

SEASONAL ABUNDANCE AND DISTRIBUTION OF *CRANGON*  
*FRANCISCORUM* AND *PALAEEMON MACRODACTYLUS*  
(DECAPODA, CARIDEA) IN THE SAN FRANCISCO  
BAY-DELTA<sup>1</sup>

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Two decapod shrimp, *Crangon franciscorum* and *Palaemon macrodactylus*, dominate the epifaunal community of the western Sacramento-San Joaquin Delta. The Franciscan bay shrimp, *C. franciscorum*, once supported an extensive commercial fishery in San Francisco Bay (Bonnot, 1932) and today supports a more restricted bait fishery. It is a common inhabitant of the continental shelf and estuaries from southeastern Alaska to California (Schmitt, 1921). Israel (1936) discussed the life history of *C. franciscorum* in the San Francisco Bay-Delta region and Ganssle (1966) provided additional qualitative information on its distribution and abundance in Suisun Bay. Recent studies have investigated aspects of the physiology and tolerance of *C. franciscorum* to various environmental factors (Khorram and Knight, 1977; Sharp *et al.*, 1978; Nelson *et al.*, 1979) but little information is available on the biology of *C. franciscorum* in the Bay-Delta.

The oriental shrimp, *Palaemon macrodactylus*, is thought to have been introduced into the San Francisco Bay Estuary in the early 1950s from water-ballast tanks of ships returning from Korea (Newman, 1963). Its presence in San Francisco Bay is thought to represent its northernmost distribution on the west coast of North America. Little is presently known about the biology of the oriental shrimp in the Bay-Delta system.

*C. franciscorum* and *P. macrodactylus* are important components of the estuarine food web, especially as food for the game fish of the estuary (Ganssle, 1966). These shrimp are also important predators of the opossum shrimp, *Neomysis mercedis*, (Siegfried *et al.*, 1978; Sitts, 1978) and may be important in nutrient cycling in the estuary (Nelson *et al.*, 1979). Information on potential interactions between the native specimens of *C. franciscorum* and the introduced specimens of *P. macrodactylus* is lacking.

MATERIALS AND METHODS

Decapod shrimp were collected from 5 to 12 stations on the Sacramento River, from Chipps Island upstream to Rio Vista, from January, 1976, through April, 1977; and from 32 stations in Suisun Bay and the Sacramento and San Joaquin Rivers from April, 1977, through October, 1978 (Fig. 1). In 1976 a few shallow, near shore stations (< 4 m deep) were sampled but in 1977-1978 all stations were located near midchannel and were 6-14 m deep. During the initial phase of the study (January, 1976-April, 1977) decapod shrimp were collected monthly by replicate tows with three #8 nets (mesh = 200  $\mu$ m) towed simultaneously at each

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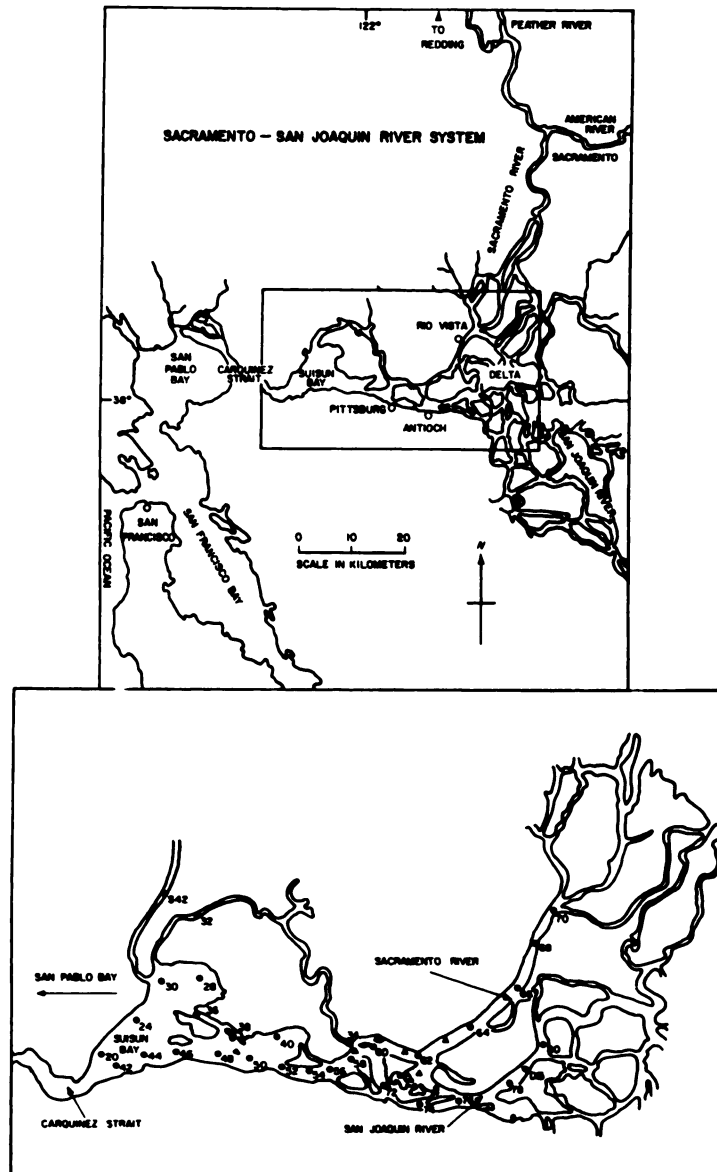


FIGURE 1. Location of study area and collection sites in Suisun Bay and the Sacramento-San Joaquin River Delta. Triangles indicate sites sampled only in 1976.

station: one just below the surface, one near mid-depth, and the third secured to a sled which maintained it just above the substrate. The nets consisted of a 1.3-m section of cylindrical netting, 50 cm in diameter, preceding a 2-m cone-shaped section which terminated in a removable plankton bucket. Each net was equipped with a current meter which was used to determine the volume sampled. From April, 1977, through October, 1978, single step-wise tows were made at biweekly intervals at the 32 stations indicated in Fig. 1. The nets used during this phase of the study were of 505- $\mu$ m mesh netting, with 29-cm-diameter mouths and were 1.48-m

long. These tows were made during a 3–5 consecutive days between  $\frac{1}{2}$  hr before and 1 hr after high neap tide by the California Department of Fish and Game, Bay-Delta Fishery Project, as part of their *N. mercedis* monitoring program. Conductivity and water-temperature data were collected at each sample site. All shrimp collected were placed in 10% buffered formalin and later transferred to 70% isopropyl alcohol.

All shrimp collected were measured from the anterior edge of the carapace (excluding the rostrum) to the posterior tip of the telson. The sex of all specimens collected in 1977 and 1978 was determined by microscopic examination of the endopodite of the second pleopod. On developing and mature males this endopodite bears an appendix masculina, whereas for females the structure is similar to those of the third pleopod (Newman, 1963; Smith and Carlton, 1975). An additional distinguishing characteristic used for *C. franciscorum* sex determination was the structure of the endopodite of the first pleopod, which is short and curved inward for males and long and straight for females. Preservation made it difficult to locate the gonopore of each shrimp so this character was not used for sex determination.

For brood-size determinations the eggs of 17 ovigerous specimens of *C. franciscorum* and 66 specimens of *P. macrodactylus* were stripped and enumerated. Only females with ova in the early developmental stages were used for determination of brood sizes.

Length-weight relationships were determined for 238 specimens of *C. franciscorum* and 183 specimens of *P. macrodactylus*. Each shrimp was measured and then dried at 60°C for 48 hr, cooled, and then weighed to the nearest 0.01 mg for shrimp > 2 mg and to the nearest 0.001 mg for shrimp < 2 mg.

## RESULTS

The size frequency distribution of specimens of *C. franciscorum* collected in the study area from November, 1977, through October, 1978, is presented in Figure 2. Specimens of *C. franciscorum* were not caught until they were about 10 mm long. The largest influx of 10–20-mm-long *C. franciscorum* specimens occurred in May. Sexual dimorphism is typical for crangonids (Lloyd and Yonge, 1947; Meredith, 1952; Allen, 1960; Price, 1962; Durkin and Lipovsky, 1977) and was evident for specimens of *C. franciscorum* from the Bay-Delta. Almost all specimens of *C. franciscorum* collected from the delta that exceeded 45 mm in length were female. The largest female collected from the delta was 72 mm long while the largest male was 52 mm long. Collections of *C. franciscorum* made in San Pablo Bay in May–June and September, 1977, indicate a significantly different population structure (Fig. 3). Samples from the delta in May–June, 1977, indicated a population made up of about 50% juvenile shrimp, median size = 34 mm and maximum size = 50 mm. Samples from San Pablo Bay indicate a population primarily of mature shrimp, median size = 50 mm and maximum size = 72 mm. In September the median of *C. franciscorum* collected in the delta was 38 mm (range 27–52 mm) while in San Pablo Bay the median size was 48 mm (29–64 mm).

No estimates of growth were made from the size frequency histograms. Immigration, emigration, and temperature–salinity differences all combine to obscure growth patterns of *C. franciscorum* in the Delta. *C. franciscorum* eggs generally hatch in the spring. Young develop into juveniles by summer and reach maturity by winter.

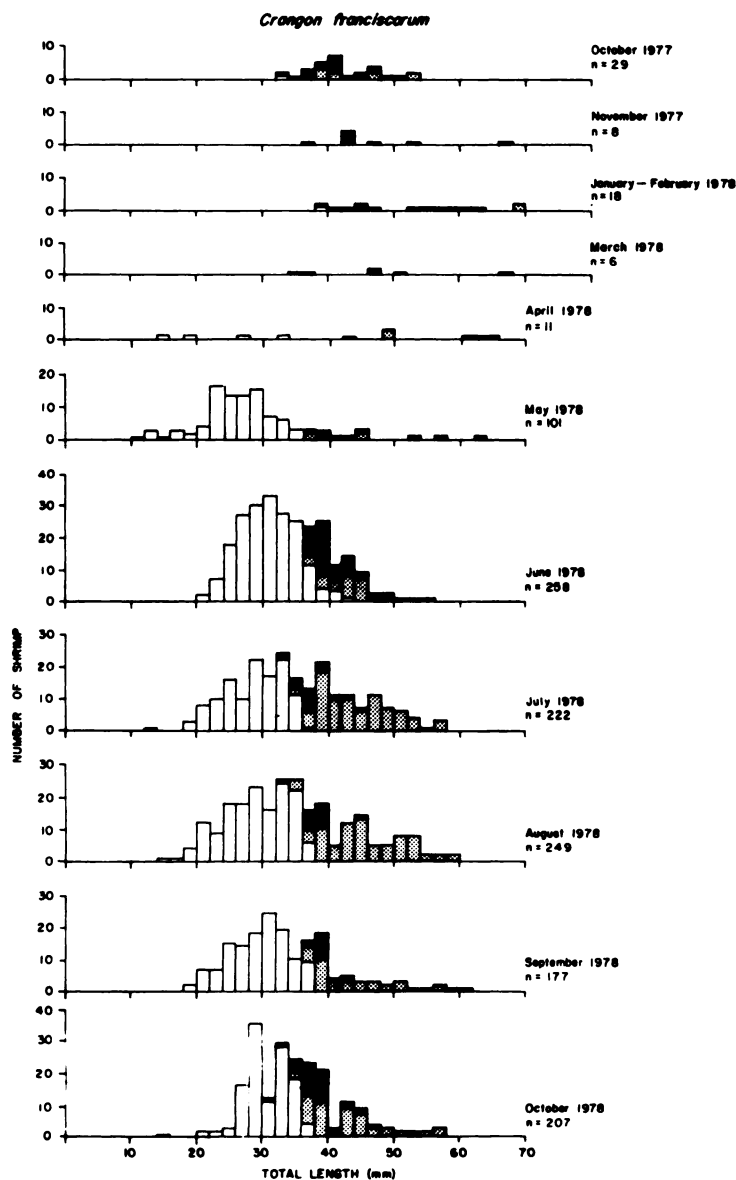


FIGURE 2. Size frequency distribution of specimens of *Crangon franciscorum* collected in the Suisun Bay, Sacramento-San Joaquin River study area, November, 1977–October, 1978. Dark bars indicate number of males, hatched bars indicate number of females, and open bars indicate number of juveniles or undetermined individuals measured.

The size frequency distribution of specimens of *P. macrodactylus* collected in the study area is presented in Figure 4. Summer is the main recruitment period for *P. macrodactylus* in the delta. Ovigerous females were collected from May through August, with a few collected in April and September. *P. macrodactylus* larvae are planktonic and are very abundant in the plankton of the delta during summer. Larval specimens of *P. macrodactylus* are photopositive (Little, 1969) but become more photonegative as they develop (Siegfried *et al.*, 1978).

Sexual dimorphism is also apparent in *P. macrodactylus*. Almost all individuals longer than 40 mm were female. Females reached *ca.* 55 mm maximum length and males *ca.* 44 mm. This is near previously reported sizes (Newman, 1963). Size at sexual maturity was not determined but secondary sexual characteristics are apparent when shrimp attain about 20 mm in length. Ovigerous females as small as 23 mm long were collected, so males would presumably mature at this or smaller sizes.

Length-weight relationships for juvenile, male and female specimens of *C. franciscorum* are presented in Figure 5. The regression equations describing these relationships are given below:

$$\text{Juveniles (n = 100) : } \log W = -5.41 + 2.58 \log L, r = 0.88$$

$$\text{Males (n = 74) : } \log W = -6.12 + 3.27 \log L, r = 0.92$$

$$\text{Non-ovigerous females (n = 57) : } \log W = -6.62 + 3.57 \log L, r = 0.96$$

(*W* = dry weight in grams and *L* = total length in mm). Analysis of covariance (Steel and Torrie, 1960) revealed significant differences in slopes between the length-weight regression of juveniles and mature shrimp. The difference is attributable, at least in part, to gonadal development.

Length-weight relationships for *P. macrodactylus* are presented in Figure 6. Regression equations describing these relationships are given below:

$$\text{Juveniles (n = 118) : } \log W = -5.44 + 2.53 \log L, r = 0.95$$

$$\text{Males (n = 45) : } \log W = -5.49 + 2.95 \log L, r = 0.97$$

$$\text{Non-ovigerous females (n = 19) : } \log W = -6.10 + 3.40 \log L, r = 0.98$$

The slopes of the above regressions are all significantly different from one another ( $\alpha = 0.05$ ). *P. macrodactylus* is more robust than *C. franciscorum*, in many cases weighing 50% more than a *C. franciscorum* of similar length.

Ovigerous specimens of *C. franciscorum* were collected in San Pablo and San Francisco Bays in the spring and fall of 1977. Most female specimens of *C. franciscorum* collected in San Francisco Bay in May were ovigerous while in

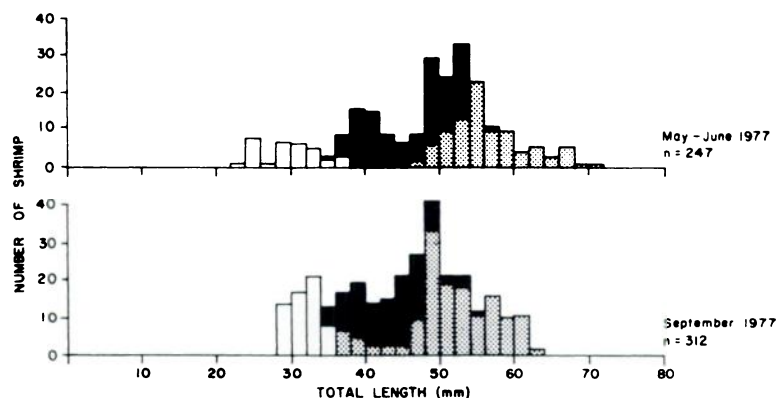


FIGURE 3. Size frequency distribution of specimens of *Crangon franciscorum* collected in San Pablo and San Francisco Bays, May-June and September, 1977. Dark bars indicate number of males, hatched bars indicate number of females and open bars indicate number of juveniles or undetermined individuals measured.

September–October, most were non-ovigerous. Ovigerous females in our samples ranged from 48 to 67 mm long.

Ovigerous specimens of *P. macrodactylus* were collected in the study area from April (1977) and May (1976, 1978) through August each year. More than

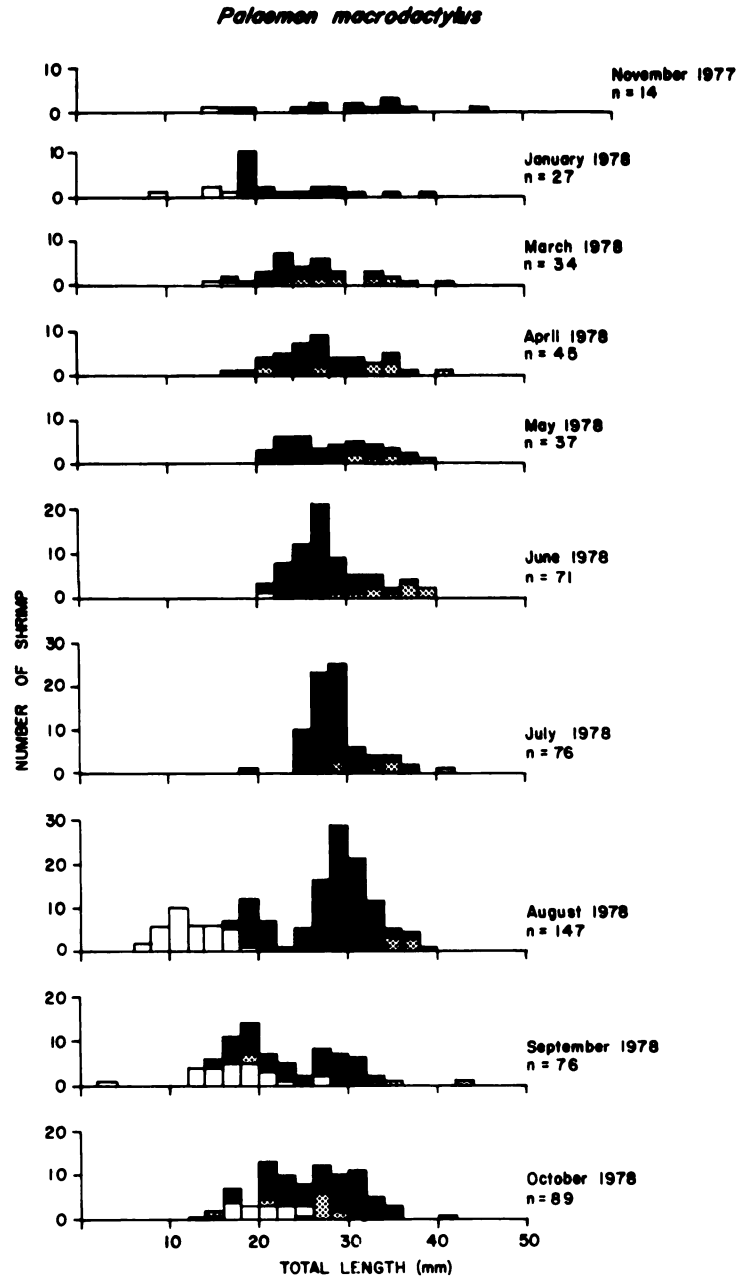


FIGURE 4. Size frequency distribution of specimens of *Palaemon macrodactylus* collected in Suisun Bay, Sacramento-San Joaquin River study area, November, 1977. Dark bars indicate number of males, hatched bars indicate number of females, and open bars indicate number of juveniles or undetermined individuals measured.

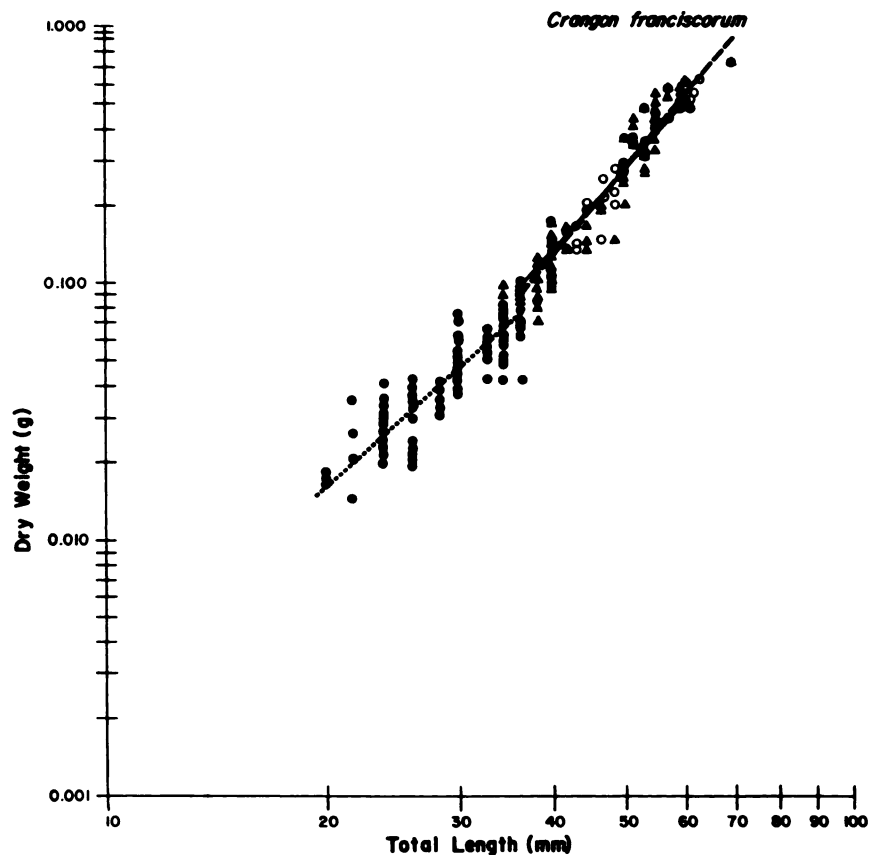


FIGURE 5. Relationship between total length (mm) and dry weight (g) of juvenile (solid circles), male (open circles), female (triangle) specimens of *Crangon franciscorum* collected from the study area, January, 1976–October, 1978.

50% of the mature females collected during these periods were ovigerous. Ovigerous females ranged in size from 23 to 48 mm long. Female specimens of *P. macrodactylus* appear capable of producing more than one brood; ovigerous females often carried a second brood in the ovaries while the first brood had not yet been released.

The brood sizes of 17 specimens of *C. franciscorum*, ranging in size from 48 to 67 mm long, and 66 specimens of *P. macrodactylus* ranging in size from 23 to 48 mm long, are presented in Figure 7. The relationships between brood size and body length are given by: *C. franciscorum*:  $\log N = -3.66 + 4.09 \log L$ ,  $r = 0.90$ ; *P. macrodactylus*:  $\log N = -1.66 + 2.96 \log L$ ,  $r = 0.81$ . The size ranges of ovigerous females of the two species have little overlap, but in the area of overlap, *P. macrodactylus* has a greater mean brood size than *C. franciscorum*.

The seasonal abundance of *C. franciscorum* and *P. macrodactylus* in various parts of the study area is shown in Figures 8 and 9. There are obvious differences between 1977 and 1978 in the location of the peak population densities. In 1977, a very dry year, salinity incursion was more extensive than in 1978, and the peak densities of both *C. franciscorum* and *P. macrodactylus* were located in the river channels. In 1978 the bulk of both populations was centered in Suisun Bay.

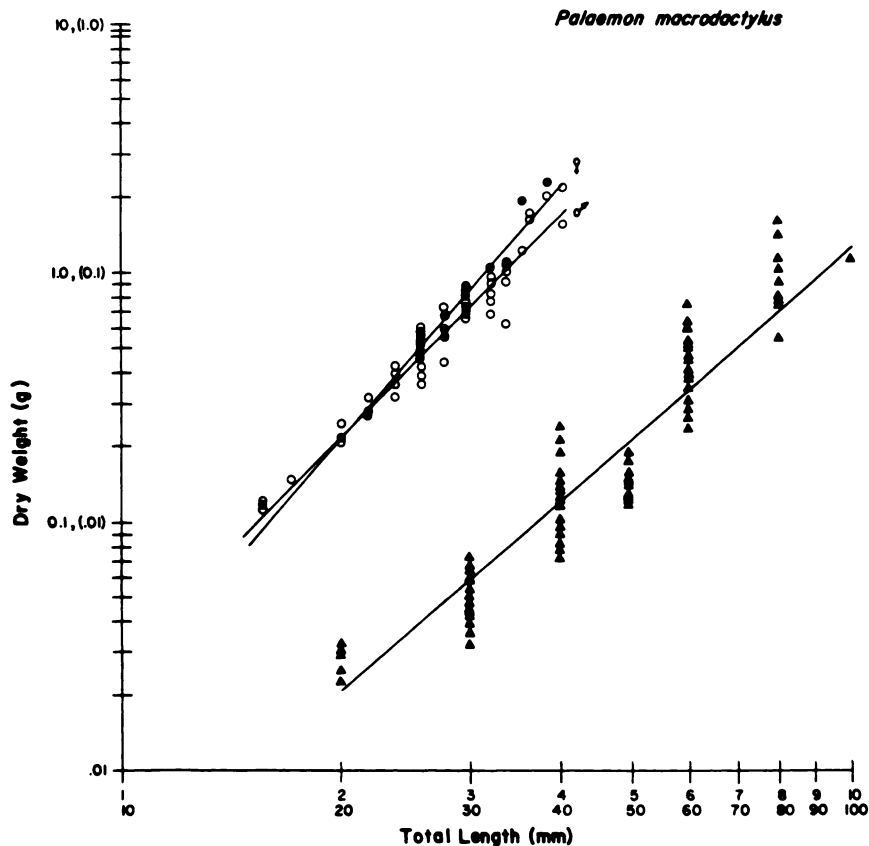


FIGURE 6. Relationships between total length (mm) and dry weight (g) of juvenile (triangle), male (open circle), female (solid circle) specimens of *Palaemon macrodactylus* collected from study area, January, 1976–October, 1978. Inner scale = juveniles, outer scale = male and female shrimp.

A significant difference between *C. franciscorum* and *P. macrodactylus* is evident in their population densities in the San Joaquin River. *P. macrodactylus* was abundant in the San Joaquin River during the summer (particularly in 1977) while *C. franciscorum* was virtually absent. The San Joaquin River receives more industrial and agricultural effluents relative to its discharge than the Sacramento River. This may create water quality differences between the two rivers that limit *C. franciscorum* distribution.

Both *C. franciscorum* and *P. macrodactylus* appeared to be limited upstream by low salinities. Few individuals of either species were collected from waters <1‰ salinity (Fig. 10). In both 1977 and 1978, the maximum concentration of *C. franciscorum* in the delta was generally in the salinity range 1–7‰ (Fig. 10).

*Palaemon* appears to be more tolerant of low salinities combined with low temperatures than is *C. franciscorum*. In the spring and fall–winter it is not unusual to collect *P. macrodactylus* in fresh or nearly fresh water. *C. franciscorum* is generally absent from the delta channels at those times but is often abundant in Suisun Slough and adjacent sloughs from January through May where salinities are near 2‰.



## DISCUSSION

The maximum size of *C. franciscorum* collected in this study is in good agreement with maximum sizes reported from Yaquina Bay, Oregon (Krygier and Horton, 1975). However, collections of *C. franciscorum* off the mouth of the Columbia River indicate a population with mean size  $> 80$  mm and maximum sizes  $> 110$  mm (Durkin and Lipovsky, 1977). Reduction of maximum size of individuals inhabiting estuaries as compared to individuals of the same species inhabiting the sea has been reported for *Crangon crangon* (Maucher, 1961). Remane and Schlieper (1971) suggest that reduction in size of marine animals, although generally slight in higher Crustacea living in brackish water, is comparable to Bergmann's law—that is, size is related to features of the physical environment. The reduction may be attributable to physiological effects of salinity, reduced food availability, or a combination of these and other factors. Studies of osmotic regulation indicate that smaller specimens of *C. franciscorum* are capable of better hyper-regulation than larger individuals and that larger ones may tend to hypo-regulate better than smaller individuals (Shaner, 1978). Thus, the migration of larger individuals from low salinity waters to high salinities would be energetically advantageous.

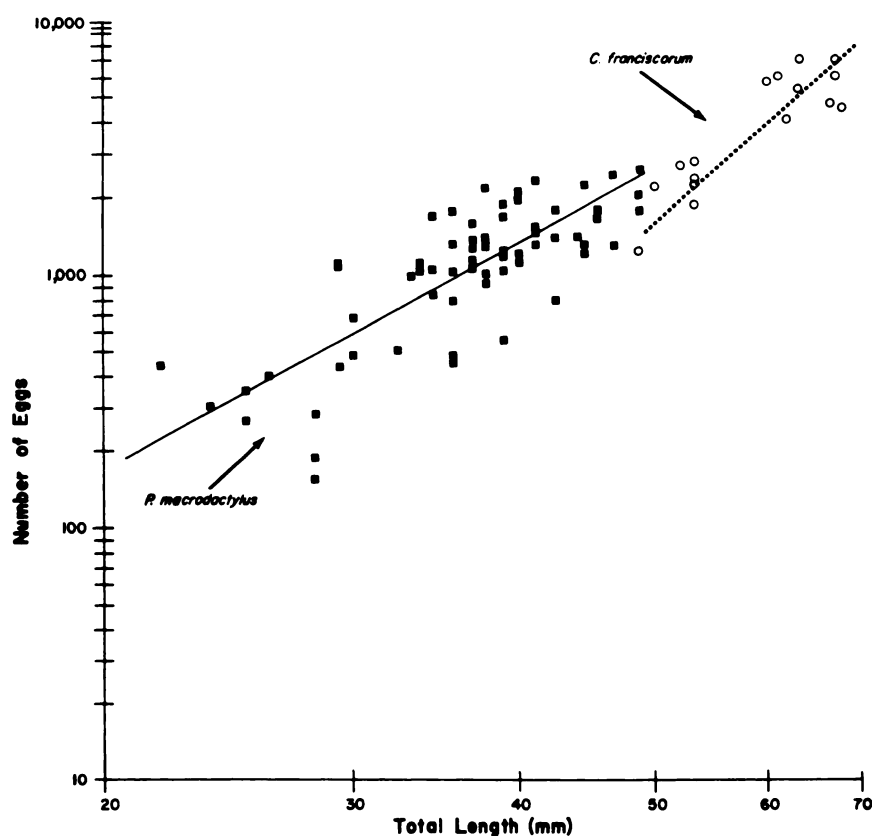


FIGURE 7. Relationship between total length (mm) and number of eggs carried by ovigerous specimens of *Crangon franciscorum* and *Palaemon macrodactylus*. All ovigerous specimens of *Crangon franciscorum* were collected in San Pablo Bay. All ovigerous specimens of *Palaemon macrodactylus* were collected in the study area.

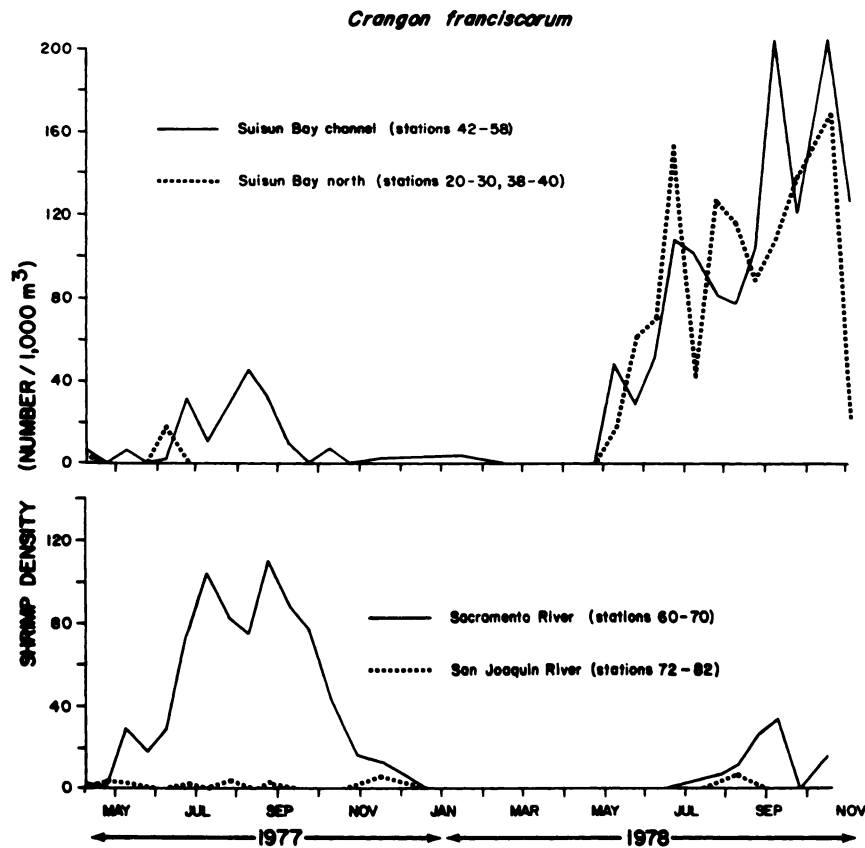


FIGURE 8. Abundance of *Crangon franciscorum* in various portions of the study area, April, 1977–October, 1978.

Although *C. franciscorum* inhabits brackish water for much of its life cycle in the delta, it requires high salinities for reproduction. No ovigerous female specimens of *C. franciscorum* were collected in the delta at any time during the study. Ovigerous females are found year-round in San Pablo and San Francisco Bays but the peak reproductive period appears to be from December through June (Isreal, 1936). Energetic demands of osmoregulation at low salinities may preclude egg development and thus reproduction in the delta. Broekema (1941) has shown that low salinities, characteristic of the delta, retard egg development in crangonids. Krygier and Horton (1975) report collecting only 1 of 120 ovigerous specimens of *C. franciscorum* at salinities below 15‰. Salinity is important not only in relation to egg development but also in larval survival. Preliminary investigation suggest that survival of larval specimens of *C. franciscorum* declines at salinities below 12‰ (Shaner, unpublished).

The life history pattern of *C. franciscorum* in San Francisco Bay appears not only to minimize the energetic demands of osmoregulation but also to minimize interspecific competition with another crangonid that is abundant in San Francisco Bay, *C. nigracauda*. These species coexist over much of their range (Krygier and Horton, 1975), partitioning their habitat temporally and spatially. In San Francisco Bay *C. franciscorum* spawns earlier in the year than *C. nigracauda* and moves

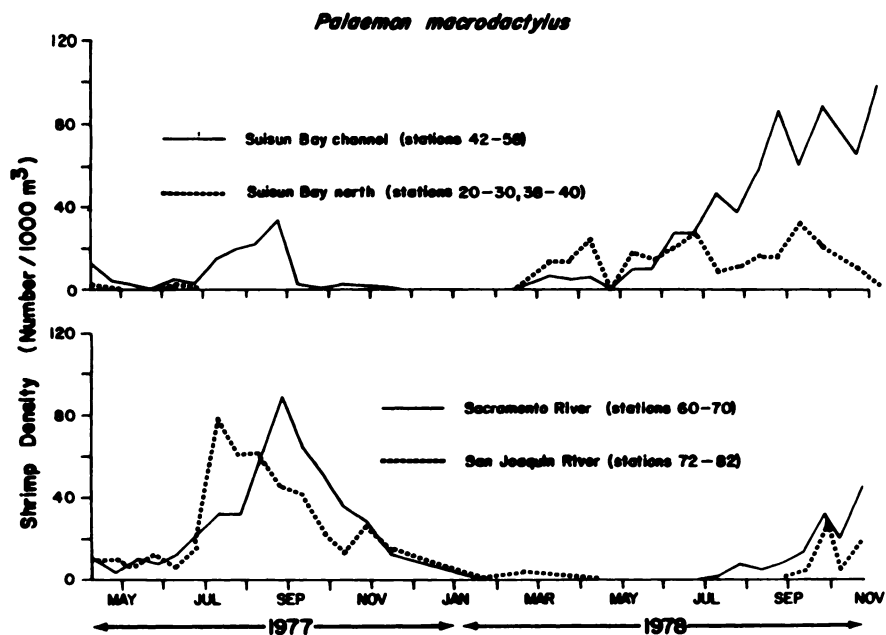


FIGURE 9. Abundance of *Palaemon macrodactylus* in various portions of the study area, April, 1977–October, 1978.

into the brackish waters of the delta in the summer. *C. nigrauda* is restricted to the higher salinity waters of the bay and ocean where it spawns during the summer months (Isreal, 1936; Siegfried, unpublished). *C. nigrauda* was collected only rarely, and then only at the highest salinities, from the study area. *C. franciscorum* is also somewhat larger than *C. nigrauda*, suggesting the potential for trophic resource partitioning based on size differences. A third crangonid, *C. nigramaculata*, also occurs in San Francisco Bay but little is known of its biology in the system.

The life history of *P. macrodactylus* differs in several important respects from that of *C. franciscorum*. Recruitment of young specimens of *P. macrodactylus* is separated both temporally and geographically from that of specimens of *C. franciscorum*. These differences reduce niche overlap between these shrimp and may provide an alternate prey for the *C. franciscorum* population. Larval and post-larval specimens of *P. macrodactylus* are preyed upon by specimens of *C. franciscorum* and may provide a "buffer" during periods of low prey availability (Siegfried, in preparation). Temporal separation of recruitment accentuates size differences between populations of *C. franciscorum* and *P. macrodactylus* and enhances trophic resource partitioning between these shrimp (Siegfried, in preparation). Differences in size and spawning season may be important factors ultimately determining the potential for coexistence of these two shrimp in the San Francisco Bay System.

Reproduction by specimens of *P. macrodactylus* is influenced by temperature, salinity, and photoperiod. Observations of *P. macrodactylus* at higher salinities in the San Francisco Bay system indicate that ovigerous females are found for a longer period than in the brackish water of the delta, *i.e.*, mid-April to late October (Little, 1969). Photoperiod appears to be an important parameter controlling spawning in *P. macrodactylus*. Spawning in the laboratory did not begin until

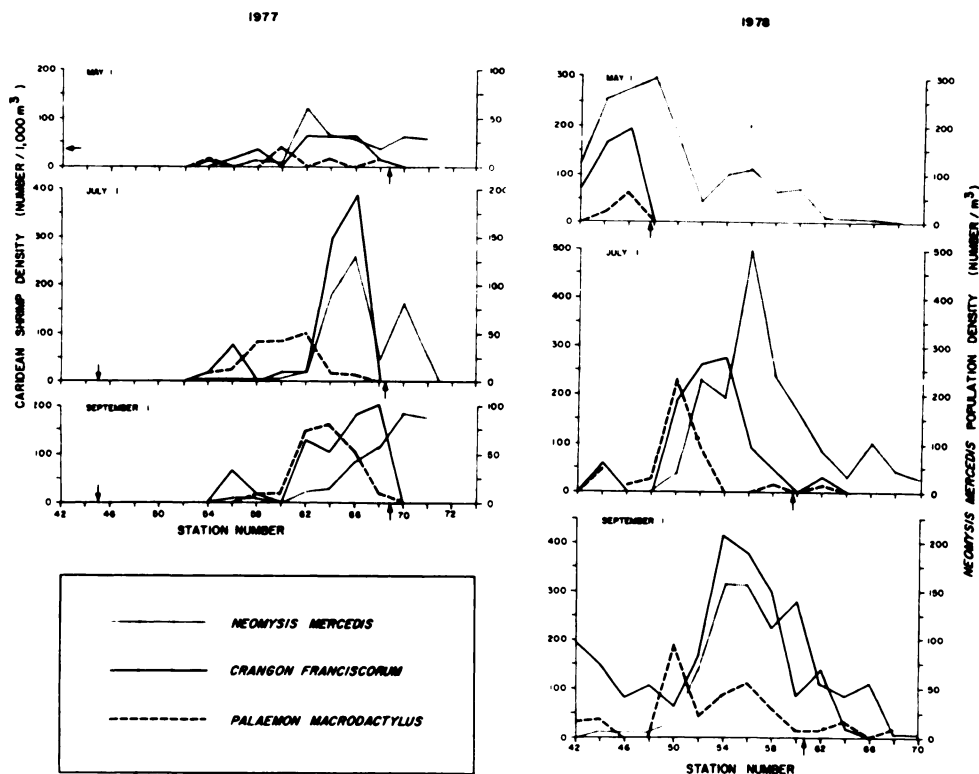


FIGURE 10. Abundance of *Crangon franciscorum*, *Palaemon macrodactylus*, and *Neomysis mercedis* at stations 42-70, on selected dates, May, 1977-September, 1978. Arrow pointing upward marks 1‰ salinity, arrow pointing downward marks 18‰ salinity.

the photoperiod was above 12 hr light:12 hr dark, *i.e.* March, and occurred repeatedly at 20°C under 16 hr photoperiod (Barclay, 1978).

Laboratory bioassay indicates optimum salinity for adult *C. franciscorum* to be around 18-20‰ (Khoram and Knight, 1977). In 1977 this salinity range was present in lower Suisan Bay (stations 42-46) yet no specimens of *C. franciscorum* were collected from that area in 1977 (Fig. 9). During 1978 that salinity range was located downstream of the study area throughout the year. More recent salinity tolerance investigations indicate juvenile *C. franciscorum* to be more tolerant of low salinity, with 100% survival at 2‰ (Shaner, unpublished). Although low salinity limits the upstream distribution of specimens of *C. franciscorum*, other factors are important in determining their downstream distribution.

The distribution of *C. franciscorum* in the delta is influenced by the availability of its principal prey species, *N. mercedis*. Analysis of gastric mill contents of *C. franciscorum* indicates that not only is *C. franciscorum* density much higher in locations where *N. mercedis* density is high (Fig. 9), but those individuals of *C. franciscorum* in areas of high prey density take more prey than those from low prey density areas (Siegfried, in preparation). The dearth of other populations of suitable prey species in the delta region may be an important factor linking the distribution of the crangonid population to that of *N. mercedis*.

TABLE I.

Calculated indices of spatial overlap ( $L$ ), and interspecific crowding between *C. franciscorum* and *P. macrodactylus* ( $Z$ ) in the San Francisco Bay Delta, April 1977–October 1978. See text for explanation. Roman numerals = different collection series.

Sample series	$L_{xy}$		$Z_{c(p)}$		$Z_{p(c)}$		Mean No. specimens of <i>Crangon</i> / Station		Mean No. specimens of <i>Palaemon</i> / Station	
	1977	1978	1977	1978	1977	1978	1977	1978	1977	1978
January		1.84		1.61		1.50		0.81		0.88
February		0		0		0		0.12		0.35
March I		0.06		1.00		0.06		0.03		0.49
March II		0		0		0.20		0.14		0.46
April I	0	0	0	6.00	.0	0.36	0.14	0.05	0.66	0.89
April II	1.42	3.47	0.33	1.22	0.11	0.85	0.13	0.24	0.23	0.35
May I	1.31	3.99	0.59	1.41	0.76	4.77	0.44	1.19	0.33	0.35
May II	0	2.12	0	2.67	0	7.27	0.17	1.62	0.20	0.59
June I	1.17	3.24	0.30	3.02	0.60	9.06	0.51	2.59	0.26	0.86
June II	1.94	2.36	1.27	3.02	2.48	12.00	1.15	4.73	0.59	1.19
July I	0.89	3.42	1.18	3.79	0.98	10.26	1.15	3.07	1.38	1.13
July II	2.59	1.57	3.11	2.33	4.30	6.77	1.67	4.27	1.21	1.47
August I	3.66	0.64	5.60	1.62	4.85	2.56	1.33	4.03	1.54	2.57
August II	3.51	1.02	7.15	3.30	5.89	5.49	1.67	4.27	2.03	2.57
September I	4.76	2.42	4.89	4.04	4.53	8.03	0.95	6.10	1.03	3.07
September II	6.66	1.00	5.24	4.44	5.77	4.82	0.85	4.67	0.77	4.30
October I	5.00	1.62	2.85	4.01	2.59	9.12	0.51	7.20	0.56	3.17
October II	2.09	1.16	2.00	3.57	0.43	3.57	0.21	3.07	0.95	3.07
November	2.53		0.78		0.58		0.23		0.31	

The diet of *P. macrodactylus* in the delta consists almost entirely of *N. mercedis* (Siegfried, in preparation). However, the numerical and functional response to prey density is not as strong as in *C. franciscorum*. *P. macrodactylus* appears, like *C. franciscorum*, to be limited downstream by the lack of prey and upstream by low salinities. Although the peak *P. macrodactylus* densities often coincide with high *N. mercedis* densities (Fig. 9), the maximum *P. macrodactylus* density is usually downstream from the maximum *N. mercedis* and *C. franciscorum* densities. This pattern may be attributable, at least in part, to interactions between the caridean shrimp populations. Further study is necessary to clarify the factors responsible for this distribution pattern.

The possible interaction between these two shrimp can be expressed in a series of indices of overlap or crowding. Hurlbert (1978) has recently reviewed overlap indices and defines niche overlap as the degree to which frequency of interspecific encounter is higher or lower than it would be if each species utilized each resource state in proportion to the resource's abundance. For spatial overlap, when each sample unit or "resource state" is considered to be equally abundant Hurlbert's index of interspecific encounter reduces to Lloyd's (1967) index of interspecies patchiness:  $L = n\sum (P_{x1} \cdot P_{y1})$  and refers to the likelihood that two organisms will bump into or somehow crowd each other during a given time interval (Hurlbert, 1978).  $L = 0$  when no distributional overlap occurs;  $L = 1$  when both species are uniformly distributed, and  $L > 1$  if each species has a clumped distribution and their distributions tend to coincide.

Spatial overlap ( $L$ ) was calculated for each collection date in 1977 and 1978 and the results are presented in Table I.  $L$  was generally greater than 1.0, indicating a higher probability of interspecific encounter than if both *C. franciscorum* and *P. macrodactylus* were distributed uniformly, *e.g.*, on July 1 1978, the probability of interspecific encounter was  $3.42\times$  higher than if both species were distributed uniformly. In 1977 spatial overlap was greatest from about August through October, whereas in 1978 spatial overlap was greatest from April through July. Spatial overlap was lower in early 1977 because a large portion of the *P. macrodactylus* population was in the San Joaquin River or in the sloughs bordering Suisun Bay. In 1978 the *P. macrodactylus* catch was high in the sloughs from August to October where no specimens of *C. franciscorum* were collected, thus leading to reduced spatial overlap.

Niche overlap is generally not reciprocal, *i.e.*, species  $x$  generally impinges on species  $y$  to a different degree than species  $y$  impinges on species  $x$  (Hurlbert, 1978). Thus, it is of interest to measure directional overlap or mean crowding of species  $x$  by species  $y$  and vice versa (Lloyd, 1967; Hurlbert, 1978):  $Z_{x(y)} = (\sum x_i \cdot y_i) / x$ . If  $Z_{x(y)} > \bar{y}$  then species  $x$  has more experience of species  $y$  on the average than would be the case if both species were independently distributed. The mean crowding values of *C. franciscorum* by *P. macrodactylus*, etc., are presented as part of Table I.  $Z_{x(y)}$  is consistently greater than  $\bar{y}$ . In 1977 the mean crowding of *Crangon* by *Palaemon*, or the average number of *Palaemon* encountered by an individual *Crangon*, was generally greater than the mean crowding of *Palaemon* by *Crangon*. The reverse was true in 1978.

Competition between these two species may not be occurring even in spite of considerable spatial overlap since space is not likely to be limiting. However, trophic overlap is also great (Siegfried, in preparation) and under some conditions the availability of prey, *i.e.*, *N. mercedis*, could be limiting. If that is the case, competition would have been most intense in 1977 when *N. mercedis* densities were about 15% of normal values (Siegfried *et al.*, 1979). It might be significant that the highest spatial overlap values occurred in the later half of 1977 when *C. franciscorum* and *P. macrodactylus* were both abundant and *N. mercedis* density was very low.

The association between *C. franciscorum* and *P. macrodactylus* is very recent in the San Francisco Bay Estuary. There is no quantitative data available to evaluate the effect, if any, on the introduction of *P. macrodactylus* on native shrimp populations of the delta. *P. macrodactylus* appears more tolerant of some environmental conditions than *C. franciscorum*, occurring not only in the same habitats as *C. franciscorum* but in additional habitats, *e.g.*, in the San Joaquin River and in pilings near shore, not used by *C. franciscorum*. This may provide a competitive advantage during periods in which resources become limiting, perhaps during droughts. Careful management of upstream diversions and water projects in the delta may be required to protect the native shrimp of the delta.

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## SUMMARY

The seasonal abundance and distribution of the native caridean shrimp, *Crangon franciscorum*, and the introduced shrimp, *Palaemon macrondactylus*, in the channel areas of the San Francisco Bay Delta were studied from April, 1977, through October, 1978. *C. franciscorum* reproduces earlier in the year and grows to a larger size than *P. macrondactylus*. *C. franciscorum* reproduction occurs from December to June in the high salinity waters of San Francisco Bay and the Pacific Ocean. *P. macrondactylus* reproduction occurs from May to September in the delta as well as in higher salinity habitats. Length-weight and length-fecundity relationships differ significantly between the two shrimp. Both shrimp are limited upstream by low salinities, few shrimp occurring at salinities < 1‰. The downstream distribution of these shrimp is related to prey availability, i.e., *Neomysis mercedis* abundance.

Indices of spatial overlap, or interspecies patchiness, indicate a high degree of overlap which varied seasonally and exhibited markedly different patterns in 1977 and 1978. Directional crowding (intraspecific patchiness) also differed between 1977 and 1978. *P. macrondactylus* appears more tolerant of varied environmental conditions than *C. franciscorum*, occurring in the same habitats and also in additional ones not utilized by *C. franciscorum*. This may give *P. macrondactylus* a competitive advantage when trophic resources become limiting.

## LITERATURE CITED

- ALLEN, J. A., 1960. On the biology of *Crangon allmani* Kinahan in Northumberland waters. *J. Mar. Biol. Assoc. U.K.*, 39: 481-508.
- BARCLAY, W., 1978. Development of spawning and mass larva-rearing techniques for the euryhaline shrimp *Palaemon macrondactylus*. Davis, California. Pp. 137-143 in A. W. Knight, Ed., *Studies on Bioenergetics, Osmoregulation, Development, Behavior, and Survival of Several Aquaculture Organisms*. Dep. Land, Air and Water Resources, Water Sci. and Eng. Paper No. 4507, University of California, Davis.
- BONNOT, P., 1932. The California shrimp industry. *Calif. Dep. Fish Game Bull.* 38: 20 pp.
- BROEKMA, M. M., 1941. Seasonal movements and the osmotic behavior of the shrimp *Crangon crangon* L. *Arch. Neerl. Zool.*, 6: 1-100.
- DURKIN, J. T., AND S. J. LIPOVSKY, 1977. *Aquatic disposal field investigations, Columbia River disposal site, Oregon. Appendix E. Demersal fish and decapod shellfish studies*. Tech. Rep. D-77-30, Environ. Effects Lab., U. S. Army Eng. Waterways Exp. Sta., Vicksburg, Mass. pp. 119-129.
- GANSSELE, D., 1966. Fishes and decapods of the San Pablo and Suisun Bays. pp. 64-94 in: D. W. Kelley, Ed., *Ecological Studies of the Sacramento-San Joaquin Estuary*. Calif. Dep. Fish Game Bull., 133.
- HULBERT, S. H., 1978. The measurement of niche overlap and some relatives. *Ecology*, 59: 67-77.
- ISREAL, H. R., 1936. A contribution toward the life histories of two California shrimps, *Crango franciscorum* (Stimpson) and *Crango migracauda* (Stimpson). *Calif. Dep. Fish Game Bull.*, 46: 1-28.
- KHORRAM, S., AND A. W. KNIGHT, 1977. Combined temperature-salinity effects on grass shrimp. *J. Environ. Eng. Div., Am. Soc. Civil Eng.*, 103: 381-388.

- KRYGIER, E. E., AND H. F. HORTON, 1975. Distribution, reproduction, and growth of *Crangon nigricauda* and *Crangon franciscorum* in Yaquina Bay, Oregon. *Northwest Sci.*, **49**: 216-240.
- LITTLE, G., 1969. The larval development of the shrimp *Palaemon macrodactylus* Rathbun, reared in the laboratory, and the effect of eyestalk extirpation and development. *Crustaceana*, **17**: 69-87.
- LLOYD, A. J., AND C. M. YONGE, 1947. A study of *Crangon vulgaris* L. in the Bristol Channel and Severn Estuary. *J. Mar. Biol. Assoc. U.K.* **26**: 626-661.
- LLOYD, M., 1967. Mean crowding. *J. Anim. Ecol.*, **36**: 1-30.
- MAUCHER, W. D., 1961. Statistische untersuchungen in den körperproportionen zwischen der Nord- und Ostform von *Crangon crangon*. *Kiel. Meeresforsch.*, **17**: 219-227.
- MEREDITH, S. S., 1952. A study of *Crangon vulgaris* in Liverpool Bay area. *Proc. Trans. Liverpool Biol. Soc.*, **1950-1952**: 75-109.
- NELSON, S. G., M. A. SIMMONS, AND A. W. KNIGHT, 1979. Ammonia excretion and its relationship to diet in a benthic estuarine shrimp, *Crangon franciscorum* Stimpson (Crustacea: Crangonidae). *Mar. Biol.* **54**: 25-31.
- NEWMAN, V. A., 1963. On the introduction of an edible oriental shrimp (Caridea, Palaemonidae) to San Francisco Bay. *Crustaceana*, **5**: 119-132.
- PRICE, K. S., JR., 1962. Biology of the sand shrimp, *Crangon septemspinosa* in the shore zone of the Delaware Bay region. *Chesapeake Sci.*, **3**: 224-255.
- REMANE, A., AND C. SCHLIEPER, 1971. Biology of brackish water. *Die Binnengewässer*, Vol. 25, 327 pp.
- SCHMITT, W. L., 1921. *The marine decapod crustacea of California*. Univ. Calif. Publ. Zool., No. 23. 470 pp.
- SHANER, S. W., 1978. Osmotic and ionic regulation in the euryhaline shrimp *Crangon franciscorum* (Stimpson) (Crustacea: Natantia). Pp. 106-121 in: A. W. Knight, Ed., *Studies on Bioenergetics, Osmoregulation, Development, Behavior, and Survival of Several Aquaculture Organisms*. Dept. Land, Air and Water Resources, Water Sci. and Eng. Paper No. 4507, Univ. of Calif., Davis, California.
- SHARP, J. W., R. M. SITTS, AND A. W. KNIGHT, 1978. Effects of Kelthane and temperature on the respiration of *Crangon franciscorum*. *Comp. Biochem. Physiol.*, **59**: 75-79.
- SIEGFRIED, C. A., A. W. KNIGHT, AND M. E. KOPACHE, 1978. *Ecological studies on the western Sacramento-San Joaquin Delta during a dry year*. Dept. Land, Air, and Water Resources, Water Sci. and Eng. Paper No. 4506. Univ. of California, Davis. 121 pp.
- SIEGFRIED, C. A., M. E. KOPACHE, AND A. W. KNIGHT, 1979. The distribution and abundance of *Neomysis mercedis* in relation to the entrapment zone in the western Sacramento-San Joaquin Delta. *Trans. Am. Fish. Soc.*, **108**: 260-268.
- SITTS, R. M., 1978. *Ecological Aspects of the Estuarine Shrimps Neomysis mercedis, Crangon franciscorum, and Palaemon macrodactylus*. Ph.D. Dissertation, University California, Davis, California, 79 pp. Diss. Abs. 7905210.
- SMITH, R. I., AND J. T. CARLTON, Eds., 1975. *Lights Manual: Intertidal Invertebrates of the Central California Coast*. University California Press, Berkeley, California. 716 pp.
- STEEL, R. G. D., AND J. H. TORRIE, 1960. *Principles and Procedures of Statistics*. McGraw Hill, New York. 481 pp.