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Interaction between diel vertical migration of a mysidacean shrimp and two-layered estuarine flow

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Abstract

Neomysis mercedis (Holmes) has a diel vertical migration pattern that interacts with two-layered estuarine flow and a turbid entrapment zone to keep the population from being swept out of the upper Sacramento-San Joaquin Estuary. In the entrapment zone mysids are found near surface on all night tides but are present at that level during day only on flood tides. In the clearer water downstream from the entrapment zone mysids are not found near surface during day. In both locations a higher percentage of juveniles than adults are near surface. Individuals swept downstream from the entrapment zone in the seaward moving surface layer are apparently transported back upstream via the bottom density current. Thus, the population circulates both vertically and longitudinally but there is no net seaward movement except in response to changes in location of the entrapment zone. Due to their greater near surface abundance on flood tides which move them upstream, neonates are less abundant than adults seaward of the entrapment zone.

Introduction

Neomysis mercedis is a planktonic mysidacean shrimp found in estuaries along the North American Pacific Coast from southern California to Alaska (Orsi & Knutson, 1979). Like all estuarine plankters, it faces the problem of maintaining its location in the estuary despite the prevailing seaward movement of the water. Oceanic, estuarine and freshwater mysids possess a diel vertical migration, moving toward the surface during darkness and returning to deeper water during daylight (Clutter, 1969; Heubach, 1969; Beeton, 1960; Mauchline, 1980). In stratified estuaries with two-layered flow, this migration pattern could enable mysids to avoid net seaward transport. Both Heubach (1969) and Siegfried *et al.* (1979) demonstrated a light regulated diel vertical migration of *N. mercedis* in the Sacramento-San Joaquin Estuary of California but neither of them presented data to show how this migration could interact with two-layered flow to stabilize the location of the mysids within the estuary.

The study by Siegfried *et al.* indicated that the vertical migration of juvenile mysids differed from that of the adults. They showed that in the entrapment zone juvenile *N. mercedis* occurred higher in the water column during daylight hours than adults did and they believed this led to a horizontal separation of these life stages as occurs in *Schistomysis ornata* (Mauchline, 1970). However, if young mysids also tend to occur higher in the water column downstream from the entrapment zone, they are more likely to be advected seaward in the surface flow and hence swept out of the estuary. It is assumed that mysids do not swim against tidal currents. Such antagonistic swimming, if successful, would keep the mysids at a single geographical location instead of within a certain salinity range. Heubach's (1969) results show that mysids remain most abundant at certain salinities throughout the year. Mysids are also unlikely to swim against non-tidal, i.e., two-layered flows, because such currents are not directly detectable.

To clarify the vertical migration and determine how it would interact with two-layered flow to stabilize the location of the species within the estuary, a field study of the migration of different life stages in and downstream from the entrapment zone was performed.

Site description

The saltwater-freshwater interface of the Sacramento-San Joaquin Estuary has been termed the 'entrapment zone' (Arthur & Ball, 1979). This zone is characterized by surface salinities of 1.2 to 5.6 °/oo, long water residence times, high turbidity, and high concentrations of suspended material, phytoplankton and zooplankton. Tides move the entrapment zone up and downstream as much as 13 km. The entrapment zone also oscillates along the axis of the estuary from San Pablo Bay to the western Delta in response to the volume of river flow.

Although the entire water column moves in the direction of the tides there is a net upstream movement of dense, saline water along the bottom, termed the bottom density current, and a net seaward transport of the fresher, surface water. This is known as two-layered flow. Vertical mixing occurs between the bottom and surface strata and a plane of no net motion is postulated to exist between them (Conomos & Peterson, 1977; Arthur & Ball, 1979).

Tidal currents during the study period had maxima from 113 to 252 cm s^{-1} (USDC 1980, 1981). The bottom density current averages 4 cm s^{-1} and the surface drift 5 cm s^{-1} (Conomos & Peterson, 1977).

Mysids were sampled in the entrapment zone at Chipps Island and downstream from it at Port Chicago. Both sites were located in the Suisun Bay area of the estuary (Fig. 1). The Chipps Island site

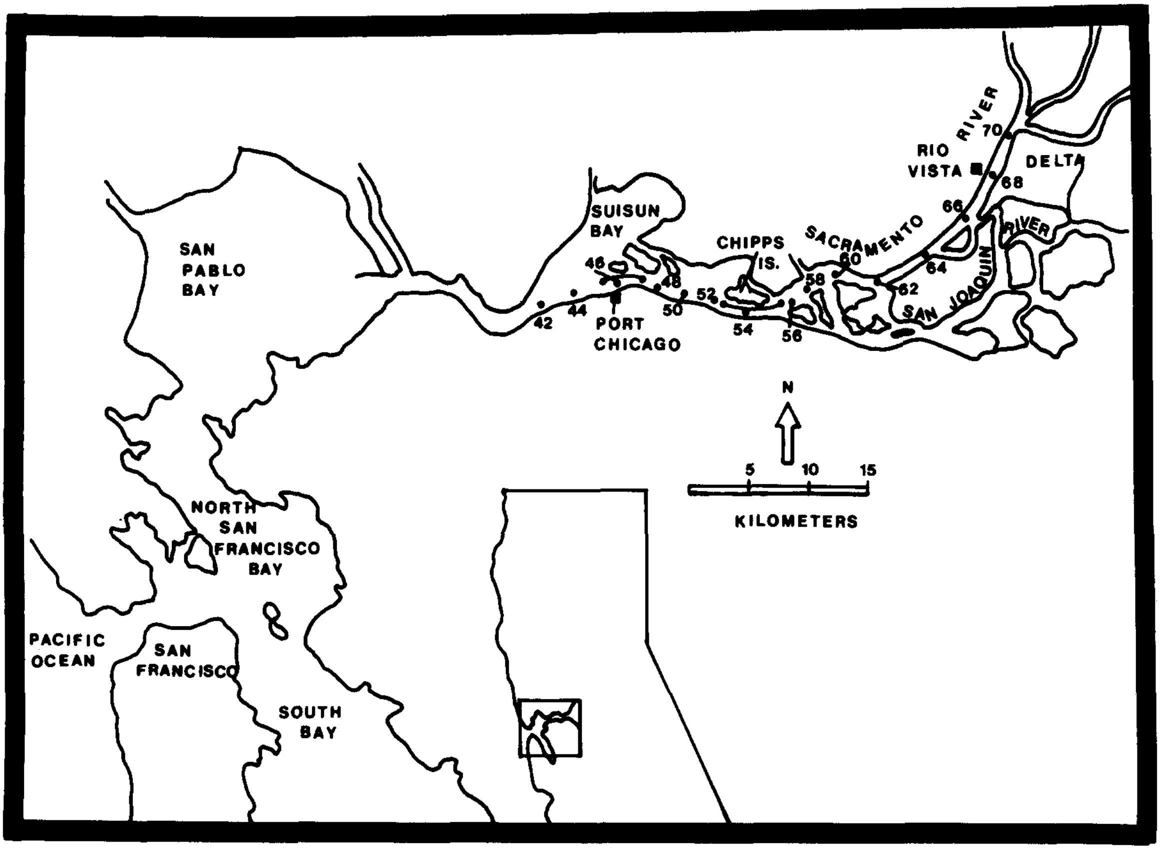

Fig. 1. Map of Sacramento-San Joaquin Estuary showing vertical migration sampling sites (● ——— ●) and regular monitoring survey stations (●).

was 56 km from the Pacific Ocean and the Port Chicago site was 46 km from it. Water depths at Chipps ranged from 7 to 15 m at lower low tide across a channel 0.8 km wide. The Port Chicago site was located in a dredged ship channel 60 m wide and 10 m deep at lower low tide. It was surrounded by shallow flats <1 to 3 m deep to lower low tide. The sampling areas extended over 6 to 8 km in an attempt to sample at a surface salinity of 3 °/oo at Chipps Island and 8–11 °/oo at Port Chicago.

Methods and materials

Sampling was conducted at approximately hourly intervals (except when prevented by strong winds) at Chipps Island (entrapment zone) on 21 – 22 August 1980 and at Port Chicago (downstream from the entrapment zone) on 16 – 17 July 1981. A 5 m boat with inboard motor was used. Mysids were caught in conical plankton nets 1.48 m long, 0.3 m mouth diameter and 505 μm mesh opening. Nets were fished in 11 – 14 m of water with the lowermost net on the bottom, the top net 1 m from the surface and the other nets equally spaced in between. Five nets were fished at Chipps Island but difficulties in handling that number caused a reduction to four at Port Chicago. Tows lasted 10 minutes at Chipps, but were lengthened to 15 minutes at Port Chicago because mysids were much less abundant at the latter location. General Oceanic digital flowmeters measured water volumes filtered. Salinity and temperature were measured at surface, midwater and bottom. A Secchi disc was used to measure water transparency. Catches were preserved in 10% formalin with Rose Bengal dye added to aid in distinguishing mysids from detritus.

Catches were corrected for the time each net fished at levels above its assigned depth while being hauled in by determining the percent of the total fishing time each net spent above depth and from this, the volume filtered and the number of mysids caught above proper depth. For example, the volume of water the second net from the surface filtered while at surface was multiplied by the number of mysids per cubic meter in the surfac net and the resulting number subtracted from the total catch. The number remaining was divided by the volume filtered at the correct depth to get the corrected number per meter in the second net.

All mysids were counted in samples with (≥ 400 individuals. Larger catches were subsampled. Lengths were determined to the nearest millimeter from eye to tip of telson. The percentage of three life stages, a) ≤ 3 mm neonates, b) 4–6 mm juveniles, c) ≥ 1 mm adults, was calculated for each water stratum, surface, midwater and bottom, on each tow. In addition, the geographical distribution of these life stages within the estuary was determined from biweekly surveys (see Knutson & Orsi, 1983 for methods).

Results

Vertical migration in the entrapment zone

Neonates avoided the surface on ebb tides of the first day (Fig. 2a). Usually ≤ 60% of them were ≥ 50 near bottom on these tides. In contrast, on the only flood tide (actually the high slack) sampled that day > 90% were in midwater. Neonates moved towards the surface on the flood tide at sunset (tow 7) when 2% of them were near surface and > 75% were in midwater. During the night varying percentages of the neonates were near surface on both ebb and flood tides with the exception of the ebb at 0155 h (two 13) when they left the surface and concentrated near bottom. Interestingly, all neonates were off bottom on the high slack at 0050 h (tow 11). Neonates were still near surface on the first day tow which was run on an ebb tide after sunrise. But on the subsequent ebb tow they went to midwater or near bottom. Significantly, on the following flood tow 5 to 20% of them were near surface with most of the rest located in midwater.

Neonates thus had a strong tendency to avoid surface on day ebb tides, (except the ebb after sunrise) but were found near surface in varying percentages on both ebb and flood night tides and on day flood tides. The vertical migration patterns of juveniles and adults were similar to that of neonates (Figs 2b and c). Adults, however, were much less abundant near surface than smaller mysids during the day on all tides.

Vertical migration downstream from the entrapment zone

Seaward of the entrapment zone neonates were

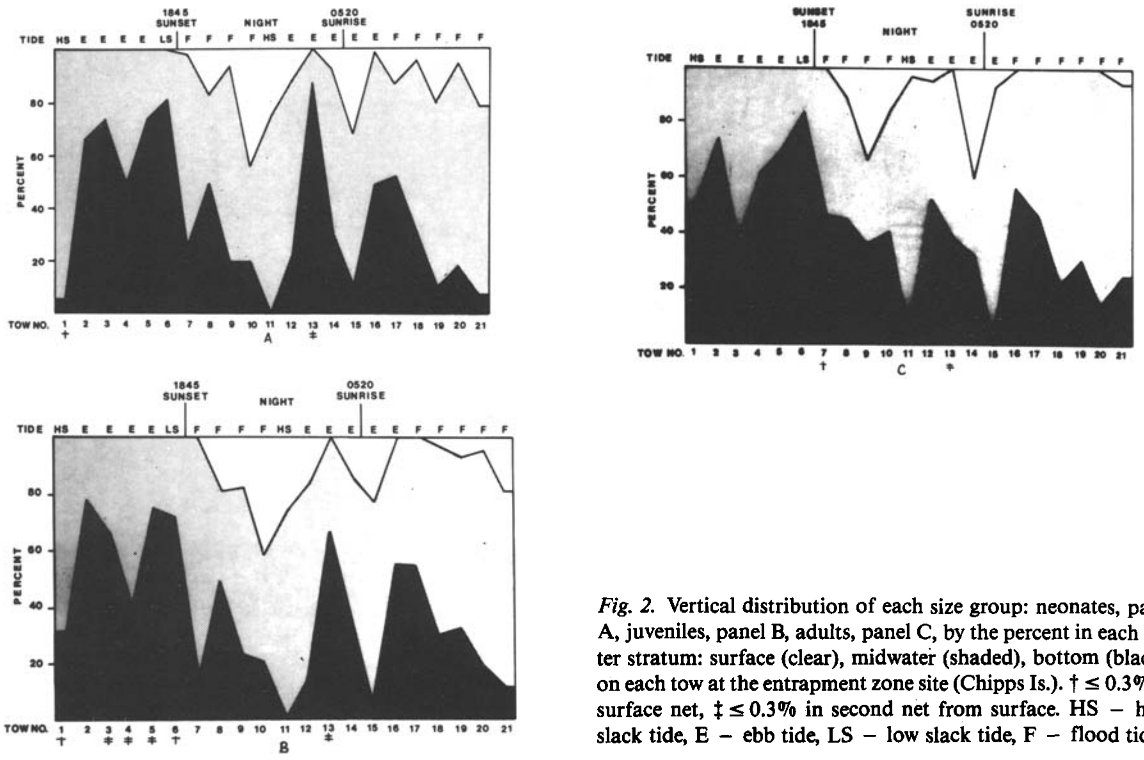

Fig. 2. Vertical distribution of each size group: neonates, panel A, juveniles, panel B, adults, panel C, by the percent in each water stratum: surface (clear), midwater (shaded), bottom (black), on each tow at the entrapment zone site (Chipps Is.). † ≤ 0.3% in surface net, ‡ ≤ 0.3% in second net from surface. HS – high slack tide, E – ebb tide, LS – low slack tide, F – flood tide.

found near surface only at night and the average percentage near bottom on all tows was higher than in the entrapment zone, often > 90% on day tides, both ebb and flood (Fig. 3a and Table 1). Juveniles also were near surface only at night and a greater percentage was near bottom than occurred in the entrapment zone (Fig. 3b and Table 1). Adults followed the pattern of the smaller mysids in that they were near surface only at night (Fig. 3c). But, as in the entrapment zone, the percentage of adults at that level was lower than those of the neonates and juveniles (Table 1).

Table 1. Vertical distribution of size groups by percent in each water stratum during day and night tows in the entrapment zone (Chipps Island) and downstream from it (Port Chicago).

	Day, below EZ			Night, below EZ		
	≤3 mm	4–6 mm	≥7 mm	≤3 mm	4–6 mm	≥7 mm
Surface	0	0	0	25	32	18
MW	10	12	14	2	21	29
Bottom	90	88	86	73	47	53

	Day, in EZ			Night, in EZ		
	≤3 mm	4–6 mm	≥7 mm	≤3 mm	4–6 mm	≥7 mm
Surface	6	3	1	26	22	12
MW	51	52	53	60	53	67
Bottom	43	45	46	14	25	21

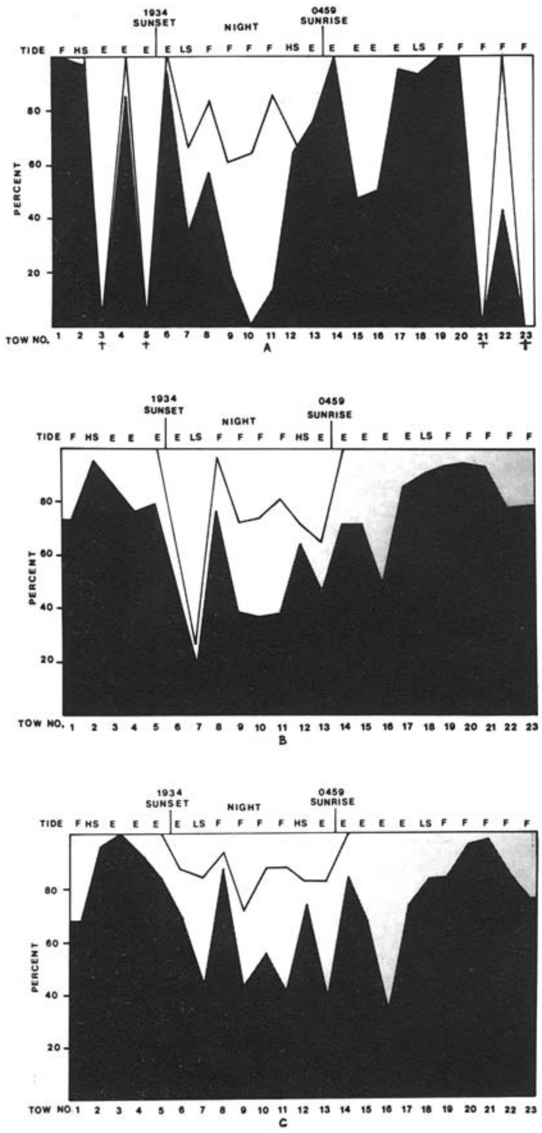

Fig. 3. Vertical distribution of each size group: neonates, panel A, juveniles, panel B, adults, pandel C, by the percent in each water stratum: surface (clear), midwater (shaded), bottom (black) on each two at the site downstream from the entrapment zone (Port Chicago). HS – high slack tide, E – ebb tide, LS – low slack tide, F – flood tide. † no neonates were taken.

Hence, the major difference in vertical migration at the two sites was the absence of any size group of mysids near surface during daytime in the clearer water downstream from the entrapment zone and a higher percentage of all groups near bottom both day and night.

Table 2. Towing times (Pacific Standard Time) and total abundance of each size group of *N. mercedis* taken in all nets combined at the entrapment zone site (Chipps Island).

Tow number	Time	Number $\cdot m^{-3}$		
		Neonates	Juveniles	Adults
1	1245	208	145	31
2	1340	612	466	43
3	1500	204	312	32
4	1545	168	399	104
5	1655	201	288	67
6	1750	500	640	181
7	1845	147	218	29
8	1945	168	372	40
9	2045	401	443	56
10	2255	466	458	51
11	2350	415	581	80
12	0050	177	346	32
13	0155	196	422	51
14	0255	63	121	19
15	0645	209	166	50
16	0750	359	469	66
17	0845	360	534	54
18	0945	347	465	62
19	1045	282	603	146
20	1145	167	283	55
21	1240	250	301	73
Mean		261	382	62

Of the three groups, juveniles were the most abundant seaward of the entrapment zone, and neonates the least abundant (Tables 2 and 3). On four of 15 daytime tows in this area no neonates were taken in any net. This differs markedly from the entrapment zone where adults were the least abundant, and neonates were caught on all tows.

Environmental factors

Light intensity and tide were identified by Heubach (1969) as the most important factors affecting the vertical migration of *N. mercedis*. The present study confirms this; all mysids were more abundant near surface at night and on flood tides. During daytime mysids were found near surface only in the more turbid entrapment zone water where Secchi disc readings ranged from 20 to 25 cm, mean 22 cm, compared to the downstream site where measurements were 35 to 59 cm, mean 44 cm.

Salinity stratification was apparently too slight to form a barrier to vertical movement. Surface sa-

Table 3. Towing times (Pacific Standard Time) and total abundance of each size group of *N. mercedis* taken in all nets combined at the site downstream from the entrapment zone (Port Chicago).

Tow number	Time	Number·m^{-3}		
		Neonates	Juveniles	Adults
1	1445	0.03	3.0	0.6
2	1620	2.4	53.6	3.6
3	1720	0	0.5	0.3
4	1825	0.5	9.3	1.4
5	1920	0	3.4	0.6
6	2015	0.2	5.8	0.7
7	2120	0.1	2.9	0.2
8	2220	0.1	4.1	1.5
9	2340	0.6	8.7	1.7
10	0130	0.3	4.8	1.5
11	0230	0.1	5.1	1.3
12	0325	0.6	10.8	0.6
13	0425	0.8	9.6	1.1
14	0525	0.2	3.5	0.7
15	0620	0.6	3.7	0.9
16	0805	0.03	2.7	0.6
17	0845	0.4	10.3	1.1
18	0950	1.2	12.4	2.3
19	1105	0.2	3.4	0.6
20	1150	0.2	4.4	1.2
21	1255	0	11.9	3.9
22	1350	0.1	2.2	1.3
23	1445	0	1.9	1.2
Mean		0.4	7.7	1.1

linities in the entrapment zone were 2.7 to 3.4 °/oo and bottom salinities ranged from 2.6 to 4.3 °/oo. Downstream from the zone, salinities ranged from 7.9 to 11.2 °/oo surface and 10.1 to 12 °/oo bottom. The mean surface-bottom difference for all entrapment zone tows was 0.4 °/oo and 1.3 °/oo for all downstream tows.

Temperature was not stratified. The water was not consistently warmer or cooler at any level. The mean surface-bottom difference was only 0.2 °C in the entrapment zone, where temperatures ranged from 19.2 to 20.8 °C, and 0.1 °C downstream from it, where the range was 19.6 to 21.5 °C.

Discussion

Effects of vertical migration on horizontal distribution

Replicate tows were not made, due in part to difficult working conditions. Replicates would help to distinguish between actual trends and random variations in the data. However, Fig. 2 and 3 show that enough consistency exists to have confidence that real differences in vertical distribution do occur between night and day, flood and ebb tide, and between the two sites.

The vertical migration pattern interacting with two-layered flow circulates mysids between the entrapment zone and the regions immediately up and downstream from it. Seaward of the entrapment zone mysids are predominantly near bottom (Table 1) and hence over a tidal cycle they will experience a net upstream movement in the bottom density current. This will eventually bring them into the entrapment zone where the reduced light penetration will encourage them to rise into midwater and surface water layers (Table 1). Mysids located in midwater should experience little net movement and hence most of the population should remain in the entrapment zone. Mysids near the bottom will continue to move upstream until the bottom current dies out in fresh water. Those mysids near the surface will experience a net downstream movement which will eventually transport them seaward of the entrapment zone.

Movement upstream from the zone should be difficult because the net flow throughout the entire water column in this area is seaward. However, if flood tides move mysids farther upstream than ebb tides return them downstream, they could be transported landwards to the limits of tidewater. The greater duration of ebb tides in this estuary would appear to make it impossible for mysids to accomplish a net movement in this manner. However, on neap tides flood current velocity may be almost twice as high as ebb velocity (USDC, 1980). This would more than compensate for the greater duration of the ebbs and would provide a mechanism to explain the presence of *N. mercedis* throughout the delta. The observed tendency for mysids to rise off the bottom on flood tides, a tendency also noted by Heubach (1969), would aid in this upstream dispersal.

This reaction of *N. mercedis* to flood tides implies an ability to detect changes in hydrostatic pressure. The existence of such an ability has been confirmed in another shallow water mysid species, *Schistomysis spiritus*, which rose to the surface of experimental tanks when pressure was increased

(Rice, 1961). In the field *S. spiritus* was found at the surface only on flood tides.

The difference between the vertical migration patterns of neonates, juveniles and adults was one of degree, not kind. Small mysids were more likely to be near the surface than large ones. Hence, because current velocities are highest at surface (California Department of Public Works, 1931), small mysids should be more subject to displacement than adults. The direction of this displacement is more likely to be upstream than seaward because in the entrapment zone during daylight hours neonates and juveniles are near surface only on flood tides. This upstream displacement is reflected in the low abundance of neonates downstream from the entrapment zone both absolutely and relative to adult abundance.

Contrarily, Siegfried *et al.* (1979) found that in the entrapment zone mysids ≥ 3 mm had 'frequent daytime midwater peaks that are not apparent for ≤ 7 mm mysids' and concluded that neonates would therefore experience a net downstream movement relative to adults rather than an upstream one. However, if neonates were off bottom only on flood tides as shown in Figs. 2 and 3, their net movement should be upstream. This conclusion is supported by the low abundance of neonates relative to adults downstream from the entrapment zone (Tables 2 and 3), and by the results of regular monitoring surveys of the Department of Fish and Game. To illustrate this, one 1976 (the year Siegfried *et al.* sampled), one 1980 and one 1981 survey of horizontal distribution of the three size groups of mysids are presented to show that (1) adults extended farther downstream from the entrapment zone and were usually more abundant there than neonates, and (2) neonates did not have abundance modes upstream from those of adults (Fig. 4).

High salinities do not appear to harm *N. mercedis* as it is present in coastal California lagoons and river mouths at salinities as elevated as 32.3 ‰ (Orsi *et al.*, 1979). Yet only very small numbers of it have been taken from San Francisco and San Pablo bays in summer. Its virtual summertime absence from these bays can be attributed to the clear water there which would keep any mysids near bottom and hence in the upstream moving density current. An alternate hypothesis is that the clear Bay water enables high predation rates on the shrimp by visual predators – fish. This hypothesis is untestable but its validity is weakened by the abundance of caridean shrimp, *Crangon spp.* in the Bays. If *Crangon* is able to thrive under these conditions it is not unreasonable to expect *N. mercedis* to do likewise.

Although the proximal cause of the vertical migration of *N. mercedis* and other mysid species is light, the 'ultimate causes' are obscure. Beeton and Bowers (1982) discuss the various hypotheses that have been developed to explain the value of vertical migration to mysids and zooplankton. Most of these hypotheses involve trophic interactions between the migrators and their predators and prey. Whatever its value is in other habitats and in other species, the vertical migration of *N. mercedis* provides a mechanism that enables it to successfully colonize the upper Sacramento-San Joaquin Estuary.

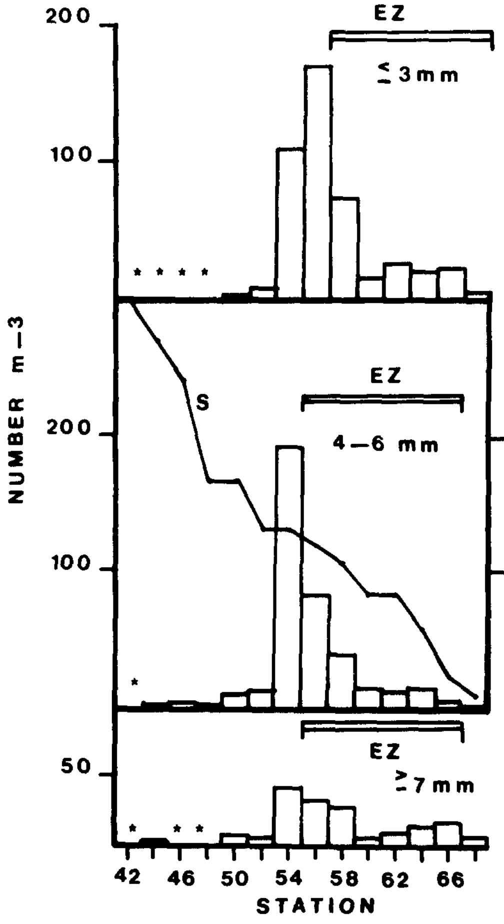

Fig. 4. See next page.

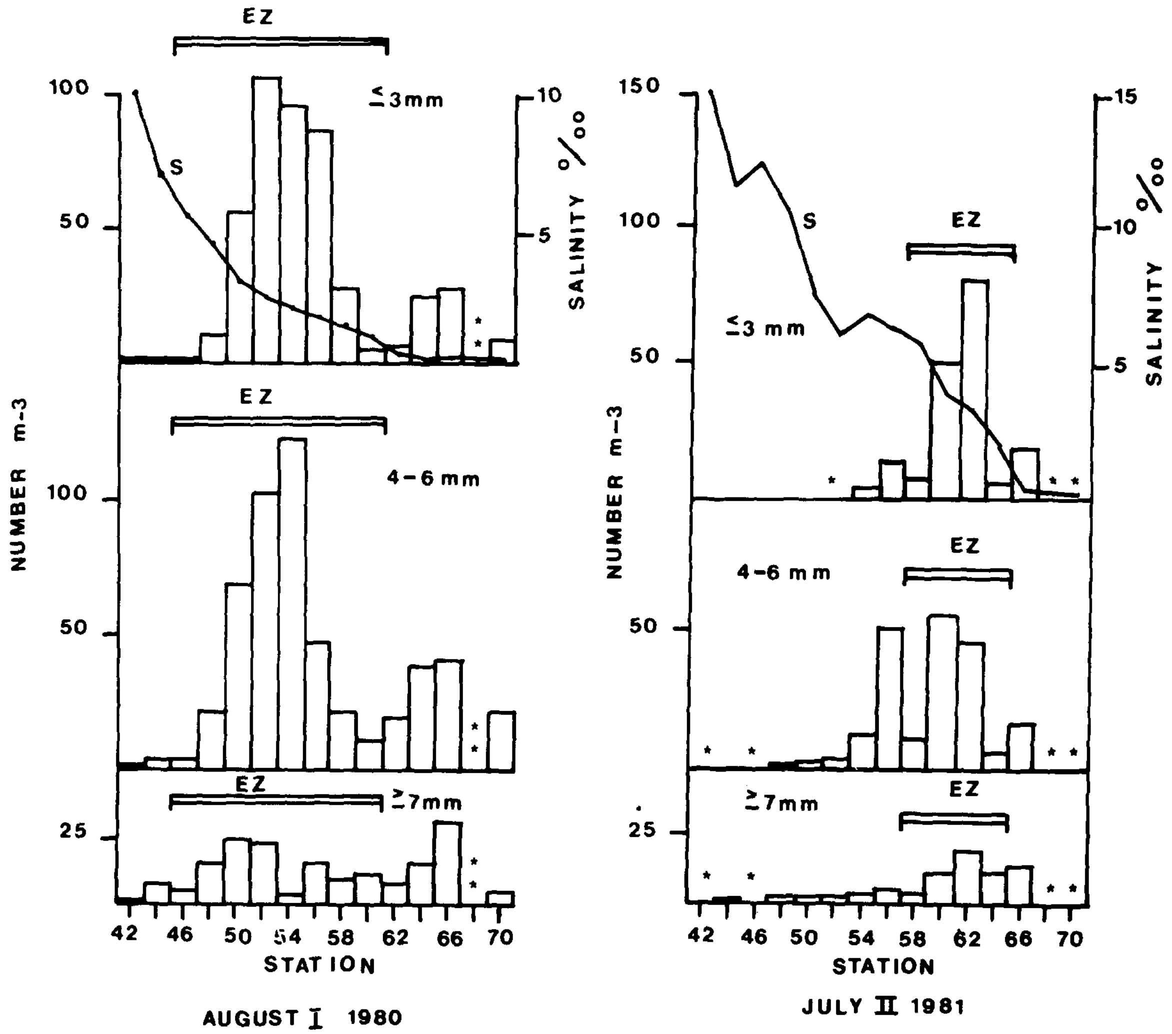

Fig. 4. Horizontal distribution of three size groups of mysids at each sampling station from western Suisun Bay to past Rio Vista on the Sacramento River on three monitoring surveys in 1976, 1980, and 1981 in relation to salinity (S) and the entrapment zone location (EZ). *<1 mysid·Bm^{-3} on July 1 and ≤0.5·Bm^{-3} on July II. ** not sampled.

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