FACTORS INFLUENCING RECAPTURE PATTERNS OF TAGGED PENAEID SHRIMP IN THE WESTERN GULF OF MEXICO

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ABSTRACT

Movements of brown shrimp, *Penaeus aztecus*, and pink shrimp, *P. duorarum*, off the adjacent states of Texas (USA) and Tamaulipas (Mexico) in the western Gulf of Mexico were examined by releasing tagged shrimp within 150 km of each side of the border during May–July 1986. Analysis of recaptures during June–August 1986 indicated that species and release location (state) significantly influenced recapture patterns. Distances travelled prior to recapture, days at large, and movement speeds were greater for shrimp released off Tamaulipas than for shrimp released off Texas. Brown shrimp were recaptured in deeper waters than pink shrimp even though all releases were made at the same depth. Within each species, shrimp released off Tamaulipas were recaptured in deeper waters than shrimp from Texas releases. Relative to shoreline, directional movement of brown shrimp tended to be offshore while that of pink shrimp tended to be alongshore. During the recapture period, fishing effort off Tamaulipas was 13% of that expended off Texas and was expended in deeper waters. Consequently, the fishing mortality was lower off Tamaulipas and tagged shrimp in Tamaulipas waters generally experienced a lower recapture rate, longer times at large, greater distances travelled, and greater depths at recapture. Catch rates off Tamaulipas were also lower than off Texas, even though both fleets used similar fishing gear.

The integration of all components of movement (distance, days at large, direction, recapture depth) was examined by standardizing recaptures north and south of release sites by fishing effort. Paired comparisons of north versus south recaptures per unit effort (R/f) for each of 22 releases indicated no significant differences in brown shrimp movements off Texas or Tamaulipas or in pink shrimp movements off Texas. A significant northward movement of pink shrimp released off Tamaulipas was found.

Brown shrimp, *Penaeus aztecus*, and pink shrimp, *P. duorarum*, are the dominant species caught by commercial shrimp fisheries of the western Gulf of Mexico. Annual landings in the adjoining states of Texas (USA) and Tamaulipas (Mexico) at present average 15,250 t (metric tons) (Klima et al. 1987b; Castro et al. 1986), of which brown shrimp are thought to comprise at least 90% (Slater[3]). In 1981, the United States National Marine Fisheries Service (NMFS) implemented a 45–60 day closure of the Texas shrimp fishery during May–July to increase yield per recruit of brown shrimp (Klima et al. 1982). Mexico has investigated the potential for a similar closure but has not enacted one (Castro y Santiago 1976).

As movement of shrimp out of U.S. waters would reduce the effectiveness of such a closure, shrimp movement patterns were assessed in a general sense by a large-scale, cooperative mark-recapture program in 1978–80 involving NMFS, Texas Parks and Wildlife Department, and Mexico's Instituto Nacional de la Pesca (INP). Tagged brown shrimp and pink shrimp were released between Galveston, TX (lat. 29°15'N, long. 94°45'W) and Tampico, Tamaulipas (lat. 22°15'N, long. 97°50'W) at various depths. Releases were made in estuaries and offshore at various times during March–November 1978–80. Long-distance movements by brown shrimp (up to 620 km) and pink shrimp (up to 428 km), some degree of transborder stock exchange, and a trend for southward movement by both species were found (Castro et al. 1985; Cody and Fuls 1981; Klima et al. 1987a; Sheridan et al. 1987). However, the program did not analyze tag recovery patterns as influenced by fishing effort that is not uniform in time or space.

To assess more precisely the short-term shrimp movements across the U.S.-Mexico border, NMFS and INP conducted a cooperative mark-recapture experiment off southern Texas and northern Tamaulipas during the summer of 1986. The objec-

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[3]Slater, B. M. Report on misclassification of commercial pink shrimp as brown shrimp, July 16, 1982 to September 30, 1982. Unpubl. manuscr., 36 p. Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

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tives of this research were to 1) test whether shrimp movement (measured in terms of distance travelled, days at large, speed, direction, or recapture depth) varied according to species, sex, or release location (state), and 2) test for directional movement after recaptures were adjusted by patterns in fishing effort.

MATERIALS AND METHODS

Collection and Tagging of Shrimp

Shrimp were collected by trawl at night off the Texas and Tamaulipas coasts. All collections were made in 16–20 m waters within 5 km of release sites. Shrimp were held in flow-through tanks before and after tagging and until released.

Shrimp were marked with colored, numbered polyethylene streamer tags as described by Marullo et al. (1976). Shrimp between 80 and 140 mm total length were selected because these sizes represented recent recruits. Tagged shrimp were released at 18 m depths within 12 hours of collection using expendable, delayed-release canisters (Emiliani 1971). Each plastic canister was weighted, filled with 50–75 tagged shrimp, sealed with a salt block, and released overboard. The salt block dissolves after 10–15 minutes under water and the canister springs open, releasing the shrimp on the sea floor.

Ten releases of tagged shrimp were made at eight sites between 24°44′N, 97°31′W and 25°57′N, 97°04′W off Tamaulipas (Fig. 1). These releases were made during 30 May–8 June 1986 from the INP ship *BIP-IX*. Twelve releases were made at six sites between 26°05′N, 97°05′W and 26°55′N, 97°17′W off Texas (Fig. 1). The Texas releases were made during 21–28 June 1986 and 7–11 July 1986 from the NOAA ships *Chapman* and *Oregon II*. The order of release sites was randomized given the following restrictions: 1) the 21 June release site was fixed due to vessel cruising speed, and 2) each Texas site was visited once before repeating any site (this was not possible off Tamaulipas). Releases were confined to sites within 150 km of the U.S.-Mexico border (25°57′N) based on shrimp movement speeds that averaged 2.5 km/d during 1978–80 (NMFS, unpubl. data) over a maximum closure of 60 days. In fact, 90% of all transborder recaptures after 1978–80 experiments resulted from releases within 120 km of the border (Sheridan et al. 1987).

No predetermined number of shrimp was set for each night's tagging due to natural variabilities in abundance and catchability. Species composition and size range of released shrimp were estimated by identification and measurement of up to 300 shrimp for each day's release. Identification and measurement of all tagged shrimp was not conducted because such handling could have increased stress and thus influenced behavior or survival of tagged shrimp. Only brown shrimp and pink shrimp were marked and released. Periodic lottery rewards of $50–$500 were offered as incentives to fishermen on both sides of the border to report capture of tagged shrimp with information on location, depth, and date of recapture (Cody and Fuls 1981).

Collection of Recaptures and Fishing Information

Port agents employed by NMFS and INP interviewed fishermen and processors in American and Mexican ports to collect recaptured tagged shrimp and information on fishing locations, landings, and effort. All recaptures during the period 30 May–31 August 1986 were checked for accuracy of date and location and were identified to species when possible. Although recaptures were made after 31 August, only recaptures during the 94 d period were chosen to best reflect summer environments. Recaptures returned with the following inconsistencies were omitted from analyses of movement (although they are included in a general summary of recaptures, Table 1): 1) not identified as brown shrimp or pink shrimp, 2) recapture dates after 31 August 1986, 3) recapture dates prior to or the same as release dates, 4) incomplete latitude and longitude, 5) depth not specified, 6) sex not specified, and 7) recaptured in trawl tows over distances exceeding 9 km. These restrictions reduced the number of usable recaptures from 5,639 (as of the date of last recapture, 5 December 1986) to 3,032 (Table 2).

Port agent interviews of fishermen throughout the U.S. Gulf of Mexico were used to estimate total brown shrimp and pink shrimp fishing effort off Texas during the period 1 June–31 August 1986. These data are collected by specific 9 m depth zones paralleling the coast within quadrangles of one degree latitude and longitude and, as such, are too coarse to examine shrimp movements in detail. Logbooks were voluntarily kept by the captains of 47 Texas shrimp vessels for the duration of the recapture period to collect precise information on starting and stopping points and times, depths, tow durations, and landings. Logbook data were assumed to reflect fishing activities of all vessels off Texas and were used to estimate the amount of total brown shrimp fishing effort (which includes pink shrimp) within 10 minute quadrangles of latitude and longi-

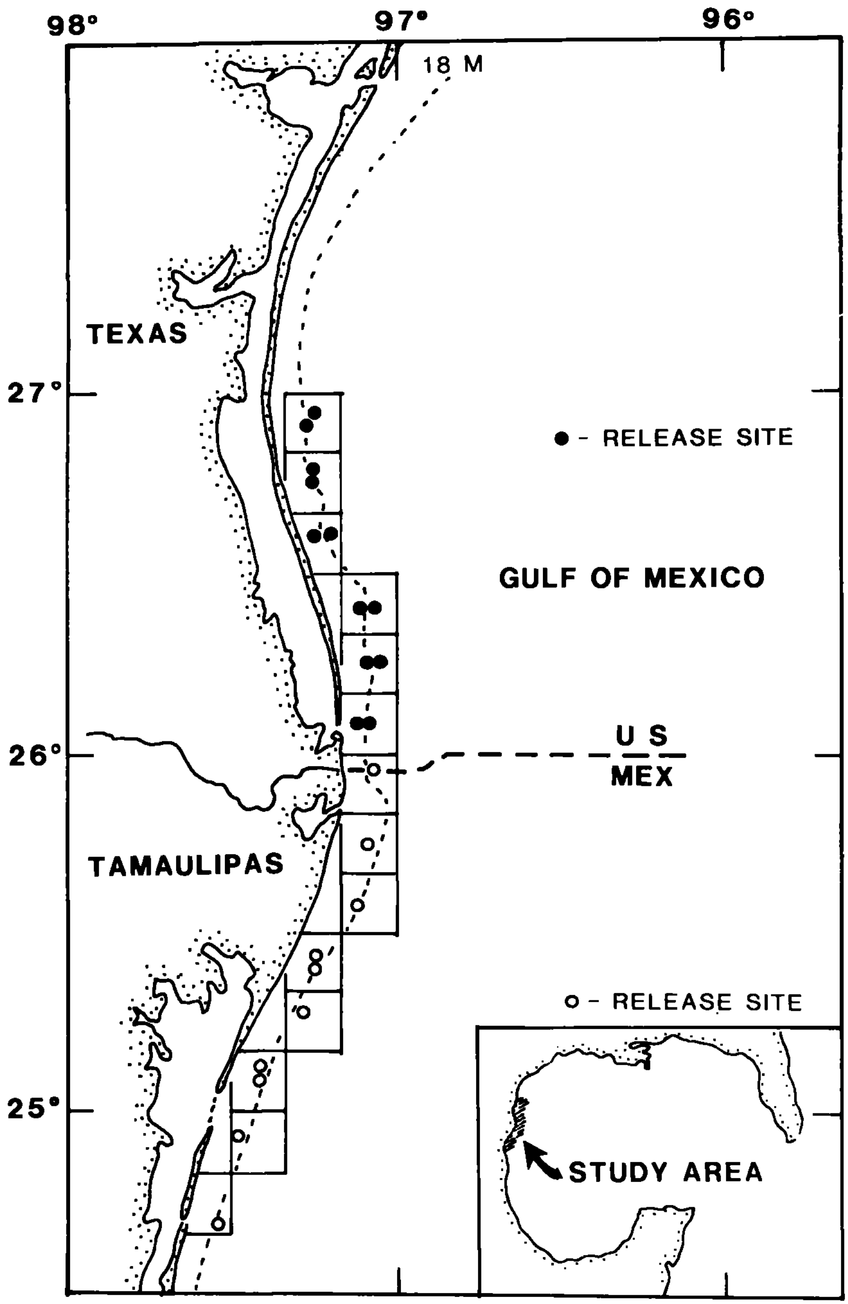

FIGURE 1.—Release sites for 1986 shrimp mark-recapture experiments.

TABLE 1.—Summary of 1986 mark-recapture experiments with brown shrimp and pink shrimp off Tamaulipas and Texas. Recaptures include all shrimp, regardless of the quality of return information, caught as of 5 December 1986, the date of last recapture.

State	Date	Release site	Number marked	Number released	Percent prerelease mortality	Number recaptured	Percent recaptured
Tamaulipas	5/30	25°36′N, 97°07′W	1,165	1,157	0.69	107	9.2
	5/31	25°17′N, 97°17′W	1,866	1,851	0.80	116	6.3
	6/1	25°24′N, 97°14′W	1,375	1,355	1.45	55	4.1
	6/2	25°57′N, 97°04′W	1,099	1,099	0.00	48	4.4
	6/3	24°41′N, 97°31′W	1,696	1,692	0.24	61	3.6
	6/4	24°56′N, 97°29′W	895	895	0.00	50	5.6
	6/5	25°06′N, 97°24′W	1,592	1,590	0.13	132	8.3
	6/6	25°08′N, 97°24′W	1,594	1,581	0.82	139	8.8
	6/7	25°26′N, 97°14′W	1,583	1,579	0.25	218	13.8
	6/8	25°45′N, 97°05′W	1,190	1,188	0.17	163	13.7
	5/30–6/8	— —	14,055	13,987	0.48	1,089	7.8
Texas	6/21	26°55′N, 97°17′W	2,305	1,931	16.26	163	8.4
	6/22	26°15′N, 97°03′W	1,995	1,898	4.36	434	22.9
	6/23	26°37′N, 97°11′W	3,188	3,024	5.14	583	19.3
	6/24	26°45′N, 97°15′W	991	939	5.25	140	14.9
	6/25	26°05′N, 97°07′W	3,288	3,157	3.98	873	27.7
	6/26	26°25′N, 97°07′W	3,690	3,661	0.79	327	8.9
	6/27	26°37′N, 97°11′W	1,784	1,729	3.08	307	17.8
	7/7	26°25′N, 97°06′W	2,009	1,993	0.80	242	12.1
	7/8	26°47′N, 97°15′W	2,063	2,056	0.34	276	13.4
	7/9	26°05′N, 97°05′W	3,617	3,600	0.47	458	12.7
	7/10	26°15′N, 97°04′W	2,447	2,399	1.96	444	18.5
	7/11	26°55′N, 97°17′W	1,864	1,849	0.80	303	16.4
	6/21–7/11	— —	29,241	28,236	3.44	4,550	16.1
Total			43,296	42,223	2.48	5,639	13.4

TABLE 2.—Comparison of shrimp species compositions for release, for all recaptures regardless of quality of return information, and for recaptures with complete and accurate return information. The latter group formed the data base for analyses of directional movement. N = number examined, * = significant difference (*t*-test, α = 0.05) between proportions of brown shrimp released and recaptured (all recaptures excluding unknowns).

Release date	Release			All recaptures				Best recaptures		
	N	% brown	% pink	*N*	% brown	% pink	% unknown	*N*	% brown	% pink
5/30	297	30.6	69.4	107	15.9*	80.4	3.7	97	13.4	86.6
5/31	294	96.3	3.7	116	70.7*	24.1	5.2	102	74.5	25.5
6/1	289	92.1	7.9	55	92.7	5.5	1.8	49	93.9	6.1
6/2	299	87.0	13.0	48	85.4	10.4	4.2	21	95.2	4.8
6/3	297	37.0	63.0	61	70.5*	24.6	4.9	56	73.2	26.8
6/4	298	93.6	6.4	50	82.0	12.0	6.0	43	88.4	11.6
6/5	295	58.6	41.4	132	51.5	45.5	3.0	120	53.3	46.7
6/6	298	85.9	14.1	139	69.1*	23.0	7.9	106	75.5	24.5
6/7	296	31.1	68.9	218	29.4	62.4	8.3	119	35.3	64.7
6/8	299	59.2	40.8	163	6.1*	87.1	6.7	54	7.4	92.6
5/30–6/8	2,962	66.9	33.1	1,089	47.1*	47.1	5.8	767	55.3	44.7
6/21	279	21.1	78.9	163	6.7*	79.8	13.5	114	4.4	95.6
6/22	298	42.9	57.1	434	8.3*	72.6	19.1	288	9.4	90.6
6/23	298	8.4	91.6	583	2.6*	82.7	14.8	345	2.9	97.1
6/24	299	57.2	42.8	140	12.9*	77.9	9.3	81	19.8	80.2
6/25	292	22.9	77.1	873	9.5*	80.9	9.6	482	.12.2	87.8
6/26	300	91.7	8.3	327	65.7	8.6	25.7	150	86.0	14.0
6/27	300	4.0	96.0	307	3.6	88.9	7.5	194	3.1	96.9
7/7	298	84.9	15.1	242	39.3	11.6	49.2	42	73.8	26.2
7/8	300	70.7	29.3	276	51.8*	38.0	10.1	43	58.1	41.9
7/9	299	85.6	14.4	458	57.9*	31.2	10.9	209	59.8	40.2
7/10	294	44.6	55.4	444	40.8	43.2	16.0	148	45.9	54.1
7/11	296	96.6	3.4	303	79.2	4.6	16.2	169	94.7	5.3
6/21–7/11	3,553	52.7	47.3	4,550	28.9*	55.5	15.6	2,265	29.2	70.8
Total	6,515	59.2	40.8	5,639	32.4*	53.9	13.7	3,032	35.8	64.2

tude, hereafter called "grids", along the Texas coast.

Port agents in Tamaulipas interviewed the captains of all vessels returning to the primary port of Tampico. Unknown, but assumed relatively small, amounts of catch and effort were potentially reported in more southerly ports. Interviewers collected catch and effort data by depth range and 10 minute lines of latitude between 22°N and 26°N. These data were then recordable either within 9 m depth zones or within grids as was done off Texas.

Interviews recorded effort by specific 9 m depth zones (Texas) or by actual depth ranges (Tamaulipas) per trip. Tamaulipas effort was assumed to fall equally into adjacent 9 m depth zones if more than one zone was covered by the stated depth range. The average fishing depth per trip was then calculated by weighting the hours expended in each 9 m depth zone by the middepth of that zone (e.g., the 10–18 m zone had a middepth of 14 m), summing over all depth zones, then dividing by the total effort expended on that trip. Average fishing depth for each fleet was then compared by a t-test corrected for unequal variances (Sokal and Rohlf 1969) using the average depth for each of 2,008 Texas trips and 505 Tamaulipas trips as observations.

Data Analysis

Three-factor, model I analysis of variance (ANOVA) with unequal cell sizes was employed to test hypotheses concerning the equivalence of treatment means for several types of observations on recaptured shrimp. The treatment factors were species (brown or pink), sex, and release state (Texas or Tamaulipas). State was chosen as a treatment because the level of fishing effort off Texas is much greater than that off Tamaulipas (approximately 200 vessels use the port of Tampico, whereas there are nearly 2,000 vessels registered in Texas alone). Four attributes of shrimp movement were examined by ANOVA: 1) distance travelled before recapture, assumed to be a straight line, 2) days at large, 3) apparent speed of movement, and 4) recapture depth. All four variables exhibited nonnormal (skewed) error distributions, as indicated by the Shapiro-Wilk test statistic (Shapiro and Wilk 1965), but the effects of nonnormality are thought to be minimal with large sample sizes (Underwood 1981). Variances of all variables were found to be heterogeneous (F-max test for unequal cell sizes; Sokal and Rohlf 1969). Data were $\log(x + 1)$-transformed prior to ANOVA (Underwood 1981), and F-max tests on transformed data indicated homogeneity of variances. Multiple comparison of treatment means of transformed data employed Fisher's LSD (least significant difference) because of unequal cell sizes (Milliken and Johnson 1984).

Circular scale data such as compass directions are a special type of interval scale data (Zar 1984) that cannot be examined by ANOVA because there is no physical reason for any zero point and high or low values are arbitrary (e.g., 45° is not a "larger" direction than 30°, and the mean of the 45° and 315° is not 180° but 0°). Examination of the raw data indicated that the assumption of unimodal distributions of recapture directions needed for hypothesis testing with the recommended parametric test (Watson-Williams statistic) would be violated. We conducted multisample testing of grouped directional data using contingency tables (Zar 1984). Before analysis, compass direction from release site to recapture site was adjusted downward by 20° off Texas and upward by 20° off Tamaulipas because northerly movement parallel to shore (hereafter termed "north") is 20° west of magnetic north (340°) off southern Texas and 20° east of magnetic north (020°) off northern Tamaulipas (Fig. 1). We grouped the adjusted directional data into eight arbitrary 45° divisions (0–44°, 45–89°, etc.) that fulfilled the requirement of having no expected cell frequency less than 4 (Zar 1984), with one exception. Only one brown shrimp and one pink shrimp released off Tamaulipas were recaptured between 270° and 359°; thus the contingency tables comparing these two data sets employed six 60° divisions (15–74°, 74–134°, etc.) to avoid low cell frequencies.

Differences in shrimp movement away from release sites were also tested by examining patterns in recaptures per unit fishing effort (R/f). R/f adjusts for temporal and spatial variations in fishing effort around each release site and integrates the effects of distance and direction travelled (Gitschlag 1986). For each release, recaptures per 10^4 hour of effort were calculated north, within, and south of the release grid from the release date through the end of the study period. "North" was defined as all grids lying between the northern latitude of the release grid and the northern latitude of the grid containing the northernmost recapture after each release. "South" was defined as all grids lying between the southern latitude of the release grid and the southern latitude of the grid containing the southernmost recapture after each release. "Within" was defined as the release grid and all grids directly east and west of it (recaptures in these grids did not show longshore movement). Two-factor, mixed model ANOVA with balanced cell sizes was used to test the hypothesis that there were no detectable differences in shrimp recapture patterns for each species off each state as indicated by R/f values. This was a randomized complete blocks design for paired comparisons of R/f values as fixed treatments (north or south) and releases of tagged shrimp (10 off Tamaulipas, 12 off Texas) as randomly chosen blocks (Sokal and Rohlf 1969; Underwood 1981).

RESULTS

Releases and Recaptures

A total of 42,223 shrimp was marked and released between 30 May and 11 July 1986, with an overall recapture of 5,639 shrimp (13.4%) by 5 December 1986, the date of last recapture (Table 1). Over the entire recapture period, 50 brown shrimp and 62 pink shrimp marked off Tamaulipas were recaptured across the border in Texas waters, while 5 brown shrimp and 2 pink shrimp marked off Texas were recaptured off Tamaulipas. General mortality among tagged shrimp prior to daily releases totalled 2.48%. For no apparent reason, prerelease mortality was higher for the June releases off Texas (5.24%) than for those off Tamaulipas (0.48%) or off Texas in July (0.86%).

Brown shrimp represented 59.2% of the overall estimated species composition at release, while pink shrimp formed 40.8% (Table 2). There was considerable variation in species composition on a daily basis at any given site as well as among sites. The largest within-site differences were between 1 June and 7 June releases near 25°25′N off Tamaulipas (brown shrimp comprised 92% and 31%, respectively) and between 21 June and 11 July releases at 26°55′N off Texas (brown shrimp comprised 21% and 97%, respectively).

Species compositions at release and after recapture (excluding unknowns; Table 2) were significantly different for 12 of 22 release dates and over all releases in each state (*t*-test for equality of proportions, $\alpha = 0.05$; Sokal and Rohlf 1969). This is likely a reflection of differences in fishing effort: experimental shrimp were collected in 16–20 m waters while commercial shrimpers fished 5–90 m waters. Other factors could act and interact to cause these proportional changes in species composition including differential natural and tag-induced mortality, depth and substrate preferences, or catchability.

A total of 2,607 recaptures was excluded due to inconsistencies in recapture information cited previously. The remaining 3,032 "best" recaptures (Table 2) were used for all remaining analyses.

Components of Movement

Species, sex, and state had variable effects on the movements of recaptured shrimp, as indicated by distances travelled before recapture, days at large, speed, direction, and recapture depth. Distance travelled before recapture was significantly affected by both species and state (Table 3). The species × state interaction was also significant. Pink shrimp moved both the greatest and least mean distances of all eight groups, depending upon where they were released. Pink shrimp released off Tamaulipas moved an average of 29.5 km (males) or 29.0 km (females), distances that were significantly greater than those of pink shrimp released off Texas (males = 9.2 km, females = 9.8 km). Brown shrimp re-

TABLE 3.—Distances travelled by recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log $(x + 1)$ - transformed data. B. Mean distances travelled. Underlined means are not significantly different (Fisher's LSD, $\alpha = 0.05$). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	F	P
A. Source of variation				
Model	7	511.07	79.50	<0.001
Species	1	53.47	58.23	<0.001
Sex	1	0.13	0.14	0.705
State	1	441.94	481.24	<0.001
Species × sex	1	0.01	<0.01	0.948
Species × state	1	12.98	14.13	<0.001
Sex × state	1	0.15	0.16	0.686
Species × sex × state	1	2.40	2.61	0.106
Error	3024	2777.04		

B. Group:	PMTa	PFTa	BFTa	BMTa	BMTx	BFTx	PFTx	PMTx
Distance (km):	29.5	29.0	25.6	23.7	13.0	11.1	9.8	9.2

leased off Tamaulipas averaged significantly greater distances than brown shrimp released off Texas (23.7 and 25.6 km versus 11.1 and 13.0 km, respectively). The distributions of recaptures by distance travelled indicated that most Texas recaptures (70%) occurred within 20 km of release sites, while only 40% of the Tamaulipas recaptures were made at close range (Fig. 2). In all but one case, percentages of total Tamaulipas recaptures in any given distance category exceeded those of Texas recaptures.

Days at large were significantly affected only by the main effects of species, sex, and state (Table 4). Mean days at large were greater for shrimp released off Tamaulipas (16.4–20.2 days) than for shrimp released off Texas (11.8–14.4 days), and within each state brown shrimp tended to be at large longer than pink shrimp. Within each species-state group, female shrimp remained at large longer than male shrimp. The distributions of recaptures by days at large indicated that 65–85% of all Texas recaptures were made 1–19 days after release, whereas only 45–50% of Tamaulipas recaptures occurred during this time period (Fig. 3). Proportions of brown shrimp recaptures in the 40–79 days at large categories were also greater than those of pink shrimp.

Movement speeds of recaptured shrimp were affected by the interaction of species and state (Table 5). This was reflected both in the significant main effect of state (shrimp released off Tamaulipas moved faster than those released off Texas, 1.67–2.34 km/d versus 1.04–1.25 km/d) and in the species × state interaction (pink shrimp released off Tamaulipas had significantly greater speeds than pink shrimp released off Texas, and the same trend was found for brown shrimp). The majority of all shrimp recaptured exhibited speeds of less than 1 km/d (Fig. 4). However, recaptures of shrimp released off Tamaulipas usually had proportionally more shrimp with speeds exceeding 4 km/d.

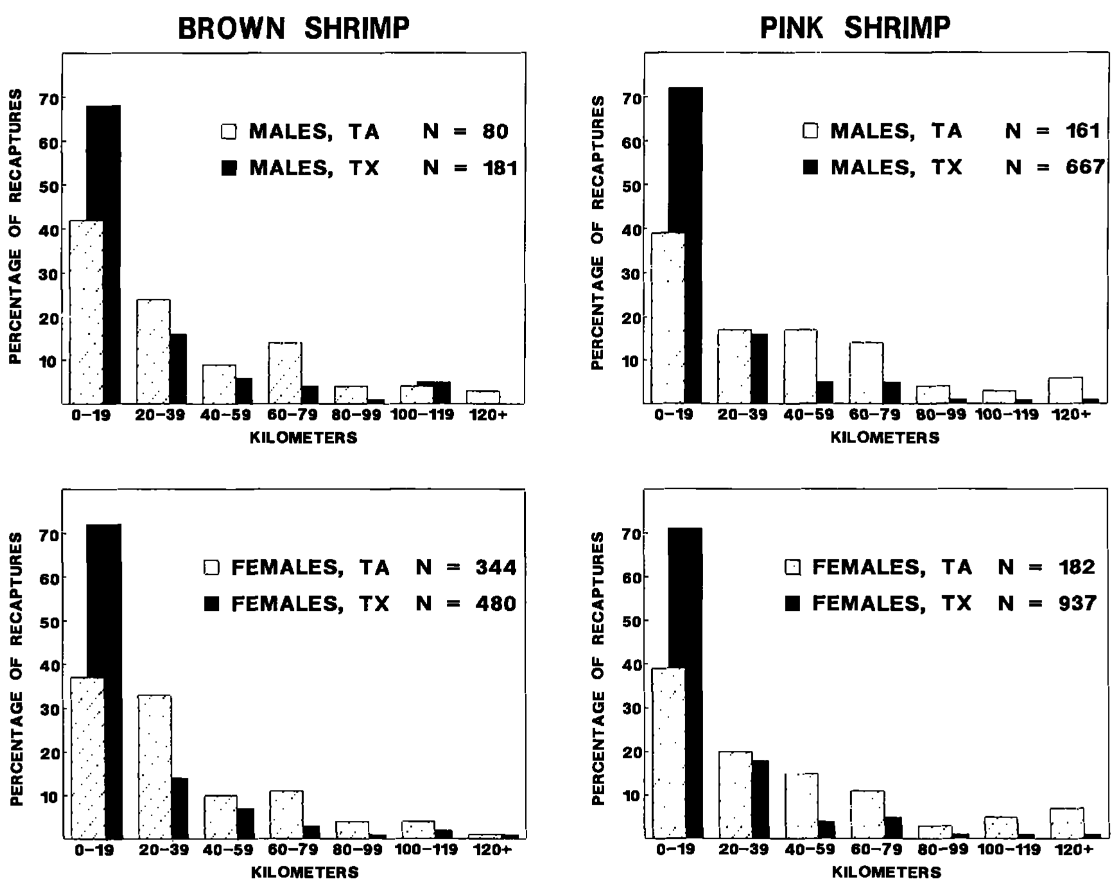

FIGURE 2.—Comparison of distances travelled by recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

TABLE 4.—Days at large for recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log (*x* + 1) - transformed data. B. Mean days at large. Underlined means are not significantly different (Fisher's LSD, α = 0.05). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	*F*	*P*
A. Source of variation				
Model	7	84.86	27.18	<0.001
Species	1	31.81	71.33	<0.001
Sex	1	2.02	4.53	0.033
State	1	50.55	113.35	<0.001
Species × sex	1	0.18	0.41	0.520
Species × state	1	0.16	0.36	0.550
Sex × state	1	0.13	0.29	0.592
Species × sex × state	1	<0.01	<0.01	0.999
Error	3024	1348.66		

B. Group:	BFTa	BMTa	PFTa	PMTa	BFTx	BMTx	PFTx	PMTx
Days at large:	20.2	19.7	16.9	16.4	14.4	13.6	12.6	11.8

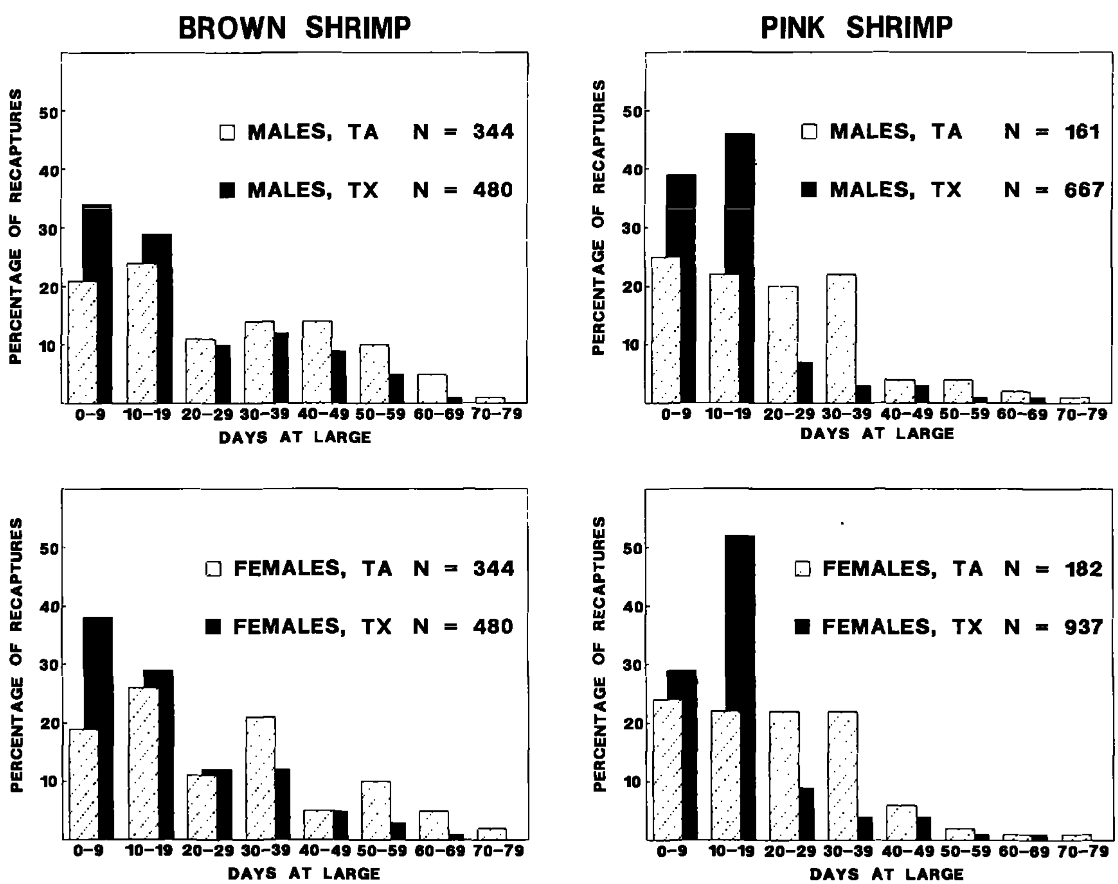

FIGURE 3.—Comparison of days at large for recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

TABLE 5.—Apparent movement speeds of recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean speeds. Underlined means are not significantly different (Fisher's LSD, α = 0.05). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	*F*	*P*
A. Source of variation				
Model	7	81.53	28.19	<0.001
Species	1	1.54	3.73	0.054
Sex	1	0.41	1.00	0.317
State	1	71.75	173.68	<0.001
Species × sex	1	0.04	0.10	0.749
Species × state	1	7.55	18.28	<0.001
Sex × state	1	<0.01	0.01	0.931
Species × sex × state	1	0.23	0.55	0.459
Error	3024	1249.30		

B. Group:	PMTa	PFTa	BMTa	BFTa	BMTx	BFTx	PFTx	PMTx
Speed (km/d):	2.34	2.24	1.73	1.67	1.25	1.07	1.04	1.04

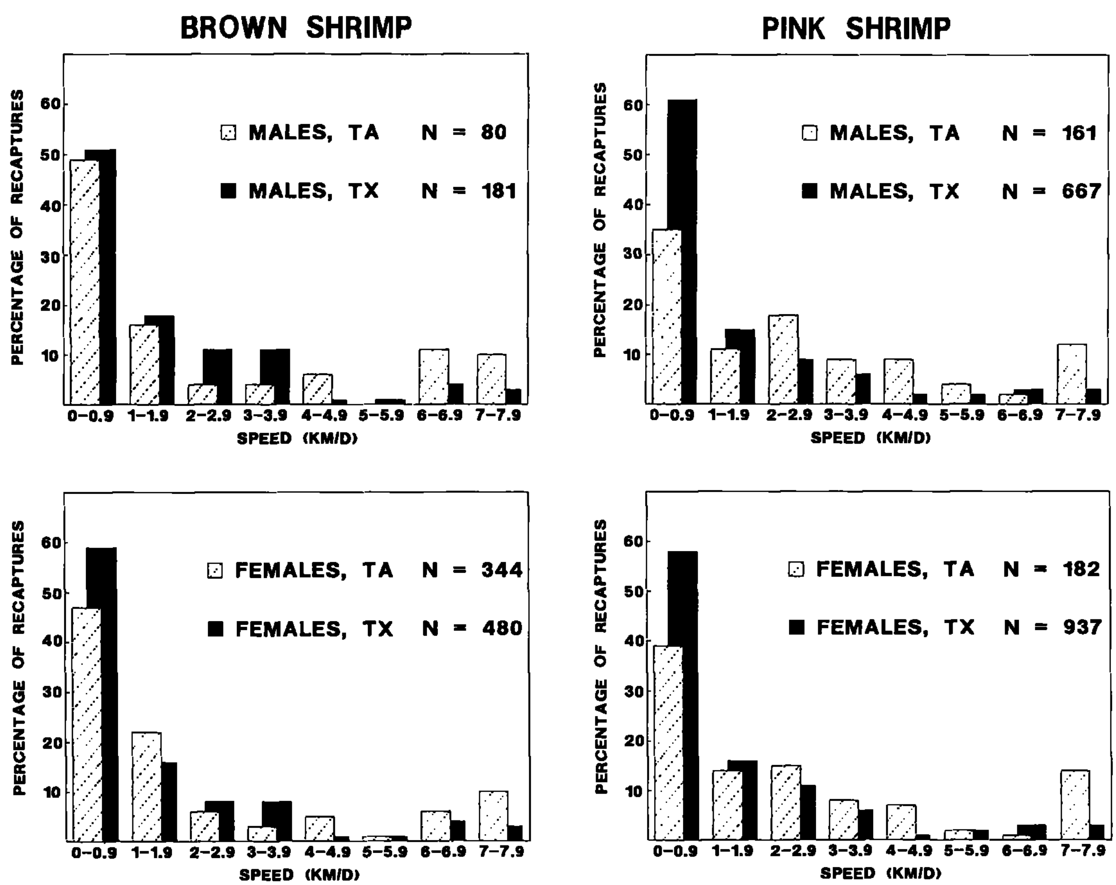

FIGURE 4.—Comparison of movement speeds of recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

Directional movement patterns of brown shrimp and pink shrimp were influenced by species and state (Table 6). The full three-factor model indicated significant differences ($P < 0.001$) in the frequency distributions of recaptures. Analysis of single factors indicated that recapture patterns based on sex alone were not significantly different. The significant species × state interaction could not be resolved further, since partitioning this interaction to within-state or within-species components still yielded significant differences in the distributions of recapture frequencies (Table 6). Graphical presentation of these analyses (Fig. 5) illustrated several points: 1) pink shrimp tended to orient alongshore (north and south) while brown shrimp had a strong offshore component (NE-SE); 2) male shrimp and

TABLE 6.—Analysis of adjusted directional movement of recaptured brown shrimp and pink shrimp using contingency tables. Directions were grouped into 45° divisions of the compass (0–44°, 45–89°, etc.) except where noted by an asterisk(*) when 60° sectors were formed (15–74°, 75–134°, etc.).

Factors	df	χ^2	P
Species × sex × state	49	1,593.63	<0.001
Species × state	21	1,569.89	<0.001
Species × Texas	7	109.15	<0.001
Species × Tamaulipas	5*	41.61	<0.001
Brown × state	7	465.39	<0.001
Pink × state	7	933.68	<0.001
Species	7	186.91	<0.001
Sex	7	5.71	0.573
State	7	1,400.36	<0.001

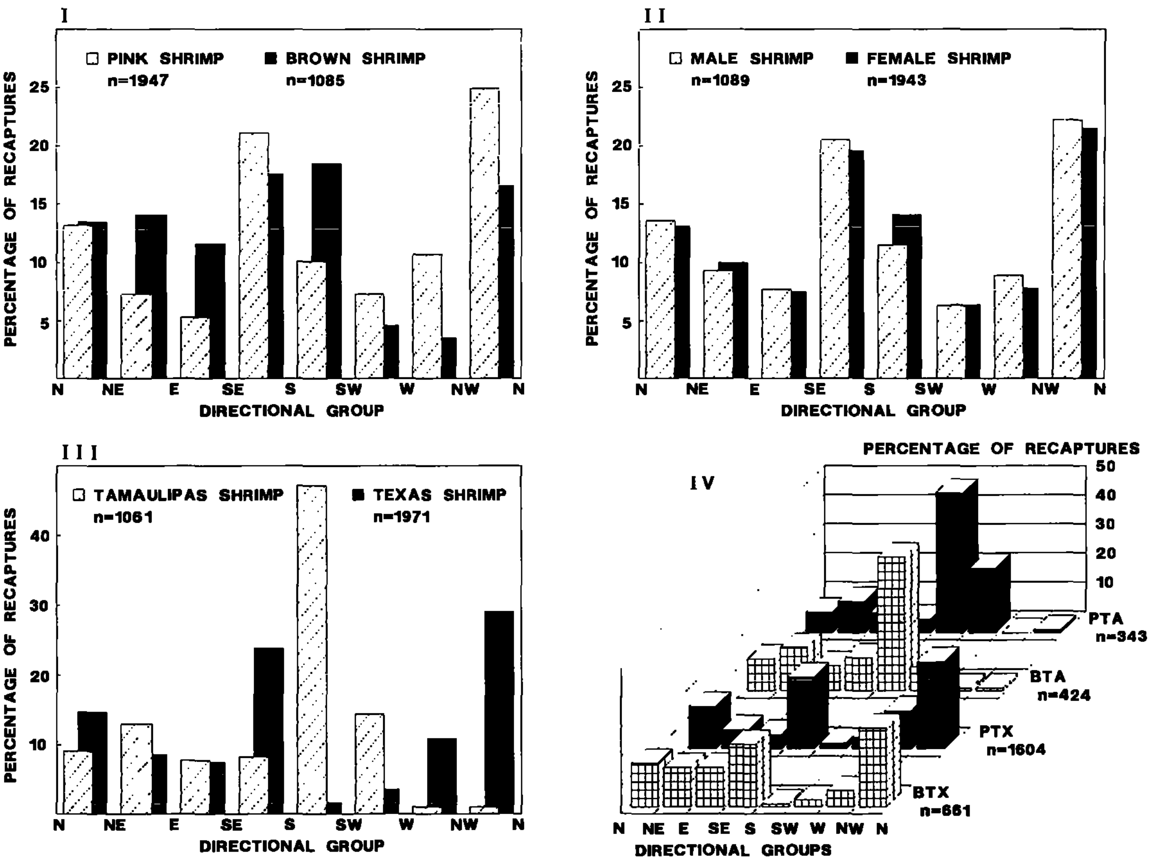

FIGURE 5.—Comparison of adjusted compass headings of recaptured brown shrimp (B) and pink shrimp (P) released off Tamaulipas (TA) and Texas (TX), where directional groups fall between compass points. n = number of recaptures. I. Frequencies by species. II. Frequencies by sex. III. Frequencies by state. IV. Frequencies by species × state interaction.

female shrimp exhibited similar recapture patterns; and 3) recaptures after Tamaulipas releases exhibited strong southward directionality and weak westerly to northerly movement compared with recaptures after Texas releases.

Recapture depth was significantly influenced by the main effects of species and state, but no interaction terms were significant (Table 7). Although all shrimp were released at 18 m depths, mean recapture depths of brown shrimp were greater than those for pink shrimp (21.5–24.0 m versus 19.6–21.5 m, respectively). Within each species, shrimp released off Tamaulipas moved to deeper waters than did shrimp released off Texas, and within each state brown shrimp moved to significantly deeper waters than pink shrimp. Most recaptures were made within 16–20 m depths, a trend that was stronger for pink shrimp than for brown shrimp (Fig. 6). Brown shrimp were more frequently recaptured in 21–25 m and 26–30 m waters than were pink shrimp.

Commercial Fishing Patterns

A total of 57,511 hours of fishing effort was recorded through interviews of fishermen landing at Tampico during the survey period, with resultant landings of 459.4 t of exportable shrimp tails. An additional 262.7 t (36% of total catch) of "pacotilla" or undersized, non-exportable shrimp tails were also landed (Castro[4]). Primary fishing areas were lat. 22°–23°N and 24°–25°N where Tamaulipas effort was concentrated off river mouths or lagoon passes (Fig. 7).

Interviews of seafood processors and of vessels landing in U.S. ports after fishing off Texas during 1 June–31 August 1986 indicated a total fishing effort of 432,175 hours with landings of 6,479 t of shrimp tails (NMFS, unpubl. data). Actual interviews of fishermen comprised 239,006 hours and 3,614 t of those totals. Logbooks kept by 47 Texas shrimp vessels (a subset of interviews) recorded 13,501 hours and 190 t; thus the detailed logbook data represented 3.1% of the total effort and 2.9% of the total landings from Texas waters. Logbook data were used to apportion total fishing effort off Texas into grids. Texas effort was more diffuse and was not clustered around river mouths or estuary passes as it was off Tamaulipas (Fig. 8).

Both fisheries operated in 1–82 m waters, of which Texas has approximately 2.3 times the continental shelf area as does Tamaulipas (U.S. Department of Commerce, NOS Chart 411). Comparison of the depth distributions of fishing effort between American and Mexican fleets (illustrated in Figure 9) indicated that American fishermen expended significantly more effort in shallower waters than did Mexican fishermen (mean fishing depths were 33.8 m and 35.1 m, respectively; *t*-test, $P = 0.009$). Overall catch rates were higher in Texas waters (6,479 t/432,175 h = 15.0 kg/h) than in Tamaulipas waters (722 t/57,511 h = 12.6 kg/h). Data collected concerning fishing gear indicated that vessels in both fleets generally employed four 12 m nets (mesh size data were unavailable).

[4]Castro M., R. G. Informe de actividades del programa MEX-US Golfo, grupo camaron Mexico. Programa MEX-US Golfo 1986. Unpubl. manuscr., 18 p. Instituto Nacional de la Pesca, Centro Regional de Investigaciones Pesqueras, Tampico, Tamaulipas, Mexico.

TABLE 7.—Recapture depth for brown shrimp and pink shrimp released in 18 m waters. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean recapture depths. Underlined means are not significantly different (Fisher's LSD, α = 0.05). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	*F*	*P*
A. Source of variation				
Model	7	13.18	35.12	<0.001
Species	1	8.84	164.94	<0.001
Sex	1	<0.01	0.13	0.722
State	1	4.15	77.36	<0.001
Species × sex	1	<0.01	0.17	0.682
Species × state	1	0.11	2.01	0.157
Sex × state	1	0.02	0.43	0.510
Species × sex × state	1	0.04	0.83	0.361
Error	3024	162.13		

B. Group:	BFTa	BMTa	BMTx	BFTx	PMTa	PFTa	PFTx	PMTx
Depth (m):	24.0	23.8	21.6	21.5	21.5	21.0	19.7	19.6

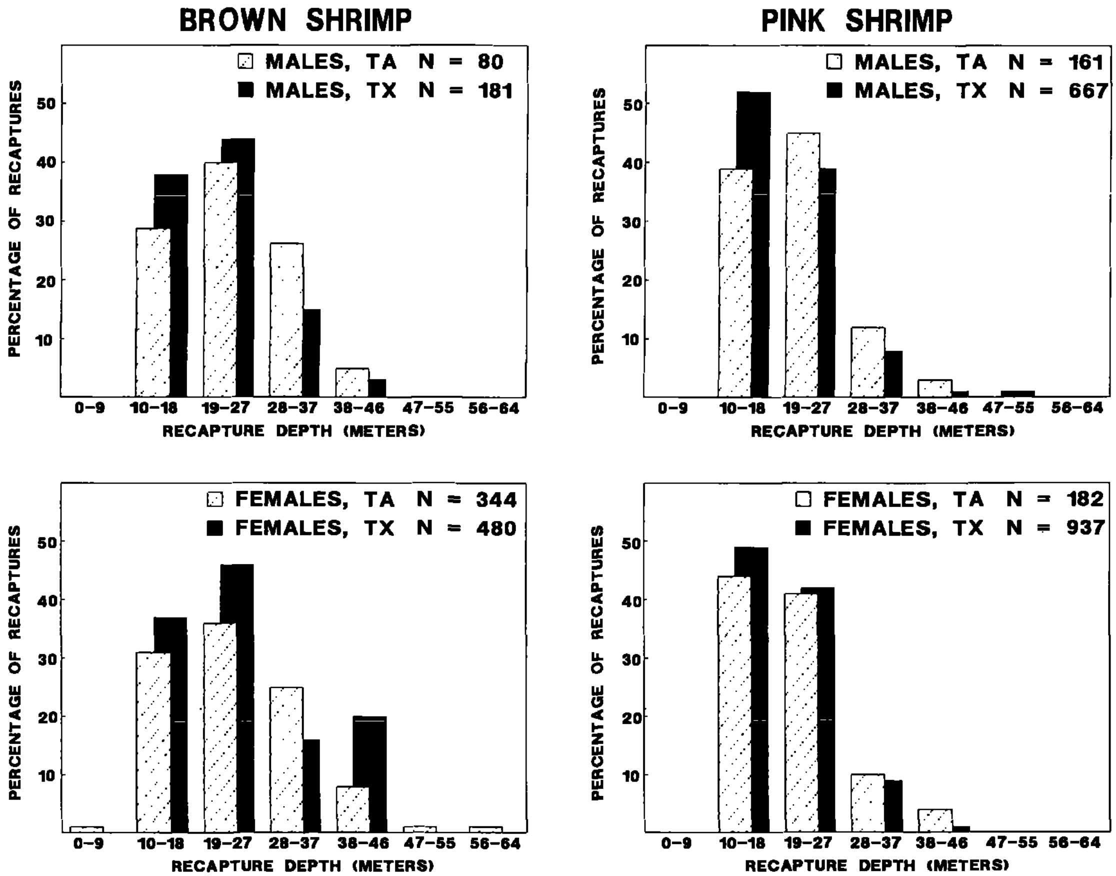

FIGURE 6.—Comparison of recapture depths of marked shrimp after release off Tamaulipas (TA) or Texas (TX).

R/f Analysis

Previous analyses indicated that sex had little to do with components of shrimp movement (except in some three-way interaction terms), so sexes were pooled for R/f analysis. North versus south comparisons of cumulative R/f values after each brown shrimp release (Table 8) indicated greater movement toward the border after 5 of 10 Tamaulipas releases and after 9 of 12 Texas releases. However, there were no significant differences in north versus south R/f values for brown shrimp in either state (Table 9). Comparisons of R/f values after pink shrimp releases indicated greater movement toward the border after 8 of 10 Tamaulipas releases and after 6 of 12 Texas releases (Table 8). Only pink shrimp released off Tamaulipas exhibited significant northward movement (Table 9).

Replicate releases on different dates were made at two sites off Tamaulipas and at all six sites off Texas (Table 8). The recapture patterns indicated that shrimp collected near, and released on, a given site did not always disperse in the same directions. Only in 6 of 8 brown shrimp releases and 4 of 8 pink shrimp releases were the paired R/f values higher in the same directions.

DISCUSSION

Variation in components of movement was linked to both species and release state. However, R/f values indicated that during the study period recaptured brown shrimp exhibited no preferred movement north or south off either Texas or Tamaulipas while recaptured pink shrimp only showed significant movement northward after Tamaulipas releases. Thus, the 1986 Texas fishery did not lose fishable biomass across the border as a result of the Texas Closure and, in fact, may have gained biomass due to the northward movement of pink shrimp off

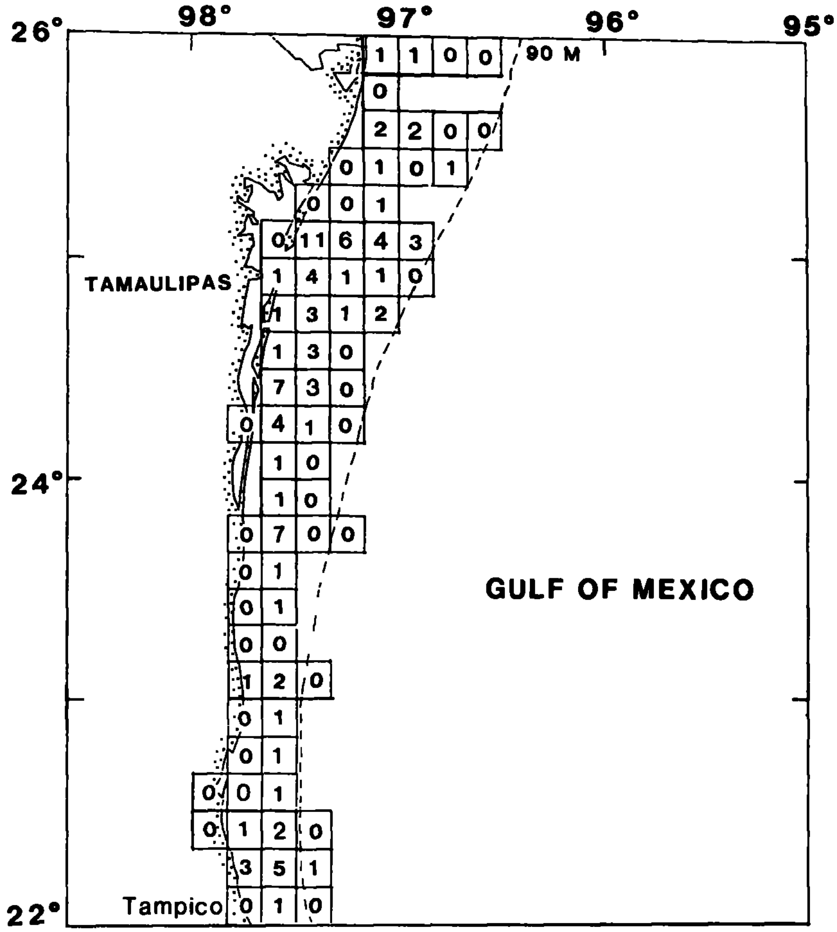

FIGURE 7.—Distribution of fishing effort by 10-minute grids of latitude and longitude for vessels fishing off Tamaulipas and landing in Tampico during 1 June–31 August 1986. Numbers in each grid are percentages of the total effort recorded by port agent interviews, where 0 = <1% of the total effort and a blank = no effort.

TABLE 8.—Directional movement of brown shrimp and pink shrimp away from Tamaulipas (TA) and Texas (TX) release sites as indicated by recaptures per 10^4 hour fished (R/f) north and south of the release sites. Sites are arranged from south to north, and an asterisk (*) indicates a replicate release.

Release		Brown shrimp R/f		Pink shrimp R/f		Release		Brown shrimp R/f		Pink shrimp R/f	
State	Site	North	South	North	South	State	Site	North	South	North	South
TA	1	2.7	23.1	1.7	7.2	TX	1	2.0	6.4	20.8	515.5
	2	5.9	7.2	2.2	0.5		1*	9.4	16.7	64.3	0.0
	3	3.2	15.1	11.7	13.8		2	1.9	6.2	10.8	83.3
	3*	13.7	13.9	7.8	4.9		2*	1.8	48.0	3.5	6.0
	4	63.2	11.3	24.8	2.0		3	2.9	13.7	2.3	0.0
	5	46.0	11.4	5.4	0.7		3*	0.9	2.0	0.0	1.4
	5*	38.0	9.3	48.9	16.0		4	0.7	1.4	13.4	17.0
	6	0.0	3.4	23.3	11.0		4*	1.1	0.6	18.7	10.2
	7	8.1	1.8	48.4	11.2		5	0.8	0.0	1.9	0.5
	8	3.7	0.0	0.1	0.0		5*	10.6	0.6	3.7	0.0
							6	0.0	1.2	1.0	6.9
							6*	3.3	15.4	0.8	0.7

TABLE 9.—ANOVA results comparing paired north versus south R/f values for brown shrimp and pink shrimp by release state (TA = Tamaulipas, TX = Texas).

Species	State	Source of error	df	SS	F	P
Brown	TA	R/f	1	389.84	1.53	0.247
		Release	9	2,612.93	1.14	0.424
		Error	9	2,290.03		
	TX	R/f	1	245.76	2.57	0.137
		Release	11	1,125.21	1.07	0.456
		Error	11	1,050.57		
Pink	TA	R/f	1	572.45	5.00	0.048
		Release	9	2,378.55	2.31	0.114
		Error	9	1,030.27		
	TX	R/f	1	10,429.20	0.98	0.343
		Release	11	125,748.12	1.08	0.452
		Error	11	116,704.83		

Tamaulipas. Previous mark-recapture studies in Texas and Tamaulipas waters indicated southward movement of brown shrimp and pink shrimp after May–June 1979 and 1980 releases in areas adjoining the border (Sheridan et al. 1987). Analysis of recaptures from those early experiments employed different methods from that used in this paper. First, recaptures "north", "within", and "south" of the release sites were located in relatively large areas delimited by one degree of latitude or longitude and by 0–90 m depths, not 10 minute grids of latitude and longitude; thus short-distance movement was not included in the analyses. Second, recaptures were standardized by landings within these large areas, not by effort. Third, recaptures and landings were accepted from the month of release through the month of last recapture, not during a restricted time period, which tended to reduce recaptures per unit landings values since ⩾50% of

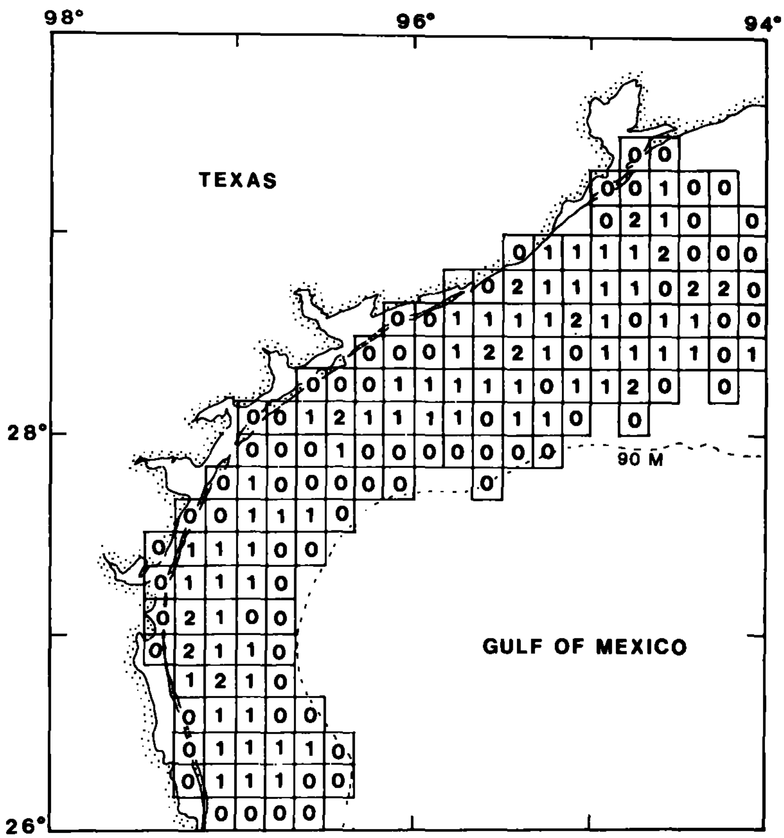

FIGURE 8.—Distribution of fishing effort by 10-minute grids of latitude and longitude for 47 vessels fishing off Texas during 1 June–31 August 1986. Numbers in each grid are percentages of total log book effort, where 0 = <1% and a blank = no effort.

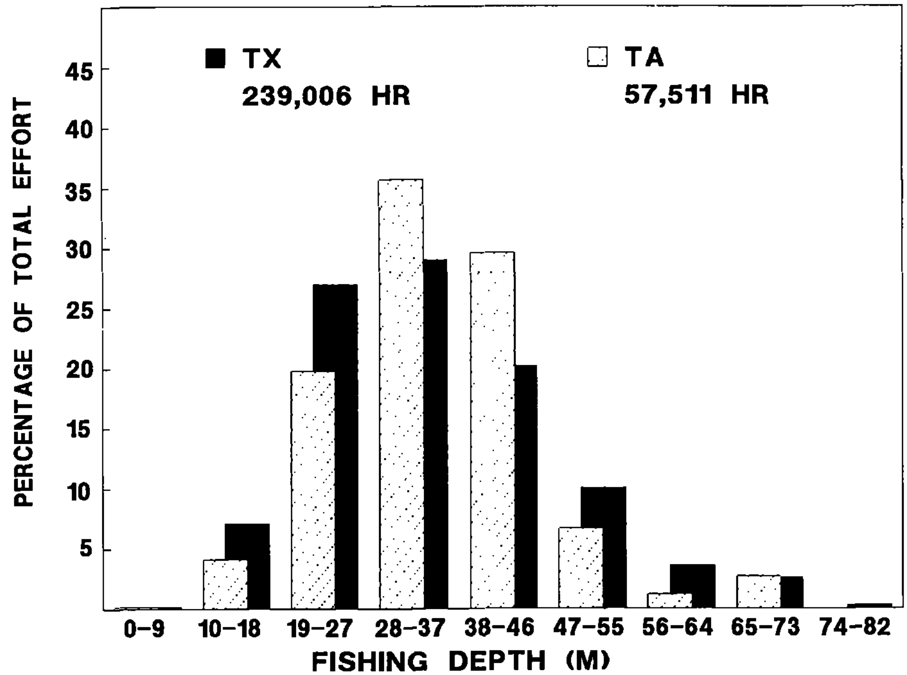

FIGURE 9.—Comparison of fishing effort (h) by depth strata between Texas (TX) and Tamaulipas (TA) interviews.

all recaptures were made within 40 days after release. Thus, in contrast to the present study, the mark-recapture analyses reported by Sheridan et al. (1987) were of limited use since they described primarily a small number of long-distance, long-duration recaptures. The difference in results is most likely due to the higher quality, finer scale data collected during the present experiments and to the use of all recaptures, not just those for shrimp moving long distances.

The factors "species" and "state" may actually describe different habitat requirements and different levels of fishing effort in the western Gulf of Mexico. Trawl catches indicate brown shrimp utilize a greater depth range (0–160 m) and are found over a wider variety of substrates (sand, silt, clay) than pink shrimp (0–65 m depth; coarse sand and shell) (Hildebrand 1954, 1955; Williams 1958; Cook and Lindner 1970; Costello and Allen 1970; Grady 1971; Renfro and Brusher 1982). Offshore substrate preferences of brown shrimp and pink shrimp have not been directly tested, however. Coarse substrates tend to lie in pockets or bands paralleling the Texas coast (McGowen and Morton 1979); thus pink shrimp recaptures could reflect longshore movement seeking these substrates. The major influence on recapture patterns was the difference in fishing activity between the two states: fishing effort off Tamaulipas was only 13% of the effort expended off Texas and occurred in deeper waters. Consequently, fishing mortality off Tamaulipas was lower and tagged shrimp generally exhibited a lesser recapture rate, greater times at large, greater distances travelled, and greater depths at recapture. Collection and utilization of fishing effort data thus seems imperative for interpretation of tag recapture patterns.

A potential source of error common to all mark-recapture experiments involves the precision of reported recapture locations. Trawl tows are of variable durations and distances, and there is no way of knowing at what point along a towing track that a marked shrimp is captured. In addition, the exact locating of recoveries depends on the precision of navigational equipment, which is usually not recorded and which could vary from dead reckoning to satellite navigation. These factors would affect estimates of distance travelled, speed, and direction but not recapture depth (shrimpers tow along, rather than across, depth contours to avoid gear adjustments) or days at large. Effects on R/f values would also be minimal since R/f does not depend on exact distances. There was no way to control for these potential difficulties other than discarding all short-distance returns, and that would have resulted in a loss of 1,173 of the 3,032 most accurate recaptures. It was believed that the initial screening of recaptures, which eliminated 2,607 of 5,639 recaptures, removed most of the inaccurate return data.

Another source of error relates to the estimated distribution of fishing effort into the grid system off Mexico. Interview coverage was 100% of all vessels coming into the port of Tampico, Tamaulipas, and likely reached a majority of Mexican vessels fishing off Tamaulipas. Captains were asked to specify fishing areas and effort but not how much time was spent in each grid. If more than one grid was fished on a trip, it was assumed that effort was divided equally among all grids fished. This would tend to reduce the estimated effort over more favored fishing grounds and increase it elsewhere, inflating R/f values over favored grounds and decreasing R/f values elsewhere. In Tamaulipas waters, effort appeared to be most concentrated between 24°20′N and 25°09′N off the Laguna Madre de Tamaulipas. Six of 10 releases were made to the north (25°10′N–25°59′N) and R/f values north of these 6 release sites could have been artificially low. This would not affect the already significant northward trend in pink shrimp movement, but would increase the nonsignificant trend in northward brown shrimp movement toward significance.

A different problem exists with the estimated distribution of fishing effort off Texas. Whereas the captains of nearly 100% of the Tamaulipas fleet were interviewed, only 3.1% of those of the Texas fleet were interviewed (via logbooks) in enough detail to estimate effort in grids. Regular port agent interviews recorded 55% of total Texas effort. Comparison of the depth distributions of effort between Texas interviews and Texas logbooks indicated no significant differences. However, comparison of the effort expended within one-degree quadrangles of latitude and longitude determined by each method indicated similar estimations of effort from 26°00′N to 26°59′N (32% of total effort by logbook, 33% by interview) but overestimation of effort from 27°00′N to 27°59′N by logbooks (38% vs. 25%). For Texas releases with recaptures north of 26°59′N (9 of 12 releases), R/f values north of release sites were probably underestimated. Since neither brown shrimp nor pink shrimp R/f values indicated significant directional movement off Texas, it is unlikely that the underestimation of northward R/f values would affect the comparisons.

Recaptures standardized by fishing effort are rarely used to analyze movement patterns of aquatic organisms. Bayliff and Rothschild (1974) and Bayliff (1979) reported movements of yellowfin tuna, *Thunnus albacares*, in terms of recaptures weighted by fishing effort in the eastern Pacific Ocean (Mexico to Ecuador). Their recapture patterns were not tested for directional movement after individual releases, and interpretation of their results could be confounded by long recapture periods (up to one year) and the large ocean surface areas addressed (0°–25°N, 80°–150°W). Gitschlag (1986) employed the R/f index as a means of reducing bias associated with nonuniform fishing effort upon apparent movement patterns of pink shrimp in an area approximating a quadrangle of one degree latitude and longitude off Florida. The only other study reporting both recaptures and effort for marked shrimp was conducted by Somers and Kirkwood (1984) on tiger prawn (*Penaeus esculentus* and *P. semisulcatus*) movements in Australia, but recaptures per unit effort were not analyzed. In reality, most mark-recapture experiments on penaeid shrimp and other organisms have been more concerned with obtaining estimates of fishing and natural mortality rates, growth rates, or stock ranges rather than assessing movements per se. We believe that employing R/f values yields more accurate information on shrimp movements than recaptures alone.

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