastward (Monreal-Gómez and Salas de León 1990), explaining, in part, the higher abundance of the neritic taxa during fall at our study site.

Neritic taxa spawn mainly in mid-shelf areas, shallower than 110 m (González-Felix 1994). Spawning of some of these taxa, including the sciaenids, is limited to the inner-shelf and these larvae are apparently unable to reach our study site. Larvae of oceanic species were more abundant than larvae of neritic species during each of the 3 seasons examined, indicating a greater influence of oceanic waters in our study area. Highest abundances of larvae were also collected at night, indicating increased gear avoidance during daylight.

In conclusion, our study area is a dynamic region of the GOM as evidenced by the large number of taxa (103) identified. Larvae were least abundant during spring and most abundant in fall for both oceanic and neritic taxa, although the richness of oceanic taxa was greatest in spring. Larvae of reef fishes were rarely found and only 3 taxa were identified.

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THE SOUTH AMERICAN NERITIC COPEPOD *CTENOCALANUS HERONAE* VEGA-PÉREZ AND BOWMAN (CALANOIDA) IN THE GULF OF MEXICO, WITH COMMENTS ON THE TAXONOMY OF THE GENUS

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ABSTRACT A single adult female specimen of the calanoid copepod *Ctenocalanus heronae* Vega-Pérez and Bowman was collected during a zooplankton survey carried out in February 1997 in Campeche Sound, the central-southeastern portion of the Gulf of Mexico. The taxonomy of the genus *Ctenocalanus* Giesbrecht is still unclear. Characters used to separate the species have been considered rather subtle. In this paper the taxonomic illustrations of the specimen collected are accompanied by a revision of the taxonomic features commonly used to identify the species. New, previously overlooked characters such as the cephalosome/urosome ratio, the shape of the 5th legs and particularly the structure of legs 1 and 2, are presented and might turn out to be useful to separate some of the species. This record of *C. heronae* in the Gulf of Mexico also represents the first reported occurrence of the genus in the Northwestern Tropical Atlantic and increases remarkably the known distribution of the species from the 24°S to the 18°N.

INTRODUCTION

The genus *Ctenocalanus* Giesbrecht belongs to the calanoid superfamily Clausocalanoidea, family Clausocalanidae. It is distributed mainly in cold neritic waters of the Antarctic, Sub-antarctic and temperate regions (Fransz 1988, Björnberg 1981, Mauchline 1998). Only 5 species of this genus (*C. vanus* Giesbrecht 1888, *C. citer* Heron and Bowman 1971, *C. campaneri* Almeida Prado-Por 1984, *C. tageae* Almeida Prado-Por 1984 and *C. heronae* Vega-Pérez and Bowman 1992) have been described (Razouls 1996, Mauchline 1998). The former 2 are the most widely distributed, mainly in the Antarctic and Sub-antarctic regions, whereas the other 3 have more restricted distributions: in the Gulf of Elat (*C. campaneri* and *C. tageae*) and in southern Brazil (*C. heronae*). According to previous reports (Owre and Foyo 1967, Reid 1990, Campos and Suárez-Morales 1994, Suárez-Morales and Gasca 1998), the genus *Ctenocalanus* has not been recorded previously in the Northwestern Tropical Atlantic.

From a zooplankton survey carried out in Campeche Sound, the central-southeastern portion of the Gulf of Mexico, a single female *Ctenocalanus heronae* was recorded. This geographic record is presented herein along with taxonomic comments, illustrations of the material examined and notes on this genus.

MATERIAL AND METHODS

Zooplankton were collected from 12–18 February 1997 (winter) during the oceanographic cruise PERFOTOXIII, carried out by the Instituto Mexicano del Petróleo on board the vessel *Justo Sierra*, of the Universidad Nacional Autónoma de Mexico. Samples were taken from 10 stations in the Campeche Sound, Gulf of Mexico, off the west coast of the Yucatan Peninsula. Copepods were sorted and then processed for identification. A single specimen of *Ctenocalanus* was recorded at station 10 on February 18. The taxonomically relevant structures for the identification of the species are illustrated herein. This specimen was deposited in the zooplankton collection of El Colegio de la Frontera Sur, Chetumal.

RESULTS

Ctenocalanus heronae Vega-Pérez and Bowman, 1992 (Figure 1)

Material. 1 adult female, ethanol-preserved, partially dissected, mounted on DEPEX medium. One locality in Campeche Bay, Gulf of Mexico at 18°46.944 N; 92°22.026W. A vial containing the cephalothorax, urosome and mounted appendages are deposited under access number ECOCH-ZOO-00412.

Remarks. The taxonomic analysis of *Ctenocalanus* in the samples resulted in the identification of an adult female of *C. heronae* (Figure 1 A–I). The genus *Ctenocalanus* can be readily distinguished by the presence of comb-like spines (ctenospines) inserted in deep notches on the outer margin of the 3rd exopods of legs 3 and 4, and by the reduced uniramous of female 5th leg (Björnberg 1981, Vega-Pérez and Bowman 1992, Mauchline 1998) (Figure 1 K). However, the taxonomic separation of the 5 species of the genus is difficult

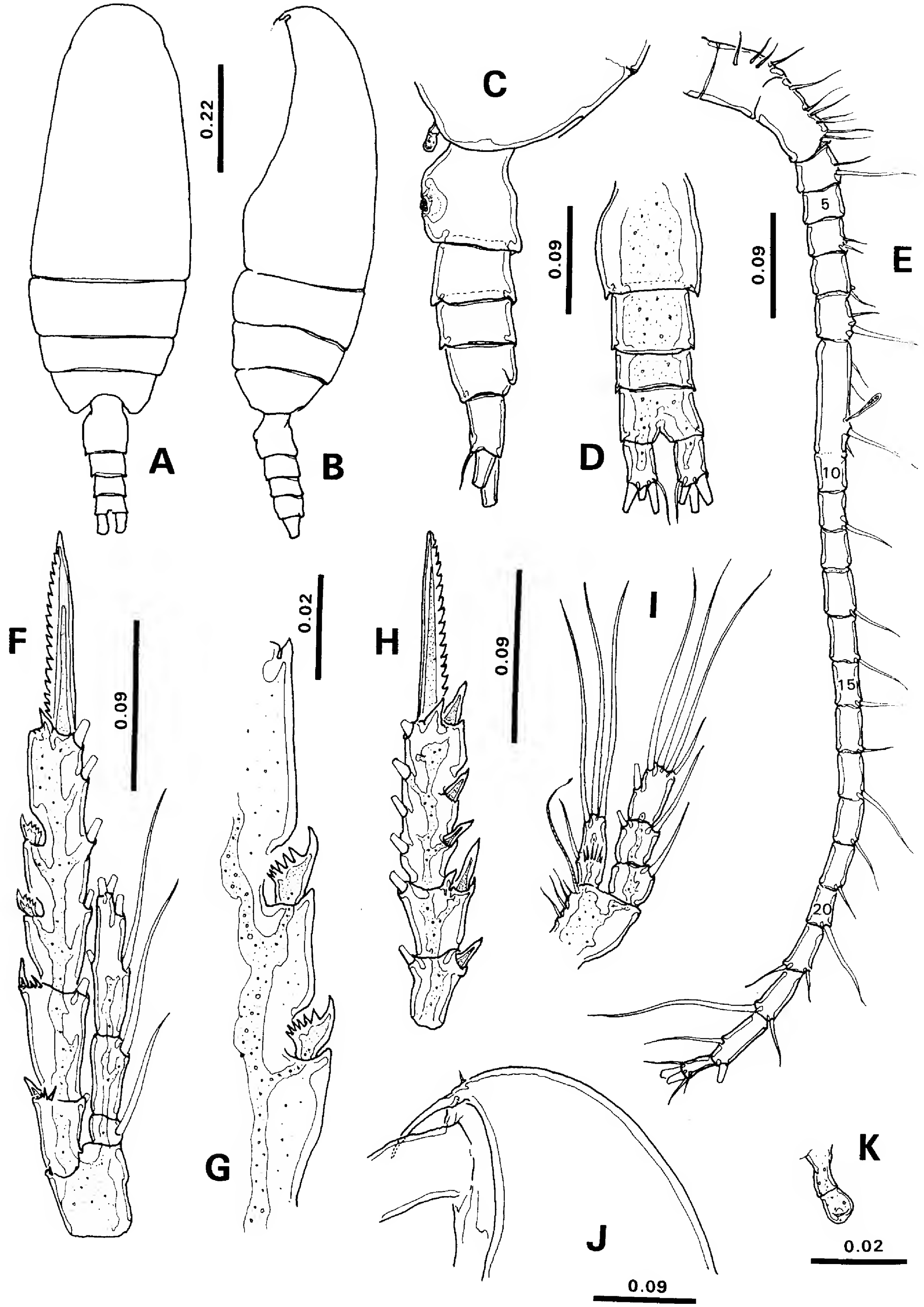

Figure 1. ***Ctenocalanus heronae*** **Vega-Pérez and Bowman, 1992. Adult female: A. Habitus, dorsal; B. habitus, lateral; C. urosome, lateral view; D. urosome, dorsal view; E. right antennule; F. third leg; G. detail of third leg ctenospines; H. second leg exopodite; I. first leg. J. head, lateral view; K. fifth leg. All scales are in mm.**

TABLE 1

Characters used to separate the known species of *Ctenocalanus*. c/u ratio = cephalosome/urosome length ratio.

	Ctenocalanus campaneri	*C. tageae*	*C. citer*	*C. vanus*	*C. heronae*	our specimen
body length (mm)	1.12	1.10	1.17	1.35	1.2–1.3	1.17
forehead	blunt	prominent	blunt	blunt	prominent	prominent
rostral points	undescribed	undescribed	long	short	long	long
genital somite	assymmetrical	symmetrical	symmetrical	symmetrical	assymmetical	asymmetrical
assymmetry	laterally (right side)	—	—	—	laterally (left side)	laterally (left side)
c/u ratio	3.58	3.96	3.80	3.98	3.37	3.43
antennular length (reach of)	anal somite distal end	beyond caudal rami	anal somite distal end	anal somite distal end	anal somite distal end	anal somite distal end
antennular articles 9–10	partially fused	separated	separated	fused	separated	partially fused
points on ctenospines	4–5	7–8	4–5	6–7	6–7	6–7
angle of ctenospines	moderately open	closed	closed	wide open	moderately open	closed
spines on leg 1 endopod	undescribed	undescribed	absent	undescribed	present	present
leg 5 (female)	uniarticulated	uniarticulated	uni- or biarticulated	biarticulated	uniarticulated	uniarticulated
shape of leg 5	blunt	mammiliform	subtriangular	assymmetrical subtriangular	rounded	rounded

because specific differences are based on a limited number of subtle characters (Vega-Pérez and Bowman 1992). The most widely used characters are the structure and orientation of the ctenospines of legs 3 and 4, and in some instances, the length of the antennules or the shape of the head (Björnberg 1981, Almeida Prado-Por 1984, Vega-Pérez and Bowman 1992). The taxonomic value of the orientation of the ctenospines was questioned by Almeida Prado-Por (1984), who pointed out that these spines are articulated at their bases, and thus, their alignment in relation with the axis of the segment is not a relevant character.

The evidence used by Almeida Prado-Por (1984) to define *C. campaneri* and *C. tageae* as new species included a set of characters which only considers the number of spines on the ctenospines, not their alignment. However, there has not been a comparative analysis of these characters for the 5 known species. The characters used by previous authors to clarify the taxonomy of the genus are presented for each species (Table 1). We examined other features such as the cephalic/urosome ratio (C/U) and the shape of the female 5th leg.

The above noted characters allow clear separation of a number of these species. For example, it is relatively easy to separate *C. heronae* from *C. campaneri* by the number of points on the ctenospines, the assymmetry of the genital somite on the right margin, the shape of the female 5th leg (Almeida Prado-Por 1984, page 86), and by the C/U ratio. *Ctenocalanus heronae* differs from *C. tageae* in the length of the antennules, which is a major difference (Vega-Pérez and Bowman 1992), in the C/U ratio, and in the shape of female leg 5 (Almeida Prado-Por 1984, page 88). It can be distinguished from *C. vanus* by its size, a genital somite which is not prominent ventrally, the C/U ratio and the biarticulated and distally subtriangular female leg 5 (Table 1). Differences become more subtle when we want to separate *C. citer* from *C. heronae*. Vega-Pérez and Bowman (1992) separated these 2 species by indicating that *C. heronae* has a wider angle of orientation of the ctenospines than *C. citer*. This difference is not valid following arguments in Almeida Prado-Por (1984) and was not considered here. We therefore analyzed other characters which might turn out to be useful to separate at least these 2 closely related species.

C/U ratio. *Ctenocalanus heronae* diverges from the other 4 species of the genus with a C/U ratio of 3.37; our specimen showed a 3.43 value (Table 1). This character might be useful to separate some of the other species as well.

First leg. In *C. heronae*, a group of spines is present on the first endopodal segment which is also observed in the Gulf of Mexico specimen. These spines are absent in *C. citer* (Heron andBowman 1971). In *C. heronae* and our specimen (Figure 1I), the outer seta on the first exopodal segment reaches more than 2/3 the margin of the succeeding segment, whereas in *C. citer* this seta barely reaches half the length of the next segment. Our specimen differs from the setation pattern described for *C. heronae* in having a relatively longer seta on the 2nd exopodal segment.

Second leg. The structure and size of the outer spines of exopodal segments 1–3 differ in both species. In *C. citer* the spine on the first exopodal segment is small and thin, whereas, it is stronger and wider at its base in *C. heronae* and in our specimen (Figure 1 H). Similarly, the spine on the 2nd segment is noticeably large in *C. heronae* and our specimen, but is distinctly smaller in *C. citer*. This spine in *C. citer* does not reach the base of the first spine of the succeeding segment, whereas, in *C. heronae* it reaches the midpoint of the spine. In *C. citer*, the proximal spine of the 3 outer spine series of the 3rd exopodal segment is very small, not reaching midway to the base of next spine. The other 2 are subequal. In *C. heronae* and in our specimen, the proximal spine is relatively larger than in *C. citer*, almost reaching the base of next spine.

Third legs. Spines on the base of the first and 2nd outer exopod segments are present, but are small in *C. citer* and well developed in *C. heronae* and in our specimen (Figure 1 F).

Number of points on ctenospines. *Ctenocalanus citer* and *C. campaneri* each have 4 or 5 points, with *C. tageae* having up to 8 points. *Ctenocalanus heronae* and our specimen has a 6–7 point pattern (Figure 1 G).

Based on these alternative characters and on the data presented in Table 1, we concluded that our specimen can be identified as *C. heronae* even though some taxonomic keys or the available descriptions and comparisons would have led us to *C. citer*. The orientation of the ctenospines is variable. For instance, in the 3rd leg these structures appear at a widely open angle (65°) in the original description of *C. heronae* (Vega-Pérez and Bowman 1992), but the angle is reduced (40–45°) in our specimen of the same species. The armature of the antennules in our specimen shows variations when compared with the *C. heronae* pattern (mainly missing setae), but those could have been lost during preservation.

Ctenocalanus heronae has been reported from the coast of Southern Brazil only (*ca.* 24°S), in a water column sample collected from the shelf of this subtropical area (Vega-Pérez and Bowman 1992). Therefore, our record in the Campeche Sound (18°N) allows a relevant northwards extension of this species from the temperate zone of the Atlantic Ocean into the tropical zone of the Northwestern Atlantic. This is also the first record of the genus in the Northwestern Tropical Atlantic.

The Surface Subtropical Water and the Surface Tropical Water comprise the upper 100m in the 0–10°S zone of the south Atlantic. While extending into lower latitudes, both layers are found in the Caribbean zone (Wüst 1964) when waters of the South Equatorial system flow into the Caribbean Basin and then into the Gulf through the Yucatan Channel. The presence of *C. heronae* could be related with this hydrologic system. This species seems to be an eurythermic tropical-subtropical form that has been recorded at 15°C in Brazil and at more than 20°C in the Gulf of Mexico.

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Relationship Between Pea Crab (*Pinnotheres maculatus*) Parasitism and Gonad Mass of the Bay Scallop (*Argopecten irradians*)

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RELATIONSHIP BETWEEN PEA CRAB (*PINNOTHERES MACULATUS*) PARASITISM AND GONAD MASS OF THE BAY SCALLOP (*ARGOPECTEN IRRADIANS*)

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ABSTRACT We investigated the prevalence of pea crabs (*Pinnotheres maculatus*) in bay scallops (*Argopecten irradians*) from 1994 through 1996 in a scallop population from St. Joseph Bay, Florida. We also assessed their impacts on scallop reproductive potential. Our results showed that prevalence in bay scallops varied between 0 and 20% and were extremely low during 1996 (<2%). Comparing Gonadal-Somatic Indices (GSI) between infested and non-infested bay scallops in samples assessed the impact of pinnotherid parasitism. Results showed that GSI was significantly reduced in infested individuals compared to non-infested individuals of the same size range ($t_{12} = 2.3$, $P < 0.04$). These results suggest that *P. maculatus* infestation may lower the reproductive potential of individual scallops, but the low rates of parasitism may only minimally impact the host population.

INTRODUCTION

Species of crabs in the family Pinnotheridae are either parasitic or commensal, and live within bivalves (Palmer 1995), gastropods (Geiger and Martin 1999), ascidians (Williams 1984) and holothurians (Takeda et al. 1997) or associated with burrows of worms (Grove and Woodin 1996) and decapods (Alves and Pezzuto 1998). They also may live on the surface of some echinoderms (Williams 1984). Members of the genus *Pinnotheres* are typically associated with bivalves and may cause substantial damage to their hosts. For example, *P. ostreum* occurs parasitically in oysters where its activities may damage the gills of its host (Christensen and McDermott 1958). However, only the presence of mature female crabs negatively affects oyster growth (Williams 1984) and reproductive potential (O'Brien and Walker 1999). *Pinnotheres maculatus* commonly occurs in scallops, mussels and a variety of other bivalves (Williams 1984, Bierbaum and Shumway 1988). Because this species actively feeds within the mantle, it is associated with stunting in scallops (Kruczynski 1975) and reductions of filtration rates in infested mussels (Bierbaum and Shumway 1988). However, little else is known about the effects of *P. maculatus* on either the growth or reproductive output of host scallops.

Bay scallops, *Argopecten irradians*, are common bivalves in many coastal seagrass communities in the Gulf of Mexico and Atlantic Coasts of the United States (Clarke 1965). Their short life span (10–24 months) and high rates of post-spawn mortality (Capuzzo and Hampton 1984) suggest that they are semelparous or a short lived iteroparous species with reproductive effort dominated by a single spawning event (Barber and Blake 1983). They are an important commercial and recreational fishery in many of these communities (Arnold et al. 1998), but have declined in abundance in some regions (Ford 1997). Consequently, impact of parasitic pinnotherid crabs may negatively affect scallop reproductive output. Here we report the prevalence of pinnotherid parasitism in an exploited population of bay scallops in St. Joseph Bay, Florida. Previous research has indicated that scallops from St. Joseph Bay show at least 2 annual peaks in reproductive output, but spawning may occur throughout the year (Bologna 1998). We also compared the effects of infestation on the Gonadal-Somatic Index (GSI) of infested bay scallops.

MATERIALS AND METHODS

St. Joseph Bay, Florida, USA (29°N, 85.5°W) is a shallow semi-enclosed lagoon with little fresh water input. Salinities in St. Joseph Bay range from 22‰ to 35‰ and temperatures from 8.5° C to 32° C (Bologna 1998). Extensive seagrass meadows occupy the shallows (<2 m) and cover about 2,300–2,400 hectares (Savastano et al. 1984, Iverson and Bittaker 1986). Seven hundred thirty-seven (737) *A. irradians* were collected between April 1994 and October 1996, frozen and returned to the laboratory. Shell height and breadth of each scallop were measured to the nearest 0.05 mm and presence of pinnotherid crabs was noted for each scallop to determine prevalence. Scallops were then dissected to assess infestation and reproductive condition. Somatic and reproductive tissues were dissected and removed from the shell. Each tissue was dried at

TABLE 1

Monthly prevalence, expressed as percent infestation, of *Pinnotheres maculatus* in *Argopecten irradians* collected from 1994 through 1996 in St. Joseph Bay, Florida. Values in parentheses indicate total number of scallops collected and dissected for analysis. † Indicates scallops were not collected during these months. NA indicates the termination of scallop collection.

Month	1994	1995	1996
January		8.00 (25)	0.00 (13)
February		0.00 (28)	10.00 (20)
March		7.14 (28)	0.00 (28)
April	10.34 (29)	13.51 (37)	0.00 (24)
May	2.22 (45)	2.38 (42)	0.00 (21)
June	20.45 (44)	5.88 (33)	0.00 (21)
July	0.00 (23)	3.22 (31)	†
August	1.11 (90)	4.17 (48)	0.00 (16)
September	†	0.00 (37)	†
October	†	18.18 (22)	0.00 (19)
November	†	†	NA
December	0.00 (6)	0.00 (6)	

80° C for 72–96 hours and weighed. Based on the weight ratio of gonadal and somatic tissue, a Gonadal-Somatic Index (GSI) was calculated for each scallop ((Gonad weight/Total weight) × 100). To assess the impact that pinnotherid crabs had on gonadal mass, comparisons were made between infested and non-infested individuals in samples. Comparisons were made using similar-sized individuals (within 5 mm shell height) from the non-infested population. Scallop GSI was then compared between non-infested and infested individuals using a paired t-test on date-averaged means. Specifically, each scallop pair in the analysis represents an independent field collection sample (e.g., June 1994). The mean GSI for each collection date was calculated for infested and non-infested scallops in the given size range. These values were then inserted as a date-averaged pair into the paired t-test analysis (e.g., June 1994, non-infested vs. infested). This process allowed meaningful comparison to be made between infested and non-infested individuals, eliminated size bias, as well as differences among dates, which might relate to seasonal spawning events and resultant changes in GSI.

RESULTS

The prevalence of *P. maculatus* in bay scallops ranged from 0 to 20% (Table 1). Prevalence was higher in 1994 and in 1995 compared to 1996. Pinnotherid parasitism occurred during 13 of 25 monthly sample collections. Results showed that infested individuals had significantly lower GSI values compared to non-infested individuals ($t_{12} = 2.3$, $P < 0.04$, Figure 1) and significantly lower gonad weights as well ($t_{12} = 2.9$, $P < 0.01$).

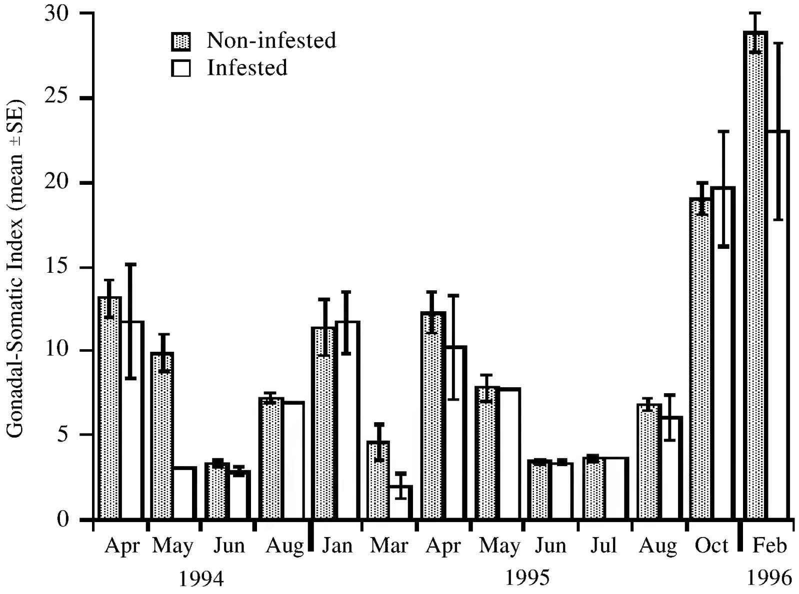

Figure 1. Comparisons of reproductive potential expressed as Gonadal-Somatic Index between infested and non-infested bay scallops, *Argopecten irradians*, collected during 1994 through 1996 from St. Joseph Bay, FL. Values represent date averaged means ±1 Standard Error. For values with no error bars, only one infested individual was available for analysis.

DISCUSSION

Pinnotherid crabs show both parasitism and amensalism in marine communities (Williams 1984, Haines et al. 1994). Previous work has shown that the presence of mature female pinnotherid crabs associated with *Mytilus edulis* can significantly reduce tissue weight, but that male and juvenile-stage crabs did not appear to significantly impact *M. edulis* (Tablado and Lopez-Gappa 1995). However, O'Brien and Walker (1999) showed that non-infested oysters (*Crassostrea virginica*) had significantly greater gonad area compared to infested individuals. Our results concur with these studies, as scallops infested by *P. maculatus* showed significantly reduced GSI (Figure 1) and gonad weight. Based on these observations, we conclude that presence of *P. maculatus* in bay scallops is detrimental to individuals and this relationship should be classified as parasitic.

One of the most striking features of this research is the relatively low percentage of infested scallops (Table 1). With maximum values of 20% parasitism, this value is well below that seen for *Sanguinolaria acuta* (90% infestation, Soong 1997) and *M. edulis* (54–72%, Tablado and Lopez-Gappa 1995), but similar to infestation rates seen by O'Brein and Walker (1999) for *C. virginica* and Kruczynski (1973) for *A. irradians*. Perhaps this relates to the short life span of *A. irradians,* limiting potential infestation, or the numerical dominance of tulip mussels (*Modiolus americanus*) that are present in this system (Valentine and Heck 1993), which could provide *P. maculatus* with an alternate host (B. Peterson, pers. comm.). Another possibility is that the relative mobility of bay scallops may impede pinnotherids from successfully infesting scallops when switching hosts in the field (*sensu* Grove and Woodin 1996). Although Sastry and Menzel (1963) showed that adult *P. maculatus* were able to identify and infest *A. irradians* in experimental trials, *P. maculatus* showed no preference for *A. irradians* over pen shells (*Atrina rigida*). Consequently, they suggested that host proximity might be most important in determining host infestation in the natural environment (Sastry and Menzel 1963). Regardless, these relatively low infestation rates (Table 1) suggest that pinnotherid parasitism may play only a minimal role in affecting the bay scallop population in St. Joseph Bay, Florida.

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Lunar Periodicity and Bioluminescence of Swarming *Odontosyllis luminosa* (Polychaeta: Syllidae) in Belize

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LUNAR PERIODICITY AND BIOLUMINESCENCE OF SWARMING *ODONTOSYLLIS LUMINOSA* (POLYCHAETA: SYLLIDAE) IN BELIZE

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ABSTRACT Few benthic polychaetes have the notoriety of the bioluminescent "glowworm", *Odontosyllis luminosa* San Martin, 1990, that inhabits soft-sediment habitats of the Caribbean. A few nights after a full moon, apparently during most months of the year, a most unusual phenomenon occurs. Female glowworms leave the sediments, swim toward the water surface, and release a bioluminescent egg mass, causing a bright green glow near the water's surface. The female's luminescence attracts the males, which also glow briefly. The tiny worm has a bright glow, and viewing it is a favorite pasttime in the Caribbean. Over 50 years ago investigators linked the bioluminescence of *Odontosyllis* with the mysterious lights described by Christopher Columbus in November 1492. Reproduction of *O. luminosa* peaks during summer, when the water's surface is brilliantly lit with females for 10–15 min on the first few evenings following a full moon. Spent females apparently survive to spawn again. They return to the sediments to build new tubes after spawning.

INTRODUCTION

The tropical grassbeds of Belize are inhabited by a unique benthic polychaete, *Odontosyllis luminosa* San Martin, 1990 (Annelida: Syllidae), that periodically leaves the sediments to reproduce at the water's surface. This is the bioluminescent "glowworm", that inhabits soft-sediment habitats of the Caribbean. The species was described only recently (San Martin 1990), but its behavior is familiar to persons throughout tropical waters of the Western Hemisphere. During evenings following a full moon, apparently during most months of the year, these worms release a glowing mass near the water's surface. This glow is surprisingly bright, and is easily visible from 30–50 m away.

Over 50 years ago investigators linked the bioluminescence of *Odontosyllis* with the mysterious lights described by Christopher Columbus in November 1492 as his ship approached an anchorage site in Rum Cay, Bahamas (Crawshay 1935). Despite this long history, details of the reproductive biology of *O. luminosa* remained undescribed. Previous authors documented the ecology of *Odontosyllis enopla* in Bermuda (Goodrich 1933, Huntsman 1948, Markert et al. 1961, Wilkens and Wolken 1981, Fischer and Fischer 1995), and assumed that it was the species that Columbus saw in the Caribbean. The description of this new Caribbean species by San Martin makes it more likely that what Columbus saw that night from the *Santa Maria* was *O. luminosa*, not *O. enopla*.

The purpose of this study was to investigate the reproductive ecology of *O. luminosa*, and describe its behavior. We also compared our observations with previous studies of *Odontosyllis* congeners and proposed directions for future studies.

MATERIALS AND METHODS

The study was conducted near South Water Caye, Belize (16°48.5'N; 88°05'W), a 6.0-ha (15-acre) island located about 32 km (20 mi) SW of Dangriga and 1.6 km (1 mi) north of the Smithsonian's Caribbean Coral Reef Ecosystems research facility on Carrie Bow Caye. South Water Caye sits astride the Belize Barrier Reef and is bordered on the west by extensive turtlegrass beds (*Thalassia testudinum*) of the barrier reef lagoon and on the east by the coral forereef. South Water Caye supports a modest human population throughout the year, and the marine ecosystems surrounding the island remain nearly pristine.

Data for this study were collected primarily during the spring, summer, and fall of 1999, with additional observations made during May 1997, and March and May of 1998. A study area about 20 m by 30 m was established over the lagoon to water depths of 2–3 m adjacent to the International Zoological Expeditions (IZE) pier for evening observations. Habitats of this area were 70% turtlegrass and 30% bare sand (coarse sand; primarily derived from coralline algae, *Halimeda opuntia*). This allowed us to count the number of swarming worms in an established region, and determine the timing of spawning activity during the days following a full moon. We also recorded weather (wind speed, direction, cloud cover) and tidal conditions during swarming events.

Females and males were collected for laboratory observations during spawning episodes of May 1998, and February, March, and May 1999. Specimens were maintained in aquaria on South Water Caye. A stereomicroscope was set up to provide magnified viewing of tube-building behavior.

Observations that we made during spring of 1997 and 1998 established that most spawning occurred during the first days following the full moon, so we focused our observation efforts at those times. We began collecting data in late May 1999 on the night preceding the full moon, and continued nightly until the activity waned (Figures 1 and 2). Observations began at dusk, and lasted until no females were seen swarming that evening. We made instantaneous observations by counting the number of females observed in the area at a set time (5-min intervals beginning at sunset). It took about 1–2 min to tally the number of females swarming in the study area at a given time. Data were pooled in Figure 2 to illustrate the timing of swarming. Error bars are not provided, because all observations occurred at the same time of day and same location (non-random sampling).

We collected benthic samples from turtlegrass beds at the NW end of South Water Caye (water 1.0 m deep) to determine population density of *O. luminosa*. Specimens of benthos were washed free of sediments on a 0.5mm sieve. Sediments were generally coarse coralline-algae sand (as above). Benthic organisms were sorted under stereomicroscopy. Additional benthic samples were collected from coral rubble in the turtlegrass beds. Fish that preyed on swarming benthos were collected with a pole-mounted sweep net (1 mm mesh), and their gut contents were sorted and identified under stereomicroscopy.

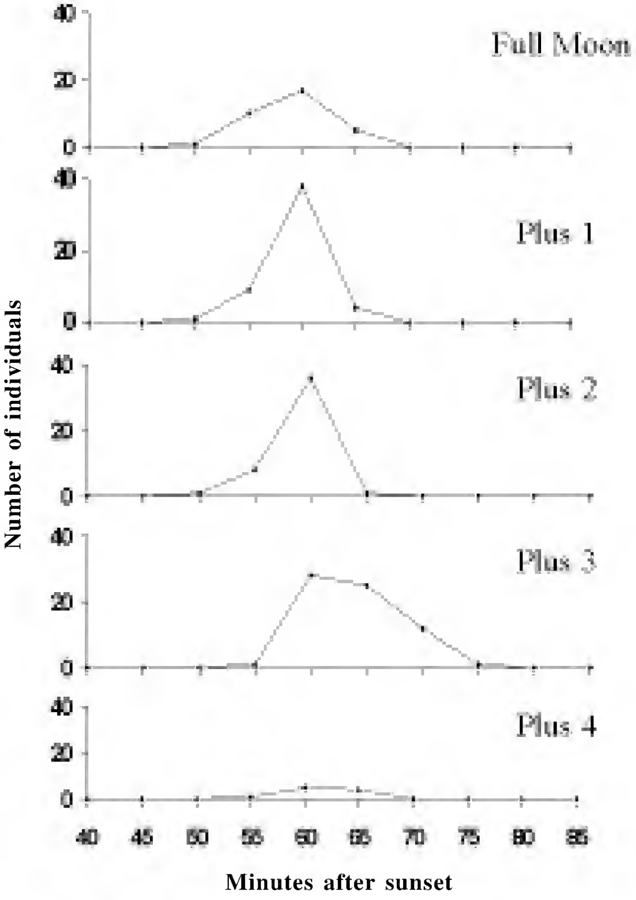

Figure 1. Numbers of female *Odontosyllis luminosa* observed luminescing in the study region (20- by 30-m area) near South Water Caye, Belize during the full moon and 4 nights that followed (30 May–3 June 1999). Data are instantaneous counts taken at 5-min intervals.

RESULTS

The greatest densities of spawning *Odontosyllis luminosa* during our 1999 study were observed on the first 3 evenings after the full moon (Figure 1). Timing of this reproductive activity was remarkably consistent from day to day, despite changes in weather conditions, tidal cycle, or current direction. For instance, cloud cover was less than 20% during the first 2 evenings of observation (Full Moon and Plus 1; Figure 1), but it was overcast with 80% cloud cover on the 3rd evening (Plus 2). As a result, it was dark much earlier on the 3rd night, yet the timing of reproductive activity remained similar. Winds were relatively calm during the first 2 evenings, and a falling tide carried the bioluminescing worms to the south. On the 3rd evening a 15-k wind blew from the NE and increased the surface currents carrying the worms southward. These differences in environmental conditions seemed to have no effect on timing of spawning activity, as evidenced by Figure 1. This consistency occurred despite the daily variance in tidal cycle (about 50 min per day).

The greatest reproductive activity of *O. luminosa* during our May–June 1999 study occurred at about 60 min after sunset (Figure 1). This timing of spawning activity is evident in Figure 2, which summarizes observations over the 5-day period. Females began bioluminescing at the surface at about 45–50 min after sunset, and peaked in activity at about 60 min; few were still spawning by 70–75 min. We noted that the peak of activity on days 1–2 after a full moon was actually at 58 min after sunset, when up to 55 females were observed in the study area, but that pattern is not reflected in the illustration since we recorded on 5-min intervals.

Specimens were observed swarming over grassbeds in various water depths, from less than 0.1 m deep near

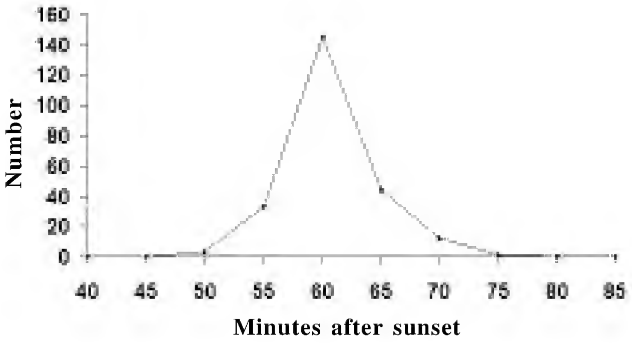

Figure 2. Total number of female *Odontosyllis luminosa* observed luminescing in the study region (20- by 30-m area) near South Water Caye, Belize, over a 5-day period. These are instantaneous counts taken at 5-min intervals beginning 40 min after sunset.

the shore to 6 m deep in the channel between South Water Caye and Carrie Bow Caye. Most activity occurred in the lagoon (where the most turtlegrass is located), but a few specimens were seen bioluminescing over the forereef on the east side of the island as well.

The reproductive behavior of *O. luminosa* was easily observed from piers and boats. Female *O. luminosa* left the bottom and drifted slowly on surface currents (within 1–2 cm of the water surface) where they periodically began luminescing. Several female specimens that we collected when they first began luminescing were full of oocytes, indicating that luminescence can occur without shedding of gametes. Specimens observed under stereomicroscopy confirmed this. Apparently both the oocytes and the bioluminescent material are released from the gonopores along the abdomen.

Males could be seen flashing a pattern of luminescence on turtlegrass blades below the females, apparently in response to glowing of the females. Males left the bottom, flashing bioluminescence as they swam rapidly toward the surface to join the females. This pattern was evident in deep water of the channel, where males swam for 5–6 m in a few seconds flashing as they went. Male *O. luminosa* (mean length, 12 mm) were generally smaller than females (mean length, 20 mm).

Once the males joined the females at the water's surface, females began quivering rapidly and periodically spinning in circles, while releasing a luminescent mass and (presumably) gametes. Males swam rapidly around the females bioluminescing and releasing their gametes. Sometimes several males encircled a single female. Each luminescent episode lasted for 45–65 sec, but some female worms repeated the episodes numerous times as they drifted near the surface. Generally, once males were attracted, the spawning of a female lasted just 2–3 min. Some females apparently were not successful in attracting males and did not undergo the oocyte-releasing behavior. Rather, they continued to periodically emit their bioluminescent mass while drifting at the surface.

A few female *O. luminosa* were observed luminescing at the water's surface following full moons during nearly every month of observation, but the greatest reproductive activity occurred during summer months (June–August). Activity increased during full moons of early spring (February and March), and counts of luminescing females numbered 2–3 per 5-min record in the observation area. Similarly low counts occurred during fall months of 1998 and 1999. Reproductive activity increased to a maximum of about 40 females bioluminescing per record during June (Figure 1; 1 female per 15 m^2). Apparently there were more *O. luminosa* spawning during July than June 1999, but an overgrowth of green algae (*Ulva rigida*) near the pier limited our observation. Although most activity occurred on evenings immediately after the full moon, a few females were seen during the first hour after sunset almost every night during May and June of 1999.

Specimens maintained in aquaria after spawning settled to the sediments to establish mucous tubes. These specimens were intact after spawning and their gametes were completely spent, characteristic of polytelic polychaetes that survive spawning events (Clark 1979). A few specimens autotomized during handling, but none of the whole specimens that we put into aquaria ruptured their body walls, even though some continued to release gametes after collection. Oocytes were observed on the bottom of the aquaria by morning, indicating that they were negatively buoyant.

The swarming *O. luminosa* were joined in the water column by other swarming benthic taxa, including amphipods, isopods, tanaids, and other species of polychaetes (nereidids, opheliids, and spionids). Several species of fish preyed on benthos as they swarmed in the water column. The most notable predatory fish was *Atherinomorus stipes*, a silverside (Atherinidae) that is common in turtlegrass beds (B. Chernoff, pers. Comm., Field Museum of Natural History, Chicago). The fishes indiscriminately fed on many of the swarming taxa as we watched and appeared to ingest *O. luminosa*. Several of the silversides began having spasms and suffered paralysis, apparently after feeding on *O. luminosa*. We collected some of these paralyzed silversides to confirm our observations, but all of them had empty guts. Apparently the fish regurgitated their ingested prey during spasms.

Odontosyllis luminosa were collected in benthic sediment samples from sandy sediments of turtlegrass beds during March 1999. Only 3 specimens were collected (density = about 1–3 m^{-2}). All 3 specimens inhabited sediments around the roots of turtlegrass short shoots, and none of those collected was sexually mature.

DISCUSSION

Odontosyllis luminosa spawning occurs during the early evenings immediately following the full moon. Activity peaks 55–60 min after sunset, notably a time when the moon is still low or beneath the horizon; thus, the water is very dark except for bioluminescence. Twilight is also a time of reduced predation pressure in the plankton (Alldredge and King 1985). The peak reproductive activity that we observed did not vary with weather conditions, nor did it match particular tidal cycles, as suggested for *O. enopla* in Bermuda (Galloway and Welsh 1911).

Summer months are the height of reproduction for *O. luminosa* in Belize. Even though not apparent during our June 1999 study, the greatest reproductive activity may occur during a mid-summer full moon. Our primary observations occurred during early summer, and local residents of South Water Caye reported that activity usually peaks the third night after the full moon in mid-summer. Our data indicated an extended period of activity on the third day (spawning lasted longer), but the number of females spawning at that time did not exceed the earlier 2 days.

Previous studies of *Odontosyllis* documented a similar pattern of reproduction on lunar cycles. The Bermuda "fireworm", *O. enopla*, reached its swarming peak 3 days after the full moon, and exhibited behaviors much like we observed (Markert et al. 1961). Females luminesced to attract males, which also luminesced. The swarming activity of *O. enopla* in Bermuda peaked at 56 min after sunset and nearly disappeared by 60 min. The entire display of *O. enopla* lasted only 15 min (Markert et al. 1961). *Odontosyllis luminosa* we observed began displaying about the same time as *O. enopla* (45–50 min), and the activity on any particular night ended within about 15 min. The cumulative data provided on Figure 2 shows that the majority of activity over a 5-day period was limited to 50–70 min after sunset.

Several authors provided reviews of the luminescence and lunar periodicity of *O. enopla* (Galloway and Welsh 1911, Goodrich 1933, Crawshay 1935, Huntsman 1948, Markert et al. 1961, Fischer and Fischer 1995) and its anatomy and physiology (Wilkens and Wolken 1981, Wolken and Florida 1984). Several other species of *Odontosyllis* are known to luminesce: *Odontosyllis hyalina* in Indonesia (Lummel 1932), *O. polycera* in New Zealand (Daly 1975), *O. undecimdonta* in Japan (Inoue et al. 1990, 1993, Tanino et al. 1996); and *O. phosphorea* in British Columbia (Potts 1913, Fraser 1915, Berkeley 1935). Eggs of *O. polycera* reportedly were negatively buoyant, as we observed for *O. luminosa*. Potts (1913) reported that males and females of *O. phosphorea* gathered at the water's surface, but males were not attracted by females as occurred with *O. luminosa* and *O. enopla*. Further, the swarming by *O. phosphorea* began before sunset and occurred during many months of the year (Berkeley 1935).

There are several dozen species of *Odontosyllis* described, but little is known about the reproductive biology or production of luminescence by most of them. Russell (1989) collected and described a new species, *O. twincayensis*, from Twin Cayes, Belize just a mile from our study site at South Water Caye. The short compound setae of *O. luminosa* distinguish them from *O. twincayensis*, and it is not known if the latter luminesces. *Odontosyllis fulgurans* and *O. detecta* are widely distributed and are known to occur in the Caribbean, but have different setae than *O. luminosa* (San Martin 1990). No other species of *Odontosyllis* are known from the region.

Crawshay (1935) compared *O. enopla* with an undescribed species that he observed in British Honduras (now Belize). The Belize species was possibly *O. luminosa*. He reported that the 2 species were "structurally similar, if not identical", but the Belize species began its reproduction "long after darkness had closed in". He observed the Belize species bioluminescing until 8:30 PM (about 2 hours after sunset). His other descriptions lacked detail, except to say that the episode of illumination by a female lasted just 5–10 min, and that the swarming might occur on successive nights, "but more usually will not recur until the same phase of a subsequent lunation". He reported that the swarming did not occur in all months (of 1921 and 1923), but was noted in January, April, May, July, October, and December. There is no way to determine for certain if Crayshaw was describing *O. luminosa*. What is certain is that its reproductive biology differed considerably from that of our observations.

There is much yet to learn about *O. luminosa*. We know little about the mechanism of its bioluminescence and almost nothing about its prespawning and postspawning behavior. It somehow maintains reproductive synchrony despite changing weather conditions, and we suspect that it avoids predation by chemical defense. This is a simple organism with a very complex reproductive ecology. It has been over 500 years since Columbus first saw this species bioluminescing in the waters of the Caribbean, yet we know little about details of its behavior. Most of its secrets remain to be explored.

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