Larval distribution and transport of penaeoid shrimps during the presence of the Tortugas Gyre in May–June 1991

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Abstract.—As part of the Southeast Florida and Caribbean Recruitment Project (SEFCAR), penaeoid shrimp larvae were collected during the spring and summer cruise of the RV *Longhorn* in the Lower Florida Keys and Dry Tortugas from 29 May to 30 June 1991. Larvae of the pink shrimp, *Penaeus duorarum*, and the rock shrimp, *Sicyonia* sp., were distributed inshore close to the Dry Tortugas Grounds, whereas larvae of the oceanic shrimp *Solenocera* sp. showed mainly an offshore distribution. Significant concentrations of *Solenocera* sp., *Sicyonia* sp., and *P. duorarum* larvae at the Tortugas transect in early June were found within and above the seasonal thermocline while the cold cyclonic Tortugas Gyre was intensively developed. For *Solenocera* sp., which spawn on the outer edge of the gyre, high concentrations of larvae were found at the inshore stations of the Tortugas transect in early June, presumably as a result of the cyclonic circulation of the gyre followed by onshore Ekman transport. *Penaeus duorarum*, which spawn in the shallow Tortugas Grounds, showed a mode of zoea II–III progressing to postlarvae I at the Tortugas Grounds during the 15 days in which the drifter *Halley* recirculated in the interior of the Tortugas Gyre. Retention of *P. duorarum* larvae by the internal circulation of the gyre at the spawning grounds may be an important mechanism for local recruitment of these shrimp to the nursery grounds of Florida Bay.

Manuscript accepted 7 December 1994.
Fishery Bulletin 93:471–482 (1995).

Penaeoid shrimps constitute the second most valuable segment of the U.S. fishing industry and are arguably one of the most valuable groups of marine species in the world. Annual stocks fluctuate widely and few spawning stock/recruitment relationships have been demonstrated (Garcia, 1983). The penaeid shrimp *Penaeus duorarum*, or pink shrimp, supports an important commercial fishery in south Florida. Pink shrimp yielded a stable catch of 9.6 million pounds per year from 1960 to 1986 (Klima et al., 1986). However, this catch has declined by more than 50% in the last four years (NMFS[1]). This fishery is directly dependent on young shrimp that migrate from nursery areas onto the fishing grounds (Nance and Patella, 1989). Animals with short life spans (≈2 years), such as pink shrimp, depend almost entirely on one year class being recruited during the year.

The life history of *P. duorarum* of the Dry Tortugas (shallow banks located about 100 km west from Key West) involves one oceanic and one estuarine phase (Garcia and Le Reste, 1981). Adults spawn offshore on the Dry Tortugas, where females lay demersal eggs (Fig. 1). The larvae undergo several changes in feeding habits and morphology including five naupliar stages, three zoeal or protozoeal, and three mysid stages. The last mysis undergoes a moult at which time it transforms into a postlarva. The average time required by *P. duorarum* to reach the first postlarval stage is approximately 20 days at 26°C (Ewald, 1965).

The first postlarval stages are still planktonic whereas those that follow are benthic. Postlarvae migrate inshore, entering the Florida Bay nursery grounds where they metamorphose to juveniles. When they have reached a length of about 10 cm, they return to the Tortugas spawning area (Allen et al., 1980).

Advective processes of *P. duorarum* and their relation to oceanographic and environmental factors are not fully understood. Research on the larval phase was performed in the mid 1960's. Munro et al. (1968) and Jones et al. (1970) studied the abundance and distribution of larvae of *P. duorarum* on the Tortugas Shelf and in the Florida Keys. These authors

[1] Jones, A. Southeast Fish. Sci. Center, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, FL 33149. Unpubl. data, 1993.

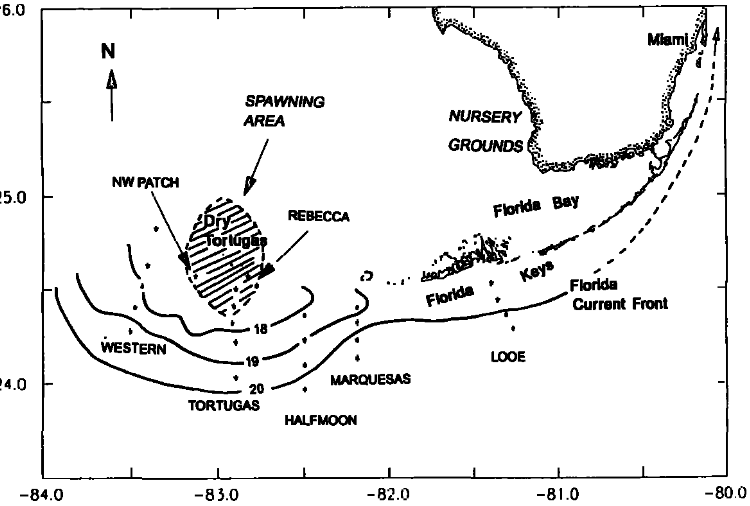

Figure 1

Location of transects and 1-m² MOCNESS sampling stations (*) of the Southeast Florida and Caribbean Recruitment Project (SEFCAR) cruise LH3, 29 May–30 June 1991 at the Dry Tortugas and Lower Florida Keys. Shaded area indicates spawning area of pink shrimp, *Penaeus duorarum*, in southeast Florida. Solid lines are the CTD temperatures at 100 m depth in late May 1991. Dashed line indicates the continuation of the Florida Current.

hypothesized that *P. duorarum* larvae migrate from where they are spawned in the Dry Tortugas by means of the Florida Current and return to Florida Bay through passes in the middle Keys. However, they had difficulty in explaining the exact migratory path in light of inconsistencies between the prevailing currents and the abundance of larvae in the pathway to the coast.

Penaeoid shrimps other than *Penaeus* are abundant in the Dry Tortugas and may occur in commercial catches (Eldred, 1959), but they are of little or no economic value. Such is the case for the rock shrimp, *Sicyonia* spp., the humpback shrimp, *Solenocera* spp., and the roughneck shrimp, *Trachypenaeus* spp. Life histories of these species are poorly known, and larval research in the Gulf of Mexico has focused on trends of seasonal distribution (Eldred et al., 1965; Temple and Fisher, 1967; Subrahmanyam, 1971b).

The Southeast Florida and Caribbean Recruitment Project (SEFCAR) has investigated the effect of oceanographic processes on plankton and regional recruitment of fishes and other reef species along the continental shelf in southeast Florida. The hydrographic conditions in the Straits of Florida are dominated by the strong Florida Current. In the southwestern part of the Florida Keys, the Florida Current is highly variable, often associated with meanders and gyres (Lee et al., 1992). The Dry Tortugas are located near the turning point where the southward-flowing Loop Current swerves abruptly east to enter the Straits of Florida (Gaby and Baig, 1983). A cyclonic gyre over the slope off the Dry Tortugas with horizontal dimensions of approximately 200 km has been described by Lee et al. (1994). The gyre, which persisted for about 100 days from mid-May to late August 1994, was observed to move eastward to the region of the Pourtales Terrace (Lee et al., 1994). Lee et al. (1992) called this gyre the Pourtales Gyre, and its effect on lobster *Scyllarus* sp. and shrimp larvae was demonstrated by the high abundance of larvae nearshore in the path of the westward flow of the gyre (Yeung and McGowan, 1991; Criales and McGowan, 1994).

The objective of this study is to describe the horizontal and vertical distribution patterns of the three most abundant penaeoid shrimp larvae in the Dry Tortugas and lower Florida Keys during the presence of the cyclonic Tortugas Gyre. This work will form a basis for later comparisons with surveys under different hydrographic conditions.

Materials and methods

Plankton and hydrographic sampling

Samples were collected between 29 May and 30 June 1991, as part of the cruise LH3 of the RV *Longhorn*, by using a 1-m² MOCNESS (multiple opening-closing net and environmental sensing system [Wiebe et al., 1976]) with 0.333-mm net mesh size. The nine nets of the MOCNESS were towed in an aperture along an oblique path at a speed of approximately 2 m·s^{-1}, and samples from the surface to near the bottom were collected. Net 1 in the set was towed obliquely from the surface down to about 200 m or to the closest multiple of 20 m if the water depth was less than 200 m. Net 2 (deepest) to net 9 (uppermost) sequentially opened or closed at controlled depths of 200–160 m, 160–130 m, 130–100 m, 100–80 m, 80–60 m, 60–40 m, 40–20 m, and 20–0 m for the deeper stations, and 50–40 m, 40–30 m, 30–20 m, 20–10 m, and 10–0 m, or 45–30 m, 30–15 m, and 15–0 m depth intervals for the shallow stations (<50 m). A flowmeter and conductivity-temperature depth (CTD) sensors were attached to the net frame. The volume of water filtered in each layer varied from 130 to 593 m³, depending on the depth strata sampled.

The cruise was divided into four legs (fifty-six stations) from west of the Dry Tortugas to Looe Key in the middle Florida Keys (Fig. 1). The sampling data are summarized in Table 1. Stations of leg 1 were repeated in the other three legs. During leg 2, one transect was added at Marquesas and another at Halfmoon. Leg 3 repeated stations of legs 1 and 2 in addition to an upstream transect (Western transect). Leg 4 included a downstream transect (Looe Key) in addition to the Tortugas, Rebecca, NW Patch, and Marquesas transects (Fig. 1).

Sampling was carried out continuously depending on the time the ship arrived at the station (Table 1). Samples were taken during the day at 35 stations and at night at the remaining 21 stations. Three moon phases were covered during this cruise. Twenty-six stations were sampled during the full moon, eight during the last quarter, and eight during the new moon.

Three ARGOS satellite-tracked surface drifters were deployed on the northern side of the gyre as part of the physical oceanographic survey. Two stations were sampled on the track of drifter *Halley* after a 15-day interval (day 1=30 May, day 15=13 June).

Larval identification and standardization

Plankton samples were preserved in 4% formaldehyde-seawater solution and later transferred to 70% ethanol. Aliquot sampling was performed after the similarity of duplicate samples was statistically evaluated (t-test, t_9=0.04, P<0.05). Each sample was adjusted to a volume of 500 mL, and the penaeoid larvae sorted from five 25-mL aliquots. The mean of the five counts was standardized to the concentration of larvae (no./100 m^3) or to abundance (no./10 m^2 of sea surface). No nauplii were caught because the mesh size of the net was too large to retain them.

Penaeoid shrimp larvae were identified to genus or species by using existing keys and larval descriptions (Heldt, 1938; Pearson, 1939; Gurney, 1943; Dobkin, 1961; Cook, 1966; Heegaard, 1966; Subrahmanyam, 1971a). Postlarvae of *Penaeus* sp. were identified from the keys of Williams (1965) and the morphometric study of Chuensri (1968). Individual stages were separated only for *P. duorarum* because it was the only species of interest for which larval stages have been described (Dobkin, 1961). The remaining penaeoid identifications were made to a generic level.

Statistical analysis

Mean abundance of total larvae caught at day (0631–2000 h; n=35, $\bar{x}$=98.3, SD=111.6) versus night (2001–0630 h; n=21, $\bar{x}$=91.4, SD=115.5) stations was not significantly different (t-test, t_{54}=0.82, P>0.05); therefore day and night data were pooled (Sokal and Rohlf, 1981).

To characterize the vertical distribution of the different larval stages per species, the depth of the center of mass (Z_m) was calculated (Röpke et al., 1993):

$$Z_m = \sum(P_i \times Z_i)$$

$$P_i = C_i \times H_i \Big/ \sum(C_i \times H_i),$$

where P_i is the standardized (no./100 m^3) number of larvae in the i^{th} depth stratum; Z_i is the mean sampling depth of the i^{th} depth stratum; C_i is the concentration of larvae in 100 m^3; and H_i is the width of i^{th} depth interval. Day and night stations were separated to determine any daily vertical larval migration. Differences in Z_m between day and night were not significant for any of the three species (*P. duorarum* t-test, t_{24}=0.63, P>0.05; *Sicyonia* sp. t-test, t_{36}=0.95; *Solenocera* sp. t-test, t_{50}=0.28, P>0.05), suggesting no daily vertical migration of larvae; therefore data were pooled. However, this may be biased by the greater number of day stations (35 day, 21 night).

Results

Horizontal distribution and abundance

Penaeus duorarum These larvae showed an onshore distribution concentrated near the Dry Tortugas (Fig. 2). The density ranged from 1.5 to 57.1 larvae/10 m^2 represented by 60.3% zoeae, 15% myses, and 24.7% postlarvae. Distribution of zoeae was nearshore; 90% were caught no farther than 25 km offshore from the Dry Tortugas. Myses were distributed a little farther offshore and eastward than zoeae but no more than 45 km from the coast. The trend of distribution of postlarvae was also close to shore; 83% of postlarvae I–III were located inshore at the Tortugas, Halfmoon, NW Patch, and Rebecca transects. The other 17% were found at the offshore stations of Marquesas associated with the Florida Current front, and no postlarvae were captured at the Looe Key transect (Fig. 2).

Larval stages in the spawning area at the NW Patch and Tortugas transects showed a progression of ages during the four legs of sampling (Fig. 3). In late May zoeae II–III showed a high concentration (33.8–45.4 larvae/10 m^2) at the spawning area, few myses were found at these stations, and no postlarvae were caught. In early June, 15 days after the first sampling, the abundance of myses and postlarvae increased. Postlarvae II–III reached their peak of con-

Table 1

Station data and abundance (no./10^2) of penaeoid shrimp larvae during the Southeast Florida and Caribbean Recruitment Project (SEFCAR) cruise LH3, 29 May–30, June 1991.

Station	Latitude N	Longitude W	Max-depth (m)	Distance offshore (km)	Date	Local time (h) (EDT)	Moon phases	Transect	*Penaeus duorarum*	*Sicyonia* sp.	*Solenocera* sp.
Leg 1, 29–31 May											
15	24.498	82.904	25	13.28	29 May	1118 day	Full	Tortugas	12.14	36.43	0.00
17	24.408	82.907	60	25.19	29 May	1242 day	Full	Tortugas	0.00	0.00	56.09
19	24.317	82.916	200	37.03	29 May	1418 day	Full	Tortugas	0.00	0.00	3.46
21	24.222	82.902	207	48.65	29 May	1621 day	Full	Tortugas	0.00	0.00	54.01
23	24.032	82.903	201	73.10	29 May	1754 day	Full	Tortugas	0.00	0.00	0.00
26	24.570	83.125	40	21.50	30 May	1947 day	Full	NW Patch	37.87	29.73	20.60
27	24.559	83.141	40	23.99	31 May	2113 night	Full	NW Patch	41.33	69.10	12.87
Leg 2, 4–7 June											
29	24.500	82.916	20	13.28	4 June	1656 day	Full	Tortugas	19.02	22.83	3.80
30	24.406	82.908	60	25.19	4 June	1816 day	Full	Tortugas	19.76	54.01	129.26
31	24.317	82.916	202	37.03	4 June	2036 night	Full	Tortugas	7.05	52.24	191.50
32	24.227	82.912	203	48.65	4 June	2237 night	Full	Tortugas	0.00	4.04	254.62
36	24.567	83.132	40	22.33	5 June	1946 day	L. quarter	NW Patch	0.00	32.85	100.29
37	24.357	82.500	48	40.28	6 June	1121 day	L. quarter	Halfmoon	36.57	200.21	84.40
38	24.229	82.499	167	47.29	6 June	1243 day	L. quarter	Halfmoon	18.96	35.17	16.64
39	24.103	83.501	197	58.03	6 June	1442 day	L. quarter	Halfmoon	2.86	9.71	21.62
40	23.972	82.503	200	71.39	6 June	1644 day	L. quarter	Halfmoon	0.00	10.46	90.89
42	24.226	82.189	198	30.09	6 June	2334 night	L. quarter	Marquesas	5.28	0.00	16.13
43	24.324	81.194	196	17.47	7 June	0209 night	L. quarter	Marquesas	0.00	0.00	43.38
44	24.403	82.191	77	7.31	7 June	0409 night	L. quarter	Marquesas	0.00	0.00	5.12
Leg 3, 12–18 June											
45	24.568	83.120	40	20.17	12 June	0914 day	New	NW Patch	6.45	3.37	24.84
46	24.833	83.359	56	35.80	12 June	1209 day	New	Western	2.45	0.00	145.05
47	24.634	83.408	57	44.96	12 June	1429 day	New	Western	0.00	0.00	103.36
48	25.524	83.445	125	57.06	12 June	1631 day	New	Western	4.27	6.76	564.17
49	24.401	83.483	202	72.29	12 June	1834 day	New	Western	0.00	0.00	67.77
50	24.280	83.522	200	88.52	13 June	2057 night	New	Western	0.00	0.00	93.78
51	24.032	82.903	200	72.76	13 June	0225 night	New	Tortugas	0.00	0.00	428.11
52	24.222	82.902	203	47.84	13 June	0503 night	New	Tortugas	0.00	0.00	37.43
53	24.317	82.916	202	34.46	13 June	0709 day	New	Tortugas	15.64	7.89	153.24
54	24.408	82.907	58	24.93	13 June	0859 day	New	Tortugas	17.74	26.72	95.20
55	24.498	82.904	21	13.58	13 June	0612 day	New	Tortugas	0.00	5.03	10.74
56	24.524	82.784	17	14.75	13 June	1437 day	New	Rebecca	16.72	22.94	13.72
62	24.403	82.191	57	2.02	17 June	1422 day	New	Marquesas	0.00	4.56	5.94
63	24.324	82.194	162	16.29	17 June	1625 day	New	Marquesas	0.00	2.58	23.66
64	24.226	82.189	162	28.28	17 June	1751 day	New	Marquesas	2.72	10.16	11.50
65	24.133	82.186	159	42.05	17 June	1924 day	New	Marquesas	6.95	17.76	6.00
66	23.972	82.503	160	71.39	17 June	2236 night	New	Halfmoon	0.00	1.95	48.16
67	24.103	82.501	163	58.03	18 June	0107 night	New	Halfmoon	0.00	0.00	50.30
68	24.231	82.501	164	47.29	18 June	0314 night	New	Halfmoon	0.00	0.00	41.40
69	24.360	82.501	15	40.28	18 June	0500 night	New	Halfmoon	0.00	15.09	11.05
70	24.524	82.784	15	14.75	18 June	0638 day	New	Rebecca	20.14	16.60	1.95
71	24.559	83.141	30	19.89	18 June	0938 day	New	NW Patch	17.63	0.00	4.64

centration (18.9 larvae/10 m^2) in mid-June. In late June the peak of zoeae II reoccurred (35.8 larvae/10 m^2).

***Sicyonia* sp.** Rock shrimp was the second most abundant species after *Solenocera* sp. The highest densities were located at the NW Patch and Halfmoon transects (Fig. 4A). Zoeae represented 31.3% of the catch and myses 68.7%. Zoeae were highly abundant at the NW Patch stations in early May (78.8 larvae/10 m^2) and early June (91.1 larvae/10 m^2), and myses were distributed in patches with two large peaks, one at the Halfmoon transect (184.8 lar-

Table 1 (continued)

Station	Latitude N	Longitude W	Max-depth (m)	Distance offshore (km)	Date	Local time (h) (EDT)	Moon phases	Transect	*Penaeus duorarum*	*Sicyonia* sp.	*Solenocera* sp.
Leg 4, 28–30 June											
77	24.032	82.903	160	73.10	28 June	1101 day	Full	Tortugas	0.00	6.60	146.53
78	24.222	82.902	160	48.65	28 June	0140 night	Full	Tortugas	0.00	5.03	10.62
79	24.317	82.916	160	36.46	28 June	1540 day	Full	Tortugas	0.00	4.11	14.38
80	24.408	82.907	57	24.93	28 June	1817 day	Full	Tortugas	1.55	8.60	4.66
81	24.498	82.904	20	13.28	28 June	1827 day	Full	Tortugas	41.34	15.64	0.00
82	24.559	83.141	28	21.95	28 June	2031 night	Full	NW Patch	57.12	151.39	0.00
83	24.570	82.832	15	27.75	28 June	2347 night	Full	Rebecca	14.09	7.05	58.13
85	24.133	82.186	160	36.46	29 June	1616 day	Full	Marquesas	1.72	1.72	3.00
86	24.226	82.189	160	24.93	29 June	1800 day	Full	Marquesas	6.85	2.81	37.73
87	24.324	82.194	158	16.28	29 June	2009 night	Full	Marquesas	0.00	5.75	39.50
88	24.403	82.191	53	2.02	29 June	2148 night	Full	Marquesas	0.00	3.10	23.94
89	24.528	81.395	25	2.16	30 June	0414 night	Full	Looe	0.00	0.00	0.00
90	24.444	81.356	160	11.49	30 June	0443 night	Full	Looe	0.00	0.00	23.69
91	24.361	81.312	161	20.82	30 June	0810 day	Full	Looe	0.00	2.42	33.53
92	24.293	81.269	160	28.27	30 June	2213 night	Full	Looe	0.00	17.31	89.51
									434.20	929.70	3531.90

vae/10 m^2) in early June and the other at the stations of NW Patch transect (60.3 larvae/10 m^2) in late June.

***Solenocera* sp.** This species represented the most abundant penaeoid larvae at the Dry Tortugas and lower Florida Keys, accounting for 72% of the total catch (Fig. 4B). The highest densities were located offshore of the Tortugas and Western transects. Abundances were lowest in late May, increased considerably in early June, and reached their peak in mid-June (Table 1). Of the catch, 29.2% was represented by zoeae and 70.8% by myses. Distribution of early zoeae was patchy; two main peaks occurred at the Western (282.9 larvae/10 m^2) and Tortugas transects (135.4 larvae/10 m^2), and mysid stages were very widely distributed throughout the area with the highest abundance at the Tortugas transect (136.6 larvae/10 m^2) (Fig. 4B). Zoeae and myses showed an offshore distribution, except at stations along the Tortugas transect in early June where high concentrations of *Solenocera* sp. larvae were found at the inshore stations while the Tortugas Gyre was well developed (Figs. 4B and 5).

Vertical distribution

Depths of the center of mass (Z_m) were calculated for the different larval stages of each species (Table 2). *Penaeus duorarum* larvae showed a shallow distribution (Z_m=18 m) which was similar among stages. *Sicyonia* sp. showed a mean Z_m of 27 m, though zoeae were distributed deeper than myses. *Solenocera* sp. larvae were widely spread throughout the water column from 0 to 100 m; the peak concentration occurred at about 42 m, and myses occurred deeper than zoeae (Table 2).

Penaeus duorarum larvae were distributed between temperatures of 23° and 29°C, *Sicyonia* sp. larvae between 20° and 28°C, and *Solenocera* sp. larvae between 15° and 29°C. Maximum concentrations were found between 22° and 26°C (Fig. 5).

Penaeus duorarum postlarvae at the offshore stations of the Marquesas transect (n=6, $Z_m\ \bar{x}$=20.8, SD=14.8) were relatively deeper than those at inshore stations (n=11, $Z_m\ \bar{x}$=11.6, SD=6.7) restricted to the seasonal thermocline (t-test, t_{15}=0.09, P>0.05).

Effect of the Tortugas Gyre on larval abundance and dispersal

Abundance and vertical distribution at Tortugas transect A general downward slope of the upper seasonal thermocline (23–27°C) toward shore was present during the four legs at the Tortugas transect (Fig. 5). *Solenocera* sp., *Sicyonia* sp., and *P. duorarum* larvae were highly concentrated above or within the seasonal thermocline. The strength of the seasonal thermocline, which is uplifted in the interior of the gyre, appears to have been a limiting factor for vertical migrations of these penaeoid larvae.

Solenocera sp. larvae were very abundant at the inshore stations between 25 and 75 m in depth during leg 2, corresponding with the strongly developed thermocline (Fig. 5). The inshore distribution of *Solenocera* sp. during this leg was noteworthy because these larvae showed an offshore distribution during the other legs.

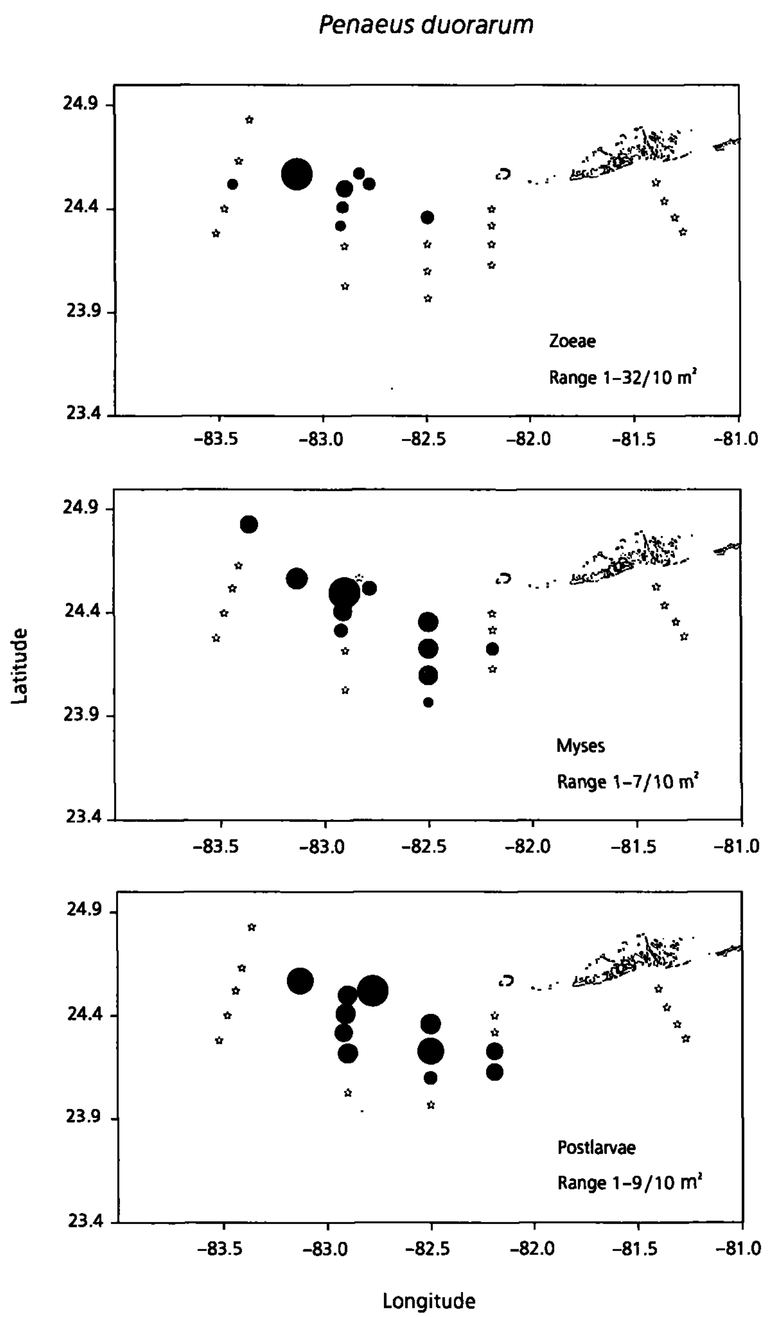

Figure 2

Horizontal distribution and relative abundance (larvae/10 m^2) of the larval stages of pink shrimp, *Penaeus duorarum*, at the sampling stations of the four legs of the LH3 cruise, 29 May–30 June 1991. Symbols are proportional in size to the abundance range and are positioned at the sampling stations. The stars = no catch.

High larval concentrations of the three species (*P. duorarum:* 1–40 larvae/100 m^3; *Sicyonia* sp.: 1–22 larvae/100 m^3; and *Solenocera* sp.: 10–60 larvae/100 m^3) were found at the Tortugas transect during leg 2 in early June within and above the seasonal thermocline between 25 and 75 m in depth (Figs. 5 and 6). Total abundances during leg 2 were much higher than those during any other leg for all three species. The abundance of *Solenocera* sp. was twice as great during leg 2, and there were highly significant differences among legs (ANOVA, $P \leq 0.05$) (Fig. 6).

Drifter circulation Drifter *Halley*, deployed on 30 May on the northern side of the Tortugas Gyre, moved south-southeast for about seven days, then turned back toward the west-northwest for about seven days (Fig. 7). The drifter spent the first 14 days in a tight recirculation in the interior of the gyre. The position of the drifter upon release initially corresponded with the position of stations 26 and 27. On 13 June, when it broke out of the gyral circulation, the drifter was located at Rebecca transect at station 56. At this point the drifter entered the Rebecca Channel between the Dry Tortugas and Rebecca Shoal where it stayed for about 10 days, undergoing tidal excursions of up to 7 km, but with no net through-flow. Relative percentages of the larval stages of *P. duorarum* at the station where the *Halley* drifter was released (Stns. 26 and 27) and at the station where this drifter broke out of the gyre circulation (Stn. 56) are plotted in Figure 7. On 30 May at stations 26 and 27, *P. duorarum* larvae showed one mode of zoeae, mainly II-III (84%). After 15 days, on 13 June, one mode of postlarvae I (67.7%) was present at station 56, a station near the departure point. The trajectory of the drifter *Halley* and the progression of age of *P. duorarum* larvae over the 15 days that the drifter spent recirculating within the gyre may indicate retention of *P. duorarum* larvae at the spawning area.

Abundance and composition of *Sicyonia* sp. larvae at the same two locations, stations 26 and 27, and at station 56 of

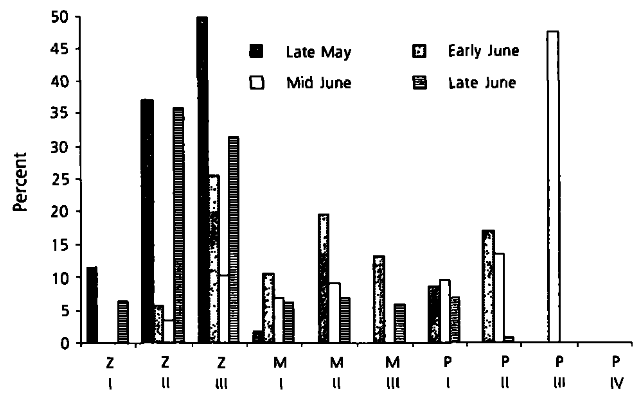

Figure 3

Percentages of the larval stages of pink shrimp, *P. duorarum*, at the Tortugas and NW Patch transects during the four legs of the cruise LH3, 29 May–30 June 1991. Z = zoeae; M = myses; and P = postlarvae.

Rebecca transect showed a similar trend to that described for *P. duorarum*: a high concentration of zoeae at the deployment of the drifter (80% zoeae) and 15 days later a dominance of myses (100% myses).

Discussion

Munro et al. (1968), in an examination of abundance and distribution of *P. duorarum* larvae in southeast Florida, could not reach firm conclusions regarding the path of migration from the Dry Tortugas to Florida Bay because of the inconsistency between the prevailing currents and the abundance of larvae in the pathway to the coast. However, they hypothesized that *P. duorarum* larvae may have been advected from where they were spawned in the Tortugas Grounds by means of the Florida Current and then were carried back into Florida Bay by tidal currents through passes in the middle Keys. The conceptual path of larval advection outlined by Munro et al. (1968) was consistent with the general current pattern known at that time. More recent oceanographic research on the Straits of Florida has shown a high variability in the Florida Current in the lower Keys and Dry Tortugas associated with meanders and gyres (Lee et al., 1992, 1994). Lee et al. (1994) showed from moored current meter data and surface drifter tracks that a cold, cyclonic gyre formed off the Dry Tortugas in mid-May and continued as a weak counterclockwise recirculation about 200 km in diameter until late August. Thus, the presence of the gyre could have acted as a larval retention and recirculation mechanism for the duration of the sampling cruise.

Table 2

Mean and standard deviation of the center of mass (Z_m ± SD) of the larval stages of three penaeoid shrimps during the SEFCAR cruise LH3, May–June 1991.

	Z (m)	SD	*n*
Solenocera sp.	42.41	20.97	52
Zoea	35.64	20.08	27
Mysis	42.18	20.69	49
Sicyonia sp.	26.85	17.02	38
Zoea	30.14	20.24	14
Mysis	25.19	13.22	36
P. duorarum	18.42	12.14	26
Zoea	15.00	9.13	15
Mysis	15.07	14.04	15
Postlarvae	16.81	18.67	17

Distributions of zoeae and myses of *P. duorarum* found in this study agree with those of Munro et al. (1968) and Jones et al. (1970) for the Tortugas shelf. However, postlarval distribution in the present study was different; most postlarvae (stages I–III) were located inshore near the area where they were spawned, rather than offshore as was found by Munro et al (1968). Composition of larval stages at the

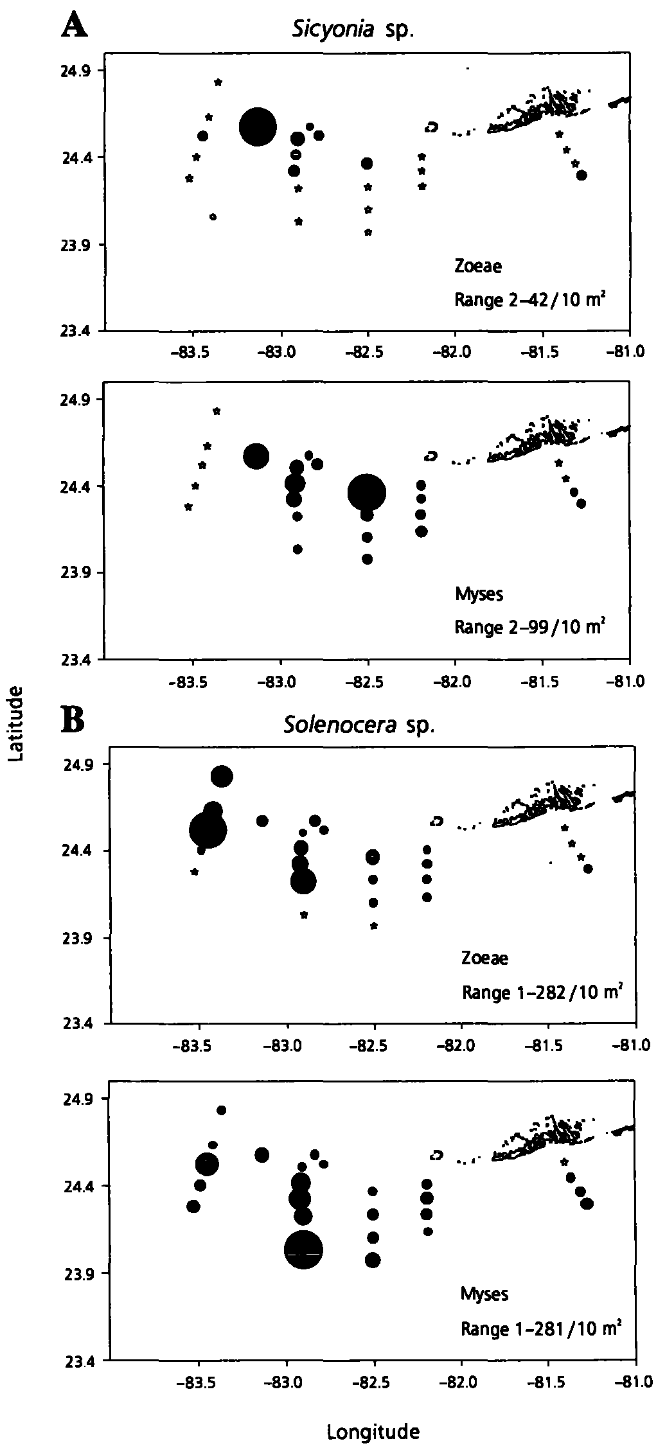

Figure 4
Horizontal distribution and relative abundance (larvae/10 m^2) of zoeal and mysid stages of (**A**) the rock shrimp *Sicyonia* sp. and (**B**) the humpback shrimp *Solenocera* sp. for the four legs of the LH3 cruise, 29 May–30 June 1991. The symbols are proportional in size to the abundance range and are positioned at the sampling stations. The stars = no catch.

Tortugas and NW Patch transects and at the two stations sampled on the track of the drifter *Halley* showed the same modal progression of zoeae to postlarvae within 15 days. This period corresponds to the time reported by Ewald (1965) for zoeae III to become postlarvae I at 26°C. This time period for larval development from zoeae to postlarvae also agrees remarkably well with the trajectory time of the drifter recirculating in the interior of the gyre. The timing of the modal progression of larval stages occurring within those 15 days of gyre recirculation at the spawning area, as shown by the drifter, may indicate that *P. duorarum* larvae were recirculating in the interior of the gyre during development. Interestingly, after the drifter broke out of the gyre circulation it moved toward the east and north toward the Florida Bay shrimp nursery grounds, suggesting a local recruitment pathway for this species.

Retention of *P. duorarum* larvae at the spawning area by the Tortugas Gyre for some days after hatching may enhance the survival of these larvae because food resources are available in the uplifted nutracline where Lee et al. (1994) found maximum concentrations of chlorophyll and copepod nauplii. Furthermore, postlarvae located in the northern (nearshore) portion of the gyre may increase their chance of settling either by escaping the offshore flow on the western side of the gyre entirely or by resisting the offshore flow, thereby drifting to the west rather than being swept offshore (Porch, 1993). Thus, the primary pathway for *P. duorarum* larvae to reach the nursery areas of Florida Bay may include retention at the spawning area by recirculation in the Tortugas Gyre followed by movement onto the Southwest Florida shelf and Florida Bay by wind and tidal currents. Those larvae that are advected eastward by the Florida Current may reach the upper and middle Keys. The latter alternative could explain the great number of postlarvae found in the middle Keys by Munro et al. (1968) and Roessler and Rehrer (1971).

Sicyonia sp. larvae showed a coastal and shallow distribution. Young zoeae were generally restricted to the inshore stations, indicating that this species may spawn near the Dry Tortugas Grounds. Myses showed the highest concentrations inshore, with a maximum concentration at the Marquesas transect. Larval stages at the two stations of the drifter showed a similar trend to that of *P. duorarum*. The time of development of *S. brevirostris* from spawning to the first postlarval stage is approximately 30 days (Cook and Murphy, 1965). Local retention of larvae at the spawning area followed by recruitment into the coastal region may be the migration mechanism for this coastal and short-lived species as well.

Early-stage zoeae of *Solenocera* sp. were widely distributed offshore; two main peaks were located at the Western and Tortugas transects at a depth of about 35 m. The age of these zoeae was estimated to be 3 to 5 days in accordance with Heldt's description (1938) of the larval development of *S. membranacea*. These data indicate that this species may have spawned somewhere in the Gulf of Mexico in a location corresponding to the outer edge of the Tortugas Gyre. Myses showed an offshore distribution in all but the Tortugas transect during leg 2, where most larvae were found inshore. The great concentration of *Solenocera* larvae at the inshore stations of the Tortugas transect in early June between 25 and 75 m in depth corresponded with the strongly developed

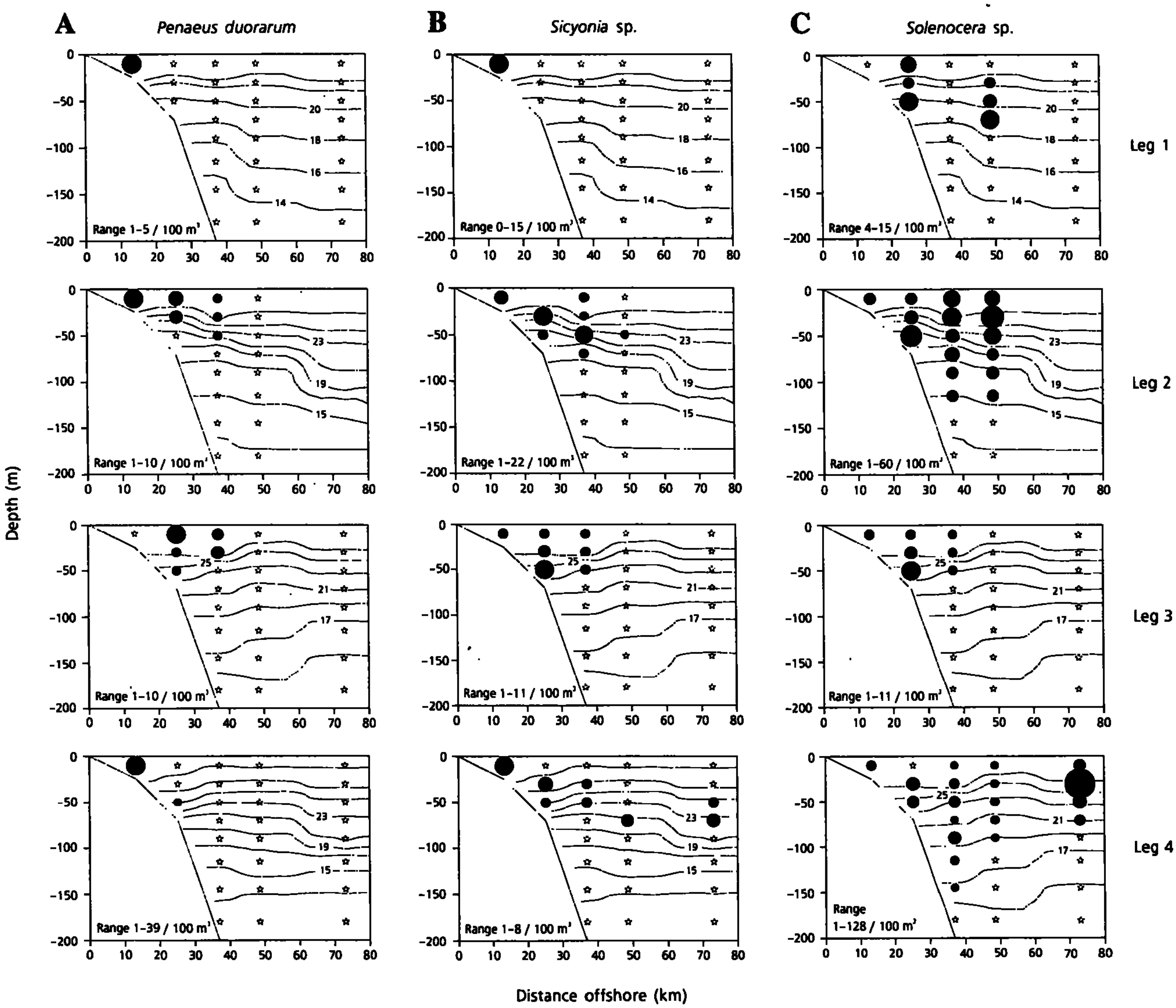

Figure 5

Cross section of Tortugas transect during the four legs showing the vertical distribution and relative concentrations (larvae/100 m³) of the three penaeoid species: pink shrimp, *Penaeus duorarum* (A); the rock shrimp *Sicyonia* sp. (B); and the humpback shrimp *Solenocera* sp. (C), superimposed over the vertical temperature profiles (°C) from the MOCNESS temperatures. Symbols are proportional in size to the abundance range. The stars = no catch.

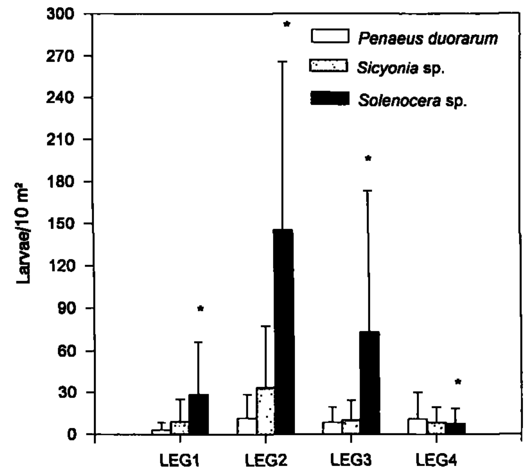

Figure 6

Mean relative abundance (larvae/10 m^2) and standard deviation of the pink shrimp, *Penaeus duorarum*, the rock shrimp *Sicyonia* sp., and the humpback shrimp, *Solenocera sp.*, at the sampling stations of the Tortugas transect during the four legs of the LH3 cruise, 29 May–30 June 1991. (*) = significant differences in mean relative abundance between legs, within species ($P \leq 0.05$).

thermocline as a consequence of the Tortugas Gyre. Criales and McGowan (1994) found *Solenocera* larvae in high abundance (62% of the penaeoid larvae) at an inshore station of Looe Reef transect during the presence of the Pourtales Gyre, whereas few larvae (only 15%) were captured in the absence of the gyre when the Florida Current intruded close to the coast.

The combination of the cyclonic gyre circulation and inshore surface Ekman transport convergence should result in a concentration of larvae in the interior of the gyre and in an onshore transport in the eastern portion. Onshore Ekman transport is expected to be relatively high in the Lower Keys and Dry Tortugas where prevalent southeast winds favor onshore transport toward the east-west oriented coast. The importance of Ekman transport on recruitment has been shown in the Florida Keys for *Scyllarus* larvae (Yeung and McGowan, 1991) and for other decapod larvae particularly brachyuran larvae in other regions (see Hobbs et al., 1992; McConnaughey et al., 1994).

Substantial gaps exist in our knowledge of the life histories of penaeoid shrimps. For example, larval development of *Solenocera* spp. has not been conducted for any of the five western Atlantic species (Perez-Farfante and Bullis, 1973), and larval development of only one of the seven western Atlantic species of *Sicyonia* spp. is known (Cook and Murphy, 1965). As long as our knowledge of the life history and larval development of these species remains limited, further conclusions regarding interactions of recruitment processes with the physical environment will remain uncertain.

This research showed the effects of the Tortugas Gyre circulation on dispersal and abundance of local coastal (*P. duorarum* and *Sicyonia* sp.) and oceanic (*Solenocera* sp.) shrimp species. The modal progression of *P. duorarum* zoeae to postlarvae within the same 15-day period in which the gyre recirculated in the Tortugas region indicates that *P. duorarum* larvae, in addition to the advective process postulated by Munro et al. (1968), may recirculate within the gyre during their development. Retention of larvae by the gyre circulation at the Dry Tortugas, combined with wind driven transport on the southeast Florida shelf, is a plausible recruitment pathway for pink shrimp recruiting to the nursery grounds of Florida Bay.

Acknowledgments

The authors gratefully acknowledge M. F. McGowan for his assistance and design of the biological sampling, W. Richards and A. Jones of the Southeast Fisheries Science Center of Miami for their continuous support during the course of this research, C. Yeung and C. Limouzy-Paris for their cooperation in the preparation of the manuscript and figures, E. Williams for analysis of oceanographic data, and the personnel of SEFCAR and crew of the RV *Long Horn* for making samples and data available. This work forms part of the Southeastern Florida and Caribbean Recruitment project (SEFCAR), funded by the National Oceanic and Atmospheric Administration through cooperative agreement No. NA90RAH00075 with the University of Miami.

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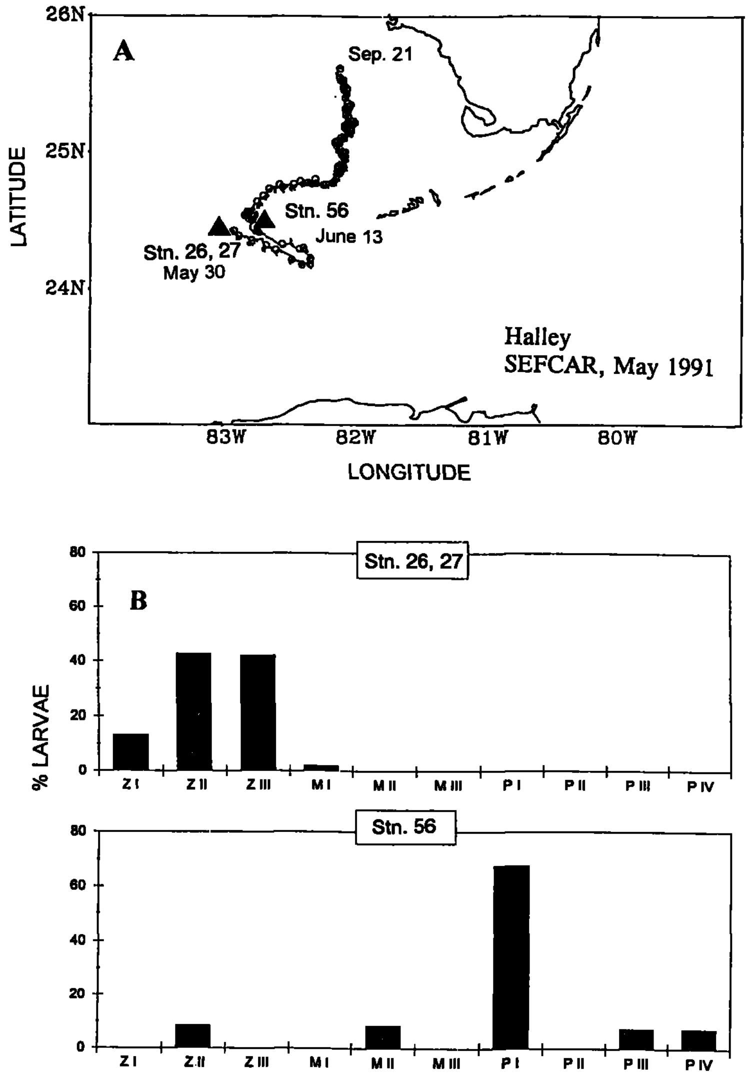

Figure 7

(A) Trajectory of the drifter *Halley* deployed during SEFCAR cruise LH3 on 30 May 1991. Stations 26 and 27 correspond to the location where the drifter was released, and station 56 with the position of the drifter when it broke out of the cyclonic circulation on 13 June 1991. (▲) = positions of stations 26, 27, and 56. (B) Percentages of the larval stages of the pink shrimp, *Penaeus duorarum*, at stations 26, 27, and 56 sampled on the track of drifter *Halley*. Z = zoeal stages; M = mysid stages; and P = postlarval stages.

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