BULLETIN OF MARINE SCIENCE, 50(1): 117-132, 1992

PARASITIZATION OF *LOXOTHYLACUS TEXANUS* ON *CALLINECTES SAPIDUS*: ASPECTS OF POPULATION BIOLOGY AND EFFECTS ON HOST MORPHOLOGY

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ABSTRACT

Loxothylacus texanus is a sacculinid rhizocephalan barnacle that parasitizes the blue crab, *Callinectes sapidus.* We collected blue crabs carrying mature *L. texanus* externae from throughout Florida nearshore Gulf of Mexico waters to (1) describe seasonal and geographic variations in *L. texanus* infection, (2) document the relationship of seasonal variation in relative abundance of parasitized crabs to that of ovigerous female crabs, and (3) evaluate the morphology of parasitized crabs compared to that of normal crabs. Overall, the proportion of blue crabs carrying mature parasite externae was low in Florida waters, particularly off southwest Florida. However, the relative abundance of these crabs varied markedly on local and regional scales. Relative abundance of crabs carrying externae was not correlated with salinity or temperature but, on a local scale, temperature was related to the proportion of crabs carrying externae; parasitized crabs were more common in water of 21–25°C. Significant seasonal increases in the relative abundance of crabs carrying mature externae temporally followed similar increases in the relative abundance of ovigerous female crabs by 4–5 months, suggesting that the life cycle of *L. texanus* is coordinated with that of *C. sapidus* such that infective female cyprids are abundant during the time that the probability of successfully infecting juvenile crabs is high. Parasitized blue crabs were, on the average, smaller than normal crabs, but the mean size of infected crabs in Florida waters was larger than elsewhere in the Gulf of Mexico. Abdominal width in both male and female crabs carrying externae was significantly wider than that of normal females, suggesting that the morphological changes induced by the parasite are more complex than simply the development of female characteristics in males.

Rhizocephalan barnacles, cirriped crustaceans that have evolved highly modified body forms to accommodate their complex life histories, parasitize decapod crustaceans. *Loxothylacus texanus,* a rhizocephalan parasite of the blue crab *Callinectes sapidus,* ranges throughout the Gulf of Mexico and Biscayne Bay, Florida (Gunter, 1950; Daugherty, 1952; Christmas, 1969; More, 1969; Park, 1969; Adkins, 1972; Ragan and Matherne, 1974; Perry, 1975; Perry and Herring, 1976; Overstreet, 1978; Perry and Stuck, 1982; Steele, 1982; Overstreet et al., 1983). In localized areas, the proportion of a blue crab population exhibiting evidence of infection by *L. texanus* can be high during certain months (Christmas, 1969; Ragan and Matherne, 1974), making the parasite a potentially important factor impacting local blue crab populations. However, virtually nothing is known of the relationship of the life cycle of *L. texanus* to that of *C. sapidus* or of the effects of this parasite on its host.

Reinhard (1950) suggested that the life cycle of *L. texanus* infecting *C. sapidus* is similar to that of *Sacculina carcini,* a well-studied related species exhibiting a life history typical of most kentrogonid rhizocephalans (Veillet, 1945; Yanagimachi, 1961; Ritchie and Høeg, 1981; Lützen, 1984; Høeg, 1990). In sacculinid barnacles, only female cyprid larvae, disproportionately produced from midsummer to fall or winter in a number of genera (e.g., *Sacculina, Lernaeodiscus*), are infective to the host; they invade by injecting a mass of primordial cells into the crab. The primordium develops into the interna which ultimately produces a virgin externa that emerges between the first and second abdominal sternites of the host and enlarges upon fertilization to effectively resemble a brachyuran egg mass in form and location. The mature externa typically persists for a year or more and frequently remains attached throughout the remainder of the life span of the crab. Both male and female crabs can become infected; the net effect of parasitization is the permanent transformation of the crab into a living chamber for the parasite. Infected crabs produce only parasite larvae, via the parasite externa.

The presence of the mature externa is an obvious visible manifestation of parasitization by sacculinids and, because it is the reproductive stage, a viable measure of the prevalence of the parasite. Moreover, because the interna stage of *L. texanus* is not visible without microscopic examination, it is the only feasible measure of the level of parasitization for population studies. Previously, studies of the life-cycle relationships of *L. texanus* and *C. sapidus* have been limited to general reports of the local relative abundance of crabs carrying externae (Christmas, 1969; Adkins, 1972; Ragan and Matherne, 1974). We here describe the temporal and spatial variation in relative abundance of blue crabs carrying externae throughout the Gulf of Mexico coastal waters off Florida in relation to that of the remainder of the Gulf. In addition, we postulate that an observed temporal relationship between the relative abundance of parasitized crabs and proportion of ovigerous females in the population is indicative of a life-cycle relationship between parasite and host. Finally, we identify external morphological changes in the host associated with parasitization and speculate upon factors that may influence an observed regional variation in size of parasitized crabs and the changes in body proportions induced by parasitization. Our study provides the first detailed information on the population biology of *L. texanus* and of the effects of this parasite on its host.

Methods

Field Sampling.—To investigate the population biology of *Loxothylacus texanus* infecting blue crabs, we examined blue crabs collected by trapping (galvanized chicken-wire blue crab traps [61 cm × 61 cm × 61 cm] baited with mullet or menhaden) at 20 stations (Table 1) distributed among five locations in the Gulf of Mexico off Florida (Fig. 1). Sampling intervals ranged 1–15 days; however, 96% ranged 4–10 days. During each sampling period, the number of crabs per trap, salinity, and water temperature were recorded at each station. Data recorded for each crab included presence or absence of an externa, sex, presence or absence of eggs (females only), and long carapace width (mm LCW; measured across the widest dimension of the carapace, including posteriolateral spines).

To compare the external morphology of normal and parasitized crabs, 179 crabs carrying externae (male : female = 1.0:1.0) and 153 normal crabs (male : mature female : immature female = 1.2:0.9:0.9) of approximately equal size distributions were collected from traps deployed in Tampa Bay and Charlotte Harbor. Data recorded for each crab included sex, claw type (crusher, pincer), and, measured to the nearest millimeter, LCW, short carapace width (SCW; measured at the base of the posteriolateral spines), carapace length (CL; measured from the notch between the eyes to the junction of the cephalothorax and abdomen), claw propodus length (PL; measured from tip of the fixed finger to the articulation of propodus and carpus), and width of the abdomen (FASW; measured at the suture line between fifth and sixth abdominal segments).

Data Analysis.—We defined blue crabs carrying mature *L. texanus* externae as parasitized and all other crabs as normal, recognizing that the category "normal" included some undetected parasitized crabs. However, because the individuals of interest to us were crabs with mature externae and because limiting the classification of parasitized crabs to those carrying mature *L. texanus* externae did not seem to obscure our results, we reasoned that the percentage of misclassified parasitized crabs included in our normal category probably was not statistically problematic.

In our study, length of sampling interval was not correlated with the number of crabs captured per trap (Hochberg, 1988); therefore, relative abundance was defined as number of crabs per trap per sampling interval. Temporal and spatial variations in the incidence of parasitized individuals were evaluated using both the proportion and relative abundance of crabs carrying externae. We assumed that the relative size frequency, sex ratio, reproductive condition, and proportion of normal and of

Table 1. Sampling periods and physical characteristics of stations sampled for *Callinectes sapidus* weekly at five locations along the west coast of Florida. Sta: station; AB: Apalachee Bay; TB: Tampa Bay; CH: Charlotte Harbor; EV: Everglades; CS–FB: Cape Sable–Florida Bay. See Figure 1 for station locations. Sample sizes for calculations of mean salinities and temperatures ranged 44–52

Location station	Sampling period	Salinity (‰) $\bar{x}$	Salinity (‰) Range	Temp (°C) $\bar{x}$	Temp (°C) Range	Depth (m)	Bottom type
AB	1/84–12/84	22	6–30	22	12–33		
Sta1		22	10–30	22	12–33	3.0	grass and mud
Sta2		22	6–30	22	12–30	3.0	grass and mud
Sta3		22	6–30	22	12–31	3.0	grass and mud
TB	11/82–10/83	25	12–33	24	13–33		
Sta4		19	15–26	23	13–31	3.0	grass and sand
Sta5		20	12–26	24	14–33	2.5	sand/shell and grass
Sta6		23	17–30	24	15–32	3.0	sand/shell and grass
Sta7		28	24–31	24	14–33	2.5	sand/shell and grass
Sta8		29	25–33	24	15–32	3.0	sand/shell
Sta9		29	25–33	24	14–33	2.5	sand/shell and grass
CH	2/84–1/85	31	15–36	25	14–31		
Sta10		30	15–36	25	14–31	2.0	dense grass and mud
Sta11		31	25–36	25	14–31	2.0	dense grass and mud
Sta12		31	25–36	25	14–31	3.0	dense grass and mud
EV	2/84–1/85	28	8–38	25	14–33		
Sta13		27	8–38	25	14–32	3.5	sand, grass and mud
Sta14		29	16–37	25	14–33	3.0	sand and grass
Sta15		28	10–38	26	15–33	2.0	grass and mud
CS–FB	1/84–12/84	32	4–40	25	17–31		
Sta16		33	27–38	25	17–30	1.5	patchy grass and mud
Sta17		35	28–40	26	17–31	1.5	patchy grass and mud
Sta18		30	21–35	25	18–31	1.5	sand and patchy grass
Sta19		31	21–34	25	18–29	1.5	sand and patchy grass
Sta20		30	4–32	25	18–30	1.5	sand and patchy grass

parasitized crabs in our samples were representative of those in the natural population over the sampling interval. Following Sokal and Rohlf (1981), we used the R × C *G*-test of independence and simultaneous test procedure for frequencies (STP) in tests for significant spatial differences in the percentages of parasitized crabs among locations and among stations within each location. At Apalachee Bay, Tampa Bay, and Charlotte Harbor, where numbers of infected individuals were sufficient for more detailed analysis, temporal variation in the incidence of parasitized crabs was evaluated using the R × C *G*-test on percentages, and analysis of variance (ANOVA) and the Student-Newman-Keuls ranked mean separation test (S-N-K) on relative abundances, of parasitized crabs.

We evaluated the relationship of temperature and salinity to the incidence of parasitized crabs using the nonparametric log-linear model (3-way *G*-test [Sokal and Rohlf, 1981]) on proportions, and Kendall's correlation coefficient (tau, calculated separately for T and S) on relative abundances, of crabs from three combinations of locations: (1) all locations, (2) Apalachee Bay, Tampa Bay, and Charlotte Harbor, and (3) Tampa Bay alone. For the 3-way *G*-tests, blue crabs were classified according to the salinity or temperature of the water at the time of collection and grouped using 5‰ or 5°C increments as classes; tau values were calculated using the data from each station at each sampling interval. In addition to the above tests, significant differences among stations in mean annual salinity (identified using ANOVA and S-N-K) and in annual proportion of parasitized crabs (identified using R × C *G*-test and STP) at Tampa Bay were compared.

We searched for a temporal relationship between the relative abundance of ovigerous female crabs and of parasitized crabs at Apalachee Bay, Tampa Bay, and Charlotte Harbor using Kendall's tau (for correlations) and the Kruskal-Wallis test followed by the nonparametric multiple comparisons test (for associations) (Sokal and Rohlf, 1981). We compared mean size of parasitized crabs to that of normal crabs within each of these locations using the *t*-test and compared mean size of parasitized crabs, and of normal crabs, among locations using ANOVA and S-N-K.

Using regression analysis, the effects of parasitization on selected components of morphology were assessed by comparing LCW versus CL, SCW versus CL, crusher PL versus pincer PL, LCW versus

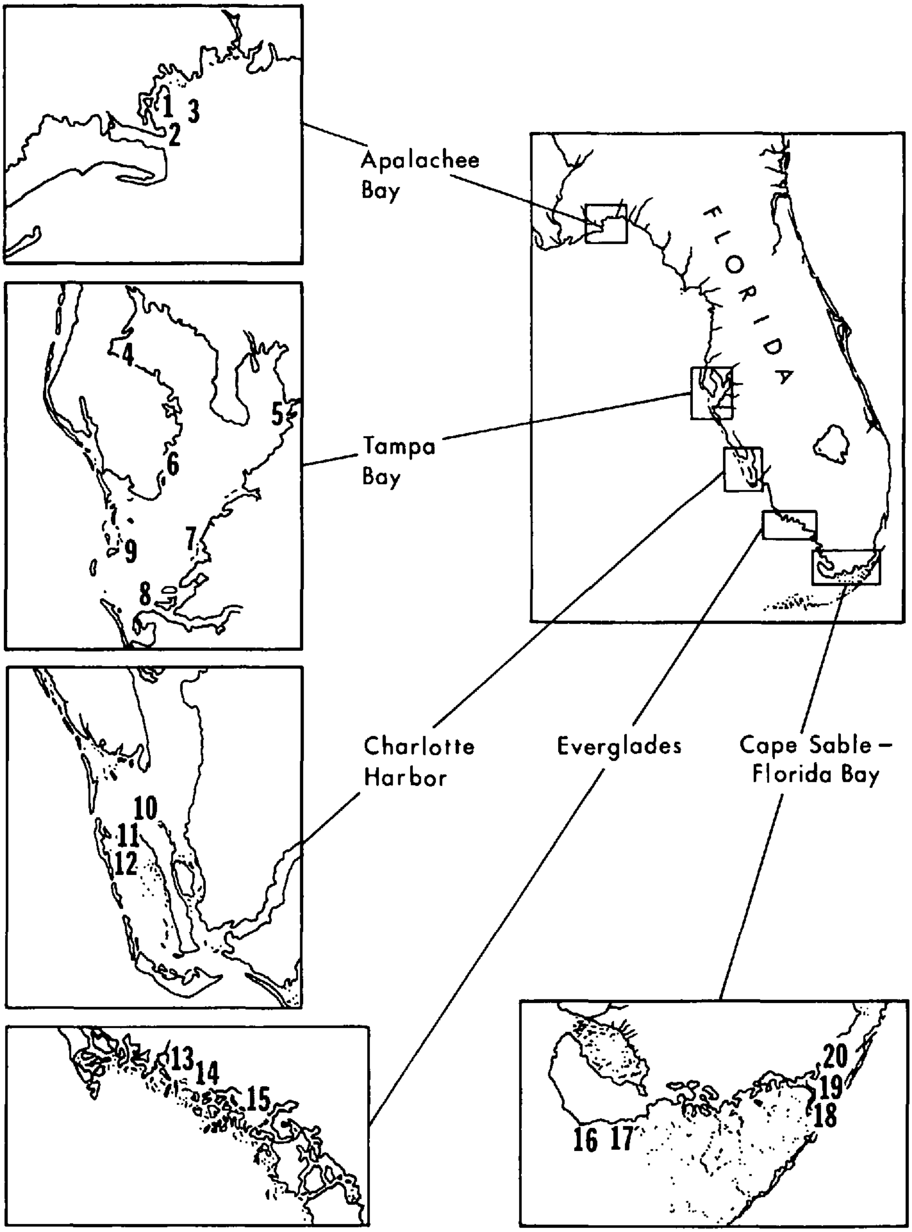

Figure 1. Locations and stations (numbered) in the nearshore Gulf of Mexico waters off Florida sampled for blue crabs (*Callinectes sapidus*) carrying externae of the parasitic sacculinid barnacle *Loxothylacus texanus.*

FASW, SCW versus FASW, CL versus FASW, and LCW versus PL and SCW versus PL of both crusher and pincer claws. For these analyses, the crabs were divided into five categories: parasitized males, parasitized females, normal males, normal sexually mature females, normal sexually immature females. All categories were included in all comparisons except LCW and SCW versus claw PL, where normal immature females were omitted. Significant differences between the slopes and elevations of the resulting regression lines for all morphological comparisons were determined using analysis of covariance.

Results

Distribution and Relative Abundance of Parasitized Crabs.—Total annual proportions of blue crabs carrying mature *L. texanus* externae were very low throughout our sampling area, but the relative percentages of infected crabs differed significantly ($P < 0.001$) among locations and were approximately 10 times higher in west-central and northwest Florida than in southwest Florida (Table 2). Blue crabs carrying externae were notably rare in southwest Florida; only 23 of the 16,282 crabs captured there carried externae. Within locations, the proportions of parasitized crabs varied little among stations except at Tampa Bay, where annual percentages of parasitized crabs ranged from extremely low (0.2% at Station 5) to the highest proportion recorded at any station (5.1% at Station 8). At Apalachee Bay, Tampa Bay, and Charlotte Harbor, both the percentages and relative abundances of parasitized crabs increased significantly ($P < 0.05$) during late summer and early fall (August–October) and increased again, but to a lesser degree, at some time during the cooler months of the year (Table 2; Fig. 2).

Neither temperature nor salinity were correlated with percentage of parasitized crabs in any of our analyses. The only effect detected was a 2-factor interaction between temperature and the percentage of crabs carrying externae at Tampa Bay; there, the G-value for the effect of temperature on parasitization was significant but the G-value for goodness-of-fit to the model was not significant. Freeman-Tukey deviates (Table 3A) and orthogonal comparisons of temperature categories (Table 3B) showed that the percentage of parasitized crabs was significantly higher in the 21–25°C class than in other temperature classes. Although the percentages of parasitized crabs were generally higher at stations with higher salinities at Tampa Bay (Table 3C), no definitive relationship between salinity and the presence of parasite externae existed.

Relationship of Host Biological and Morphological Characteristics to Parasitization.—The relative abundances of both infected individuals and ovigerous females were temporally bimodal at each location analyzed (Fig. 2), but seasonal increases in abundance of ovigerous females were neither coincident with, nor correlated to, seasonal increases in relative abundance of parasitized crabs. However, both the well-defined primary (spring) and less clearly defined secondary (late summer–fall) increases in relative abundance of ovigerous females were succeeded approximately 4–5 months later by respective, similar primary and secondary increases in relative abundance of crabs carrying mature externae.

Mean sizes of parasitized blue crabs were significantly smaller ($P < 0.001$) than those of their normal conspecifics at the locations tested (Fig. 3). The observed differences in size may have been somewhat exaggerated due to the differential ability of commercial blue crab traps to retain smaller (<127 mm LCW) parasitized crabs versus normal crabs (R.J.H., pers. observ.). However, we collected no parasitized crabs greater than 170 mm LCW, whereas approximately 7% of the normal crabs we collected were 170 mm LCW or greater, supporting the idea that blue crabs carrying *L. texanus* externae are, on the average, smaller than normal crabs. Mean size of parasitized crabs was significantly smaller ($P < 0.001$) at Apalachee Bay (Fig. 3) compared to other locations examined. Mean size of normal crabs differed significantly ($P < 0.001$) among each of the three locations; however with sample sizes as large as ours, extremely small departures from identity are deemed significant by statistical analyses.

Of the allometric relationships examined for differences among our five categories of crabs, the relationships of SCW to FASW (Fig. 4) and SCW to crusher PL (Fig. 5) showed significant differences associated with parasitization. For each

Table 2. Monthly values for sample size, proportion of *Callinectes sapidus* carrying *Loxothylacus texanus* externae (Pcrabs), and average water temperature (°C) at five locations in the nearshore Gulf of Mexico waters of Florida. Asterisks denote months constituting a homogeneous group having significantly higher proportions of Pcrabs within each location. Numbers in parentheses show ranges of the percentages of Pcrabs found among stations within each location

	Month												
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Apalachee Bay													
No. traps	180	178	225	179	177	190	177	220	178	179	227	180	2,290
Total No. crabs	317	766	1,131	843	1,033	1,201	1,409	876	269	65	565	469	8,944
No. Pcrabs	14	19	15	9	7	12	6	64	12	12	10	22	202
% Pcrabs	4.4	2.5	1.3	1.1	0.7	1.0	0.4	7.3*	4.5	18.5*	1.6	4.7	2.3 (1.8–2.5)
Mean water temp.	12.6	15.2	18.0	20.5	27.8	27.5	28.3	29.5	26.8	25.2	18.1	17.3	
Tampa Bay													
No. traps	358	357	434	358	376	415	350	445	344	358	408	360	4,563
Total No. crabs	1,237	1,422	1,884	1,653	1,888	1,760	1,728	1,592	925	951	885	853	16,778
No. Pcrabs	5	8	24	7	26	6	7	17	54	31	20	5	210
% Pcrabs	0.4	0.6	1.3	0.4	1.4	0.3	0.4	1.1	5.8*	3.3	2.3	0.6	1.3 (0.2–5.1)
Mean water temp.	16.4	16.4	18.7	21.5	25.5	29.1	30.8	30.7	28.8	26.5	22.7	19.9	
Charlotte Harbor													
No. traps	226	180	174	214	174	149	207	175	158	221	175	181	2,234
Total No. crabs	6	839	582	657	764	454	624	598	298	63	26	43	4,954
No. Pcrabs	2	27	16	9	5	3	18	44	23	4	1	2	154
% Pcrabs	33.3*	3.2	2.7	1.4	0.7	0.7	2.9	7.4*	7.7*	6.3	3.8	4.7	3.1 (2.2–3.5)
Mean water temp.	17.2	18.8	20.0	23.5	27.2	27.4	29.2	29.8	28.5	24.1	20.2	22.1	

Table 2. Continued

	Month												Total
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	
Everglades													
No. traps	220	127	216	136	223	177	210	150	186	156	158	158	2,177
Total No. crabs	701	484	460	430	399	470	827	655	357	374	845	400	6,402
No. Pcrabs	0	1	0	0	2	1	1	0	1	0	1	0	7
% Pcrabs	0.0	0.2	0.0	0.0	0.5	0.2	0.1	0.0	0.3	0.0	0.1	0.0	0.1 (0.0–0.2)
Mean water temp.	22.5	20.7	21.2	24.4	27.4	28.4	29.3	32.2	27.1	26.2	23.0	23.5	
Cape Sable–Florida Bay													
No. traps	224	279	263	285	285	266	318	262	282	291	291	285	3,331
Total No. crabs	893	1,450	1,253	1,021	673	553	644	600	809	535	518	930	9,879
No. Pcrabs	1	3	2	3	2	1	1	1	0	1	1	0	16
% Pcrabs	0.1	0.2	0.2	0.3	0.3	0.2	0.2	0.2	0.0	0.2	0.2	0.0	0.2 (0.1–0.4)
Mean water temp.	21.2	22.4	24.3	26.5	28.5	27.3	28.1	29.7	27.3	25.7	22.1	22.6	

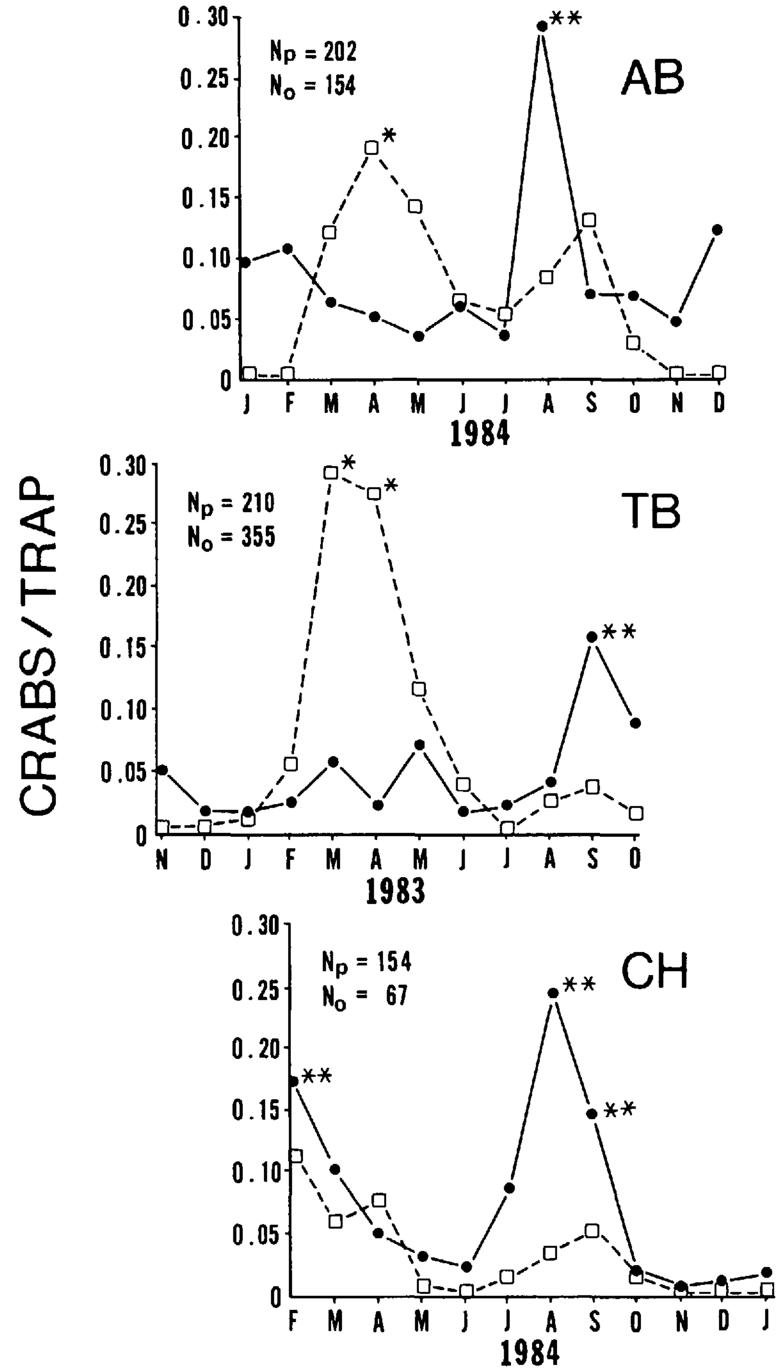

Figure 2. Temporal variation in relative abundance (mean number of crabs per trap per sampling interval) of female *Callinectes sapidus* carrying *Loxothylacus texanus* externae (solid lines) and of ovigerous female *C. sapidus* (dashed lines) at three locations in nearshore Gulf of Mexico waters off Florida. Asterisks denote months during which the relative abundances of ovigerous crabs (*) and of crabs carrying externae (**) formed statistically homogeneous groups ($P < 0.05$) with relatively higher abundances within each sampling location. N_o: number of ovigerous females; N_p: number of parasitized blue crabs.

Table 3. Relationship of the percentage of *Callinectes sapidus* carrying *Loxothylacus texanus* externae (P) to temperature (T) in Tampa Bay, Florida. T classes: 1: 11–15°C; 2: 16–20°C; 3: 21–25°C; 4: 26–30°C; 5: 31–35°C. Salinity (S) classes: 3: 16–20‰; 4: 21–25‰; 5: 26–30‰; 6: 31–35‰. A. Freeman-Tukey deviates showing pattern of deviation from the log-linear model of the effects of T on P. Significant deviates (marked by asterisk) indicate that significantly fewer (negative values), or more (positive values), individuals than expected occurred in a T-S class. N: not parasitized. B. Orthogonal comparisons of the relationship of T to P. Significant values between categories (groups of T classes) indicate that the effect of T on P differed between categories. C. Relationship of P to station and S. Single asterisks denote stations that formed a statistically homogeneous group ($P < 0.05$) with significantly higher mean annual salinities. Double asterisk denotes the station at which a significantly higher percentage ($P < 0.001$) of blue crabs carried parasite externae. See Figure 1 for station locations

A

T Class	S Class	Expected values P	Expected values N	Freeman-Tukey deviates P	Freeman-Tukey deviates N
1	5	3.81	62.19	−0.884*	0.258
2	3	3.62	88.38	−0.788*	0.198
2	4	5.67	179.33	−0.630*	0.143
2	5	38.66	630.34	−1.074*	0.274
2	6	1.53	30.47	−0.254	0.139
3	3	1.61	39.39	3.571*	−1.367*
3	4	3.77	119.23	1.464*	−0.274
3	5	27.51	448.49	1.710*	−0.438
3	6	4.86	93.32	0.655*	−0.111
4	3	35.64	869.36	−0.066	0.030
4	4	16.68	527.32	0.825*	−0.134
4	5	31.72	517.28	0.267	−0.045
4	6	8.21	133.79	−0.722*	0.211
5	3	12.13	295.87	−1.942*	0.369
5	4	9.87	312.13	−1.677*	0.288
5	5	6.30	102.70	−0.883*	0.250

B

T categories	G-value	Probability
1 + 2 + 5 vs. 4	9.386	0.097
3 vs. 4	22.697	<0.001
1 + 2 + 5 vs. 3	37.759	<0.001
1 + 2 + 4 + 5 vs. 3	30.749	<0.001

C

Station	Mean annual salinity (‰) $\bar{x}$	Mean annual salinity (‰) Range	Tot. traps (No.)	Tot. crabs (No.)	Proportion Pcrabs
4	19	15–26	784	3,490	1.4
5	20	12–26	770	3,759	0.2
6	23	17–30	750	4,091	0.3
7*	28	24–31	755	2,066	1.9
8*	29	25–33	760	1,500	5.1**
9*	29	25–33	744	1,872	1.2

category, the regression for SCW versus FASW was significant ($P < 0.001$), and the slopes and elevations of all regressions were significantly different ($P < 0.05$) from each other. In relation to carapace width, the average abdominal width of parasitized crabs of each sex was wider than that of normal females. The regression of SCW versus crusher claw PL also was significant ($P < 0.001$) for each category of crabs analyzed. The allometric proportions of crusher claw PL and SCW for visibly parasitized females, normal females, and parasitized males were not dis-

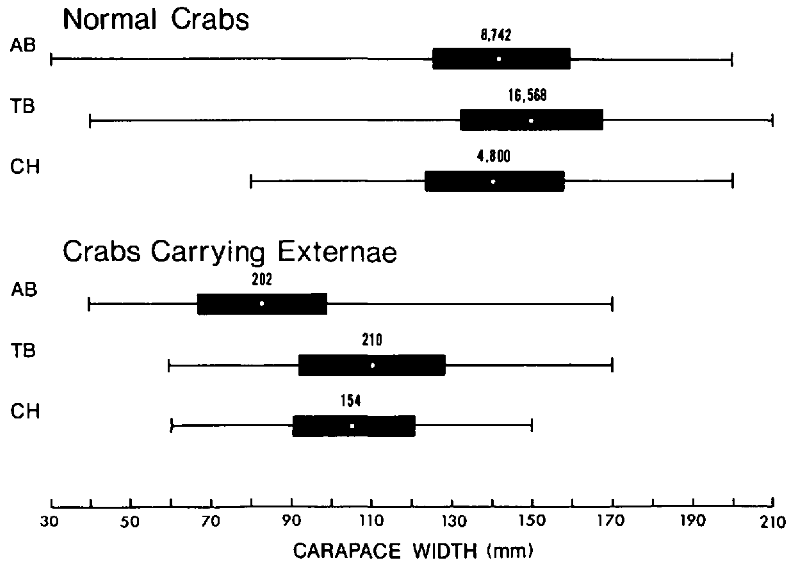

Figure 3. Size distribution of *Callinectes sapidus* carrying *Loxothylacus texanus* externae and of normal *C. sapidus* at three locations along the west coast of Florida. Bars show standard deviation; horizontal lines show range; numbers above bars are sample sizes. Mean sizes (mm long carapace width): Apalachee Bay (AB) normal crabs ($\bar{x}_n$): 142.6, crabs carrying externae ($\bar{x}_p$): 83.1; Tampa Bay (TB) $\bar{x}_n$: 150.1, $\bar{x}_p$: 110.5; Charlotte Harbor (CH) $\bar{x}_n$: 140.5, $\bar{x}_p$: 105.5.

tinguishable but both the slope and elevation of the regression for normal males were significantly different ($P < 0.05$) from those of the other three categories.

Discussion

Parasite Distribution and Relative Abundance.—*Loxothylacus texanus* parasitizes *Callinectes sapidus* throughout the Gulf of Mexico. In Florida waters, the annual average proportion of crabs carrying *L. texanus* externae varies widely around a mean of 1.5%. Generally, the annual average percentage of parasitized crabs in Florida waters is comparable to that reported for Texas waters (Gunter, 1950; More, 1969) but less than that reported for Louisiana and Mississippi estuaries (Ragan and Matherne, 1974; Perry and Stuck, 1982; Perry et al., 1984). Throughout the Gulf, the percentage of parasitized crabs can fluctuate sporadically or seasonally (Daugherty, 1952; More, 1969; Adkins, 1972; Overstreet, 1978; present study). In Florida, the proportion of crabs carrying externae can exceed 10%, principally during late summer and early fall. Clearly, the incidence of blue crabs carrying *L. texanus* externae varies temporally and spatially on both macrogeographic and microgeographic scales in the Gulf of Mexico. Nevertheless, the pattern of geographic variation seems to be that the parasite is more common in the northern Gulf and that relative abundance decreases with movement southward, particularly in Florida waters.

The uniformly low numbers of parasitized crabs captured at all stations in our southwest Florida locations (Everglades, Cape Sable–Florida Bay) support the idea that the number of crabs carrying mature externae is indeed low in southwest Florida. The near absence of crabs with externae in that region may be the consequence of environmental conditions, a combination of biological and environmental factors, or more likely, geographic location. Population densities are usu-

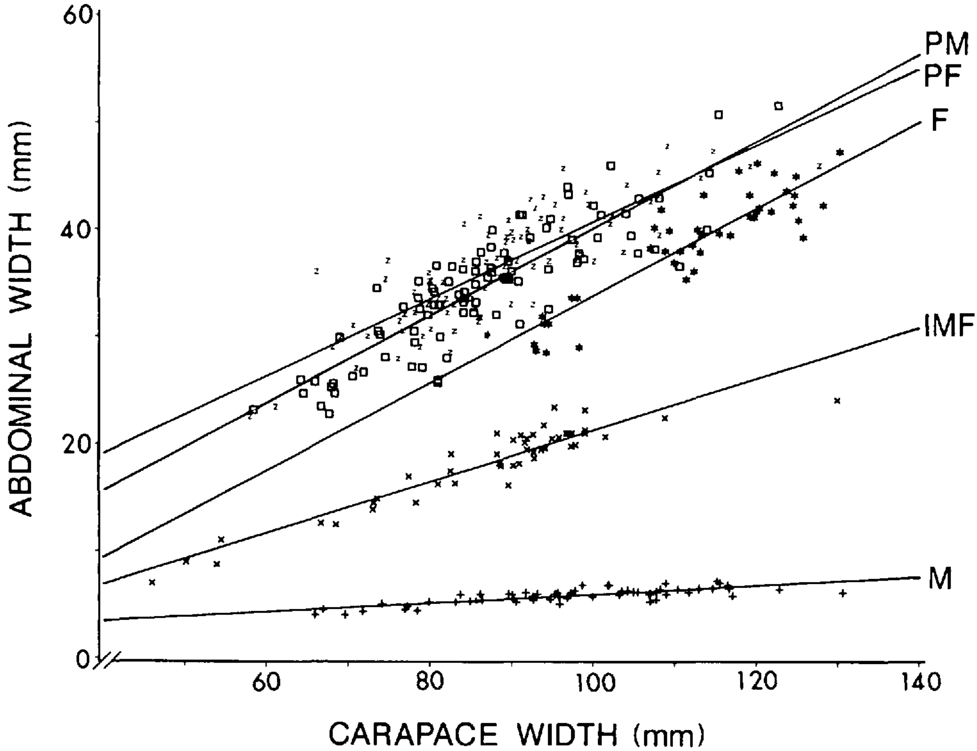

Figure 4. Relationship of abdominal width at the fifth abdominal suture to carapace width (without posteriolateral spine [SCW]) in *Callinectes sapidus* carrying *Loxothylacus texanus* externae and in normal *Callinectes sapidus*. M: normal males ($Y = 0.04X + 1.82$, $r^2 = 0.89$, $N = 59$); F: normal, sexually mature females ($Y = 0.40X - 7.00$, $r^2 = 0.95$, $N = 48$); IMF: normal immature females ($Y = 0.24X - 2.78$, $r^2 = 0.96$, $N = 46$); PM: males carrying externae ($Y = 0.41X - 6.30$, $r^2 = 0.93$, $N = 90$); PF: females carrying externae ($Y = 0.36X + 4.39$, $r^2 = 0.92$, $N = 89$).

ally low near the limits of the geographical range of a species (Andrewartha and Birch, 1954). If parasite density falls below a critical threshold, the probability that infective female cyprid larvae will encounter susceptible hosts or that male cyprids will encounter crabs carrying virgin externae is reduced (O'Brien, 1984), and could perpetuate low population levels.

Studies conducted in Louisiana and Texas suggest that blue crabs with *L. texanus* externae are more common in waters with estuarine salinities (More, 1969; Adkins, 1972; Ragan and Matherne, 1974). Our data indicate that the presence of mature *L. texanus* externae on blue crabs is not associated with salinity but is related to temperature; crabs with externae are more common in water temperatures that correspond to those occurring during spring and fall in Florida. The relationship between temperature and percentage of parasitized crabs may be facultative, associated with a temporal relationship in developmental timing of the parasite and host.

Relationship of Parasite and Host Life Cycles.—In a brachyuran-rhizocephalan association, one might expect that the parasite had evolved such that the probability of infecting the host was maximized. This would occur if a maximal number of female cyprid larvae at the developmental stage suitable for infection were in the water column during the time when the availability of susceptible crabs (usually

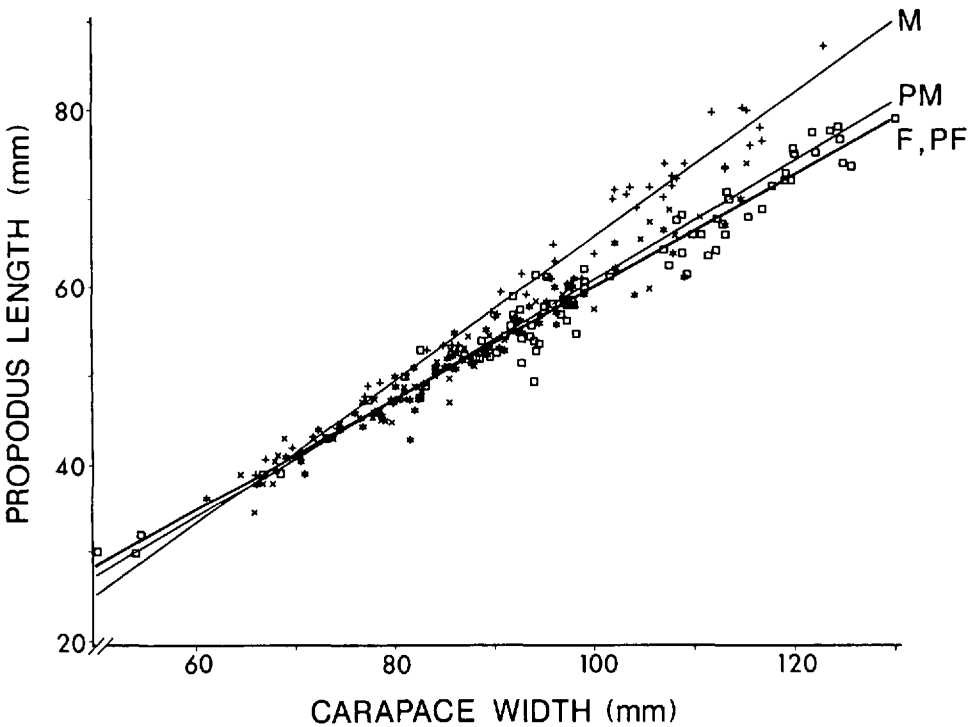

Figure 5. Relationship of crusher propodus length to carapace width (without posteriolateral spine [SCW]) in blue crabs carrying *Loxothylacus texanus* externae and in normal blue crabs. M: normal males ($Y = 0.81X - 15.35$, $r^2 = 0.99$, N = 59); F: normal, sexually mature females ($Y = 0.63X - 3.25$, $r^2 = 0.99$, N = 48); PM: parasitized males ($Y = 0.67X - 6.29$, $r^2 = 0.99$, N = 90); PF: parasitized females ($Y = 0.63X - 3.14$, $r^2 = 0.98$, N = 89).

juveniles [Smith, 1906; Veillet, 1945; Payen et al., 1981; Høeg, 1984]) was greatest (Day, 1935; Lützen, 1984). For example, the life cycle of *S. carcini* appears to be coordinated with that of its host (*Carcinus maenas*) such that the abundance of larvae peaks when juvenile crabs are most abundant (Lützen, 1984). The relationship of seasonal variation in relative abundance of ovigerous female blue crabs to that of crabs with parasite externae and the comparatively small mean size of crabs that carry externae suggest that such a relationship exists for the *C. sapidus–L. texanus* association.

The length of time necessary for development from fertilized egg to first crab stage in blue crabs is approximately 1.5–3 months (Jaworski, 1972; McConaugha et al., 1983), depending upon water temperature and salinity conditions (Costlow and Bookout, 1959; Costlow, 1967; Leffler, 1972). Size-at-age estimates for juvenile blue crabs developed by Hochberg (1988) using a growth curve derived from a relationship between size-at-instar (Newcombe et al., 1949) and mean length of intermolt period (Milliken and Williams, 1984) predict that the size of most blue crabs hatched during spring would be between approximately 10 mm LCW and 40 mm LCW during autumn and early winter. The relative abundance of blue crabs carrying mature *L. texanus* externae is highest during August–September (Adkins, 1972; present study). In kentrogonid rhizocephalans, larval developmental time from maturation of the externa to infective female cyprid stage is approximately 4–6 weeks (Ritchie and Høeg, 1981; Lützen, 1984), and nauplii can be produced for approximately three months after the externa matures (Lützen, 1981). If these aspects of the life cycle of *L. texanus* are similar to those of other kentrogonids, the relative abundance of infective female cyprid larvae should be high from October through December, the period during which juvenile blue crabs would be comparatively abundant. Similarly, the midwinter–early spring increase in relative abundance of mature externae may be timed to synchronize with the increase in abundance of juvenile blue crabs developing from the September secondary elevation in spawning.

Although crab growth continues throughout development of the interna stage (Lützen, 1984), parasitic anecdysis occurs when the externa emerges (Lützen, 1981; O'Brien and Van Wyck, 1985; O'Brien and Skinner, 1990), and growth in blue crabs parasitized by sacculinids can be inhibited in response to infection (Veillet, 1945; O'Brien, 1984). Thus, the average size of blue crabs carrying mature externae would be smaller than that of normal adult crabs if infection of most crabs occurred during juvenile ontogeny and if duration of the interna stage was short compared to the length of time required for blue crabs to attain full adult size.

Host Morphological Changes Associated with Parasitization.—Both mean size and size range of parasitized blue crabs in Florida are considerably larger than those recorded in the northern and western Gulf of Mexico (Reinhard, 1950; Christmas, 1969; Adkins, 1972; Ragan and Matherne, 1974; Overstreet et al., 1983). These regional differences probably are not an artifact of a difference between our sampling technique (trapping) and the techniques used in the other studies (trawling, seining). Visibly parasitized crabs greater than 95 mm LCW have not been reported elsewhere in the Gulf, whereas fully 51% of the crabs with externae that we collected were 100 mm LCW or greater. Parasitized crabs of this size class would have been collected from other regions of the Gulf if they existed in the populations. Rather than a sampling bias, the pattern of variation in size of parasitized crabs may be environmentally related. The benthic marine environment of the inner continental shelf of peninsular Florida is markedly different than that of the rest of the Gulf of Mexico, and the Apalachee Bay region is the location of a major geological (Wilheim and Ewing, 1972; Brooks, 1973) and biological (Earle, 1969; Briggs, 1974) boundary zone separating these two environments. The unique habitat of peninsular Florida could affect pre- and/or post-infection growth rates of blue crabs in that area, or the species of *Loxothylacus* present in Florida may differ from the species occupying the northern and western Gulf.

A comparatively small average size of brachyurans carrying rhizocephalan externae has been recorded for a number of species (Smith, 1906; Veillet, 1945; Reinhard, 1950; O'Brien, 1984) but the significant difference in mean size of blue crabs carrying *L. texanus* externae at Apalachee Bay compared to other locations in Florida was unexpected. The average size of blue crabs carrying mature *L. texanus* externae in Apalachee Bay is intermediate between the mean sizes of peninsular Florida and of northern and western Gulf of Mexico populations and may reflect the combining of two populational components: smaller resident parasitized crabs and larger parasitized crabs that have migrated northward from peninsular Florida. During spawning season, female blue crabs in peninsular Florida Gulf waters undertake a peculiar, presumably reproductively related, mass migration northward toward Apalachee Bay (Osterling and Evink, 1977; Steele, in press). Rhizocephalan parasites secrete polypeptide mimics of host hormones (Bishop and Cannon, 1979) and pheromones (DeVries et al., 1989) that stimulate various reproductively-associated female behaviors in parasitized crabs of both sexes, including migrations to spawning grounds (Rasmussen, 1959; Bishop and Cannon, 1979; Sloan, 1984). It may be that the relatively large-sized parasitized crabs inhabiting peninsular Florida also are stimulated to migrate northward along the west Florida coast, and some mix with the presumably smaller parasitized crabs that constitute the local Apalachee Bay population.

Host modification in body proportions is a phenotypic manifestation of the neurological (Veillet, 1955; Veillet and Graf, 1959; Rubiliani, 1983) and hormonal (Rubiliani and Payen, 1979) changes occurring in brachyurans infected with rhizocephalan parasites. As in other sexually dimorphic crab species (Hartnoll, 1967; Phillips and Cannon, 1978), male blue crabs parasitized by *L. texanus* undergo morphological changes that result in the development of characteristics resembling those of females. However, abdominal width in both male and female crabs carrying externae is significantly wider than that of ovigerous females. The mechanism(s) of action utilized by *L. texanus* to orchestrate morphological change in *C. sapidus* must induce alterations in the body structure of both sexes that facilitate the development and reproduction of the parasite. Most morphological alterations associated with the feminization of males (e.g., the changes in abdominal width and relative size of crusher claw) may be pleiotropic effects hormonally or genetically coupled to the specific behavioral, physiological, and morphological changes targeted by the parasite to facilitate the completion of its life cycle.

Acknowledgments

We thank Dr. J. Quinn, Jr., D. Parish, and a number of commercial fishermen for assisting with collection of parasitized crabs, D. Peebles for illustrations, and the first mate of the R/V Scrapper, K. Killam, for assistance and support throughout the project. We also gratefully acknowledge W. Arnold, Dr. N. Blake, D. Camp, D. Crewz, J. Leiby, T. Perkins, Dr. G. Rodrick, Dr. J. Torres, and two anonymous reviewers for reading various versions of the manuscript. This research constituted the basis for an M.S. thesis in the Department of Marine Science at the University of South Florida (R.J.H.) and was funded by grants from the Department of Commerce National Oceanographic and Atmospheric Administration to the Florida Department of Natural Resources (P.L. 88-309 [Project 2-408-R] and P.L. 99-659 [Project 2-IJ-2]) and by the Florida Department of Natural Resources, Florida Marine Research Institute.

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DATE ACCEPTED: April 12, 1991.

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