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PREDATION BY THE ESTUARINE SHRIMPS CRANGON FRANCISCORUM STIMPSON AND PALAEMON MACRODACTYLUS RATHBUN

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Crangon franciscorum and Palaemon macrodactylus are caridean shrimps coexisting in the Sacramento-San Joaquin Estuary of California. C. franciscorum is native to estuaries along the northeastern Pacific Ocean, while P. macrodactylus is a form introduced from the Orient (Newman, 1963). No previous reports were found which deal with the feeding habits of any species of Crangon or Palaemon in estuaries along the Pacific Ocean. Investigations of Crangon and Palaemon species in estuaries and coastal waters elsewhere have reported that some species are carnivorous (Lloyd and Yonge, 1947; Allen, 1960; Price, 1962; Herman, 1963; B. L. Welsh, unpublished Masters Thesis, University of Maryland, 1970; Wilcox and Jeffries, 1974; Subrahmanyam, 1975).

Research on vertical migrations of C. franciscorum, P. macrodactylus, and a coexisting smaller and much more abundant mysid shrimp Neomysis mercedis (Sitts and Knight, unpublished), indicate that the mysid may be an important food resource for C. franciscorum and P. macrodactylus, just as it is for many smaller fishes of the estuary (Gannsle, 1966). All three shrimps undergo nocturnal vertical migrations (Sitts and Knight, unpublished). Visual estimates of C. franciscorum, P. macrodactylus and N. mercedis biomass indicate that during some seasons N. mercedis biomass was equaled or exceeded by the biomass of the other two species. If N. mercedis was a major prey of C. franciscorum or P. macrodactylus, predation might change with vertical migration, and, if the biomasses were similar, the amount of predation could limit mysid abundance. Also, since the mysid is an important trophic resource for fish, predation on N. mercedis by the caridean shrimps may affect fish production.

This study was done to quantify and compare the biomasses of *C. franciscorum*, *P. macrodactylus*, and *N. mercedis*, and to determine and compare the feeding habits of *C. franciscorum* and *P. macrodactylus*.

MATERIALS AND METHODS

Shrimp were collected in the main channel of the Sacramento-San Joaquin Estuary of central California (long 121° 54′ 50″ W, lat 38° 02′ 51″ N). Details of sampling and the physical and chemical characteristics of the study site are given by Sitts (1978). Simultaneous collections were made of organisms at depths of 1, 5, and 9 m (bottom) about every three hrs over diel cycles on February 25–26, May 6–7, July 19–20, September 17–18 and 23–24, and November 30–December 1 of 1976. The diel samplings will be referred to by month, with the latter three

referred to as mid and late September and late November. Nets with 50-cm-diameter mouths and #8 (200- μ m) mesh were used. Samples were preserved in the field in 5% formalin, then, within seven days, the preservative was changed to 70% ethanol. All specimens of C. franciscorum and P. macrodactylus with carapace lengths >2 mm were counted and measured. All specimens of N. mercedis were counted and measured except when large catches necessitated subsampling.

Length vs. dry-weight equations were obtained for fresh specimens of each species. Lengths of individuals were determined to the nearest mm under a 10× dissecting microscope. Total lengths of N. mercedis specimens were measured from the anterior of the eyes to the anterior of the telson. Specimens of C. franciscorum and P. macrodactylus were measured for shortest dorsal carapace length from the anteriodorsal midpoint between the posterior edges of the eye sockets to the posteriodorsal edge of the carapace. Dry weights were measured after live lengths were obtained and organisms were dried at 50° C for ≥36 hrs, a period assumed sufficient for complete drying. Seventy-five specimens of N. mercedis were weighed to the nearest µg on a precalibrated electrobalance. Fifty-five specimens of C. franciscorum and 30 specimens of P. macrodactylus were weighed to the nearest 0.01 mg on a precalibrated precision balance. Additional unpublished length and weight data for N. mercedis specimens were available from an earlier study (Simmons and Knight, 1975). Since these data fit well with the present data at similar lengths, they were incorporated into the analysis to extend the lengthweight relationship.

Live lengths did not differ significantly (t-test, $\alpha 0.05$) from preserved lengths for 28 N. mercedis individuals and 15 C. franciscorum forms measured live then preserved for seven days in 5% formalin followed by seven days in 70% ETOH. P. macrodactylus was assumed also to be unchanged by preservation.

All specimens of C. franciscorum and P. macrodactylus in each field sample were measured. Up to 75 specimens of N. mercedis were measured in each sample. If over 150 specimens of N. mercedis were in a sample, 75 individuals were selected randomly from each aliquot of the entire sample. In samples with 76 to 150 mysids, 75 were measured in perpendicular sweeps crossing near the middle of the tray. The proportion of individuals of N. mercedis in each size class relative to the total number of individuals measured was extrapolated to the number of individuals of each size per m^3 . Then, the dry weight (mg) per m^3 was calculated for each size class. The dry weight (mg) for each specimen of C. franciscorum and P. macrodactylus in a sample was calculated, followed by estimates of the mean dry weight (mg) per individual and per m^3 .

Foregut contents of up to five specimens of *C. franciscorum* and five specimens of *P. macrodactylus* from each sample were examined. In samples with more than five specimens of *C. franciscorum* and five specimens of *P. macrodactylus*, five individuals of each species were chosen randomly. Carapace lengths were measured, and foreguts were removed intact, placed on a depression slide, and teased open. Foregut contents were removed with dissecting needle to water in the depression, and spread. Recognizable contents were identified and enumerated. Foregut contents of 352 specimens of *C. franciscorum* and 198

specimens of *P. macrodactylus* were examined. Percent frequency of occurrence of various food items was compared to derive an understanding of each one's relative importance in the diet of *C. franciscorum* and *P. macrodactylus*.

To determine whether certain lengths of N. mercedis individuals were being selected over others, Ivlev's (1961) index of electivity (E) was employed: $E = (F - A) \div (F + A)$, where F is the proportion in the foregut of a given length of specimens of N. mercedis relative to all lengths consumed, and A is the proportion available of the same length as F relative to all lengths available. E ranges from -1.0 to +1.0, with strong electivity of a length indicated in values near +1.0, and strong electivity against indicated in values near -1.0.

C. franciscorum and P. macrodactylus predation on N. mercedis populations was measured in each diel cycle in terms of the percent loss per m^3 per day of individuals and biomass (%I and %B below). Percentages were calculated as follows:

$$I = 3CN$$
 %I = 100I/(DI + I)
 $B = \sum_{l=2}^{m} (I P_l W_l)$ %B = 100B/(D_B + B)

where I and B are respectively, the number of individuals and the dry weight (mg) of N. mercedis consumed per m³ per day by specimens of C. franciscorum or P. macrodactylus, C represents the number of specimens of C. franciscorum or P. macrodactylus per m³, N represents the mean number of specimens of N. mercedis per C. franciscorum or P. macrodactylus foregut over a diel cycle, and P1 represents the number of foregut clearances per day by either predator. P1 the proportion of each total length class P1 relative to the number of specimens of P2. mercedis in all length classes for a diel cycle, with P3 being the longest class. P4 is the dry weight for each length class of specimens of P4. mercedis determined from the equation given in Table I. P4 and P5 are respectively, the mean number of individuals and biomass (mg dry wt) of P4. mercedis per m³ for a diel cycle. The foregut clearance value of P3 was obtained from unpublished preliminary experiments conducted here by P5. Louks on specimens of P6. franciscorum, which indicated a 6-hr foregut clearance time, and from the estimate by Wilcox and Jeffries (1974) of 6 to 12 hrs for P5. septemspinosa. We used an 8-hr clearance time as

TABLE I

Equations for length vs. dry weight equations for specimens of Crangon franciscorum, Palaemon macrodactylus, and Neomysis mercedis. $100\ R^2$ is the coefficient of determination in percent (variation accounted for by the equation), n is the number of samples, W is the dry weight (mg), l is the total length (mm), and CL is carapace length (mm).

Species	n	Equation	100 R ²		
C. franciscorum P. macrodactylus N. mercedis	53 31 176	$W_{\rm CL} = 0.8789 \; ({\rm CL})^{2.474}$ $W_{\rm CL} = 0.6390 \; ({\rm CL})^{2.632}$ $W_1 = 0.01 \cdot 0.6145 \; (1)^{2.710}$	92 95		

an approximation for C, franciscorum and applied it arbitrarily to P, macrodactylus. Statistical comparisons followed procedures of Steel and Torrie (1960).

RESULTS

Table I gives equations for estimating dry weight from length for specimens of Crangon franciscorum, Palaemon macrodactylus, and Neomysis mercedis. All have coefficients of determination (100R), or the percent of variation in weight accounted for by the equation, that are $\geq 92\%$.

The mean dry weight (mg) per m³ for each diel cycle differed between species (Fig. 1). The biomass of the N. mercedis population was greater than the biomass of populations of C. franciscorum and P. macrodactylus in February and May. In July, the biomass of the population of N. mercedis was greater than the population biomass of P. macrodactylus but equaled the population biomass of

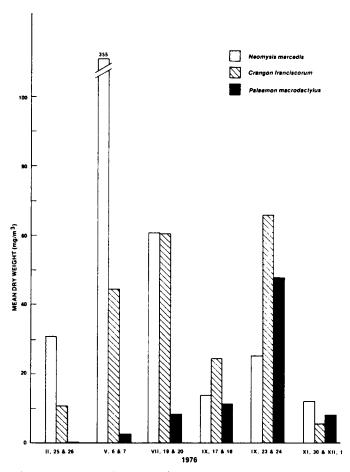


FIGURE 1. The mean dry weight (mg)/m³ of specimens of Neomysis mercedis, Crangon franciscorum, and Palaemon macrodactylus over diel cycles during 1976.

C. franciscorum. In September, the population biomass of N. mercedis was less than that for the population of C. franciscorum and was approximated and exceeded by the P. macrodactylus population. In July through late November diel samplings,

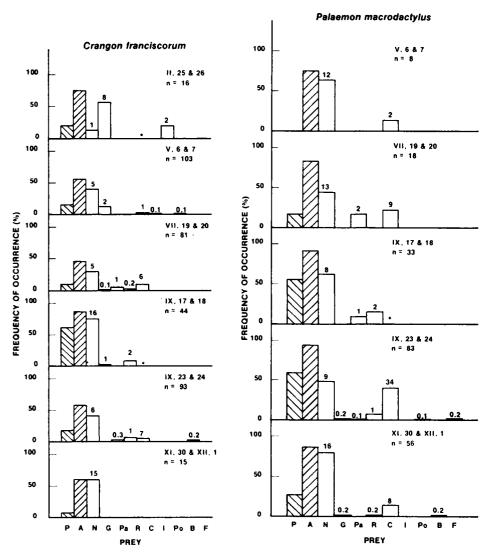


FIGURE 2. The frequency of occurrence of various items in the foreguts of specimens of Crangon franciscorum and Palaemon macrodactylus during 1976. Categories are plant fragments (P), animals or animal fragments (A), specimens of Neomysis mercedis (N), gammarid amphipods (G), larvae of Palaemon macrodactylus (Pa) and the mud crab Rhithropanopcus harrisii (R), copepods (C), insects (I), polychaetes (Po), bivalves (B), and fish larvae (F). A star indicates that copepods were not counted. The number over a bar is the average number of that prey item per 10 foreguts over the diel cycle. The single Palemon macrodactylus in February (II, 25 & 26) was excluded.

N. mercedis biomass was equaled or exceeded by the sum of C. franciscorum plus P. macrodactylus biomass.

Each species peaked in biomass at different times (Fig. 1). The biomass of *N. mercedis* was greatest in the May evaluation. *C. franciscorum* was most abundant in the May through September diel samplings, while *P. macrodactylus* biomass steadily climbed to a maximum in the late September diel cycle.

Foregut contents of *C. franciscorum* and *P. macrodactylus* indicate that those two species are mainly predacious. The frequency of occurrence of animals or animal fragments (A) always exceeded that of plant fragments (P) by at least

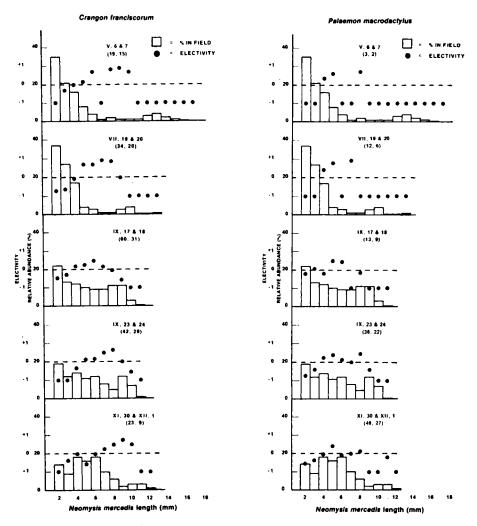


FIGURE 3. Size electivity (E) of Crangon franciscorum and Palaemon macrodactylus for specimens of Neomysis mercedis during diel cycles in 1976, and the relative abundance (%) of the total N. mercedis population in each length class.

25% (Fig. 2). Plant fragments were always small, and algae were rarely observed. The frequency of occurrence of animal fragments ranged from 46 to 86% in C. franciscorum and from 75 to 93% in P. macrodactylus. The frequency of plant fragments ranged from 7 to 61% in C. franciscorum, and from 0 to 59% in P. macrodactylus.

A variety of prey items were found in the foreguts of *C. franciscorum* and *P. macrodactylus*. Prey of both species included *N. mercedis*, gammarid amphipods including *Corophium* spp., larvae of *P. macrodactylus* and the mud crab *Rhithropanopeus harrisii*, copepods, polychaetes, bivalves, and fish larvae (closely resembling larval anchovies, *Engraulis mordax*). *N. mercedis* was the most frequently occurring item in both predators, found in 12 to 75% (February and September, respectively) of the *C. franciscorum* specimens and 44 to 79% (July and late November, respectively) of the *P. macrodactylus* specimens. The only difference in prey between the predators was that insect fragments were found only in specimens of *C. franciscorum*.

The prey items most abundant in the foreguts of specimens of *C. franciscorum* and *P. macrodactylus* were *N. mercedis* and copepods (Fig. 2). The number of specimens of *N. mercedis* per ten foreguts ranged from 1 to 16 for *C. franciscorum*, and from 8 to 16 for *P. macrodactylus*. Copepods per ten foreguts ranged from 0 to 6 for *C. franciscorum*, and from 2 to 34 for *P. macrodactylus*.

C. franciscorum selected N. mercedis specimens of intermediate sizes (Fig. 3). Consistently, mysids in the range of 6 to 9 mm long had the greatest positive electivity values. Selection was strongly against the most abundant smaller sizes, as well as the longer forms, with some electivity values of -1.0. Larger individuals of C. franciscorum contained larger specimens of N. mercedis (Fig. 4). The mean length of specimens of N. mercedis consumed increased significantly from 4 to 8 mm as the carapace length of specimens of C. franciscorum increased from 5 to 10 mm. The mean length of N. mercedis specimens was only 5 mm for 11 mm specimens of C. franciscorum.

 $P.\ macrodactylus$ tended to select intermediate size specimens of $N.\ mercedis$ (Fig. 3), as evident from the higher positive electivity values for 4 to 8 mm mysids. As with $C.\ franciscorum$, $P.\ macrodactylus$ selected against both the most abundant shorter lengths and the longer specimens of $N.\ mercedis$, which equaled or surpassed the abundance of intermediate lengths in May through late September diel samplings. Larger specimens of $P.\ macrodactylus$ consumed larger specimens of $N.\ mercedis$ (Fig. 4). This relationship was consistent over all carapace lengths evaluated. The average length of specimens of $N.\ mercedis$ consumed increased significantly (from 5 to 8 mm) with an increase in $P.\ macrodactylus$ carapace length from 5 to 12 mm.

Variation in the number of specimens of N. mercedis per C. franciscorum foregut between depths was not significant (F-test, $\alpha 0.05$) either during the day or night except for day data in May. Here, the mean number of specimens of N. mercedis per C. franciscorum foregut was greater at 9 m (0.76) than at 5 m (0.27), with no specimens of C. franciscorum present at 1 m. Since depth made little difference, all depths were combined in comparisons between day and night feeding data.

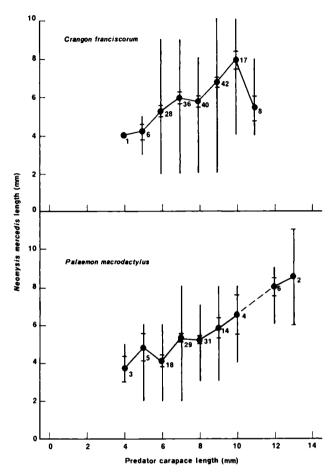


FIGURE 4. Range (vertical bar), mean (closed circle), and \pm standard error (horizontal bars on range lines) of *Neomysis mercedis* lengths found in each carapace length (mm) class of *Crangon franciscorum* and *Palaemon macrodactylus*.

The number of specimens of N. mercedis per C. franciscorum foregut at night equaled or exceeded the day level. In the first four diel samplings, F-tests for variation in mysids per C. franciscorum foregut between day and night were not significant ($\alpha 0.05$) for means which ranged from 0.20 to 1.56 and 0.00 to 1.68 for day and night data, respectively. The late September night mean of 0.75 specimens of N. mercedis per C. franciscorum forgeut was significantly ($\alpha 0.05$) greater than the day mean of 0.33. Similarly, the mean number of specimens of N. mercedis per C. franciscorum foregut in late November was significantly ($\alpha 0.01$) greater at night (3.00) than during the day (0.56).

Variation in the number of N. mercedis specimens per P. macrodactylus foregut between depths was significant (F-tests, $\alpha 0.05$) at night in late September and late November (specimens of P. macrodactylus were caught at only one depth

(9 m) during the day). The mean number of mysids per foregut at 1, 5, and 9 m at night in late September and late November were respectively, 0.00, 0.58, 1.07, and 0.33, 1.23, 1.83.

There was no significant ($\alpha 0.05$) difference in the number of specimens of N. mercedis per P. macrodactylus foregut between day and night samples in May, mid and late September, and late November. (F-tests for February and July data were not possible.) In these cases, mean mysids per P. macrodactylus ranged from 0.83 to 1.60 for day and 0.79 to 2.50 for night.

C. franciscorum and P. macrodactylus consumed N. mercedis before being caught and concentrated in the nets. The longest tows were near five minutes duration, and it is assumed that this period is insufficient for either predator to capture, macerate, swallow, and digest N. mercedis to the point that the lengths would be unmeasurable. Of the 144 specimens of C. franciscorum and 117 specimens of P. macrodactylus containing N. mercedis specimens respectively, 39% and 65% contained specimens of N. mercedis digested beyond the point at which the form of the carapace and abdomen fragments were sufficient for length determination.

N. mercedis standing crop consumed daily varied seasonally, with the extent of predation varying similarly among C. franciscorum and P. macrodactylus

TABLE II

Losses of Neomysis mercedis standing crop, in terms of individuals and biomass, to predation by populations of Crangon franciscorum and Palaemon macrodactylus during each diel sampling. Percentages (% L) are for loss relative to standing crop plus loss. \bar{x} N.m./100 m^3 is the mean number of Neomysis mercedis specimens per 100 m^3 . N_C and N_P are the individuals or biomass of Neomysis mercedis consumed per 100 m^3 per day by populations of Crangon franciscorum (N_C) and Palaemon macrodactylus (N_P), and N_T is the total consumption by both predator populations. % BCC and % BPC are percents of the mean dry weight (m_B)/ m^3 of Crangon franciscorum (BCC) and Palaemon macrodactylus (BPC) populations that each predator population consumed as Neomysis mercedis for each diel period.

Dates of diel samplings in 1976 (mo., days)	₹ N.m./100 m³	Nc	% L	% всс	Nρ	% L	% BPC	Nт	%
		indiv	iduals						
Feb. 25, 26	1,900	2	0.1		0	0	_	2	0.1
May 6, 7	38,400	33	0.1		5	0.01		38	0.1
Jul. 19, 20	14,600	77	0.5		15	0.1	_	92	0.6
Sep. 17, 18	1,600	105	6.2		34	2.1	—	139	8.0
Sep. 23, 24	2,500	103	4.0	—	127	4.8		230	8.4
Nov. 30 and Dec. 1	1,500	12	0.8		47	3.0	_	59	3.8
		bio	mass						
Feb. 25, 26	3,100	_		_	0	0			
May 6, 7	35,500	39	0.1	0.9	4	0.01	1.5	43	0.1
Jul. 19, 20	6,100	65	1.1	1.1	9	0.1	1.1	74	1.2
Sep. 17, 18	1,400	76	5.1	3.1	17	1.2	1.5	93	6.2
Sep. 23, 24	2,500	131	5.0	2.0	97	3.7	2.0	228	8.4
Nov. 30 and Dec. 1	1,200	16	1.3	2.9	33	2.7	4.1	49	3.9

(Table II). The percent of *N. mercedis* standing crop consumed was minimal during diel periods in February, May, and July. Mysid standing crop consumed by both predators was greatest in the September diel cycles. The decrease in *N. mercedis* standing crop due to *C. franciscorum* and *P. macrodactylus* predation combined were greatest during the late September diel cycle, with 8.4% of both the individuals (230) and dry weight (228 mg) of *N. mercedis* consumed per 100 m³ per day. *C. franciscorum* consumed more *N. mercedis* individuals than *P. macrodactylus* in all diel samplings except those in late September and late November. Also, except for the late November diel cycle, *C. franciscorum* consumed more *N. mercedis* biomass than did *P. macrodactylus*.

Discussion

C. franciscorum and P. macrodactylus are mainly carnivorous and N. mercedis is the major identifiable prey for both species. The carnivore role probably exceeds the detritivore role more than is indicated by the frequency-of-occurrence results (Fig. 2). Plant fragments observed in the foreguts of both predators were filamentous strands, small in size relative to other material, and often could have originated in the foreguts of consumed prey.

Mysids were the major prey item mainly because they occurred most frequently in foreguts, except for C. franciscorum in February. Also, with the additional exception in P. macrodactylus in late September, there were more N. mercedis specimens per foregut than any other prey. N. mercedis individuals were the largest size prey consumed except for the infrequent polychaetes. Copepods were abundant in foreguts of P. macrodactylus specimens; however, since they are small they contribute less biomass than mysids.

C. franciscorum and P. macrodactylus are affecting the mysid population structure by preying mainly on intermediate sized (4 to 7 mm) specimens of N. mercedis. The more abundant smaller sizes may be too difficult to locate, while the larger sizes, which are often more abundant than intermediate sizes (Fig. 3), may be too quick to capture. By not preying mainly on larger sizes, N. mercedis recruitment and subsequent availability are enhanced because female mysids begin to become gravid when they are 7 mm long (Heubach, 1969).

C. franciscorum and P. macrodactylus are unable to exploit the greater daytime abundance of their major food resource near the bottom. The daytime average of N. mercedis specimens per predator foregut never exceeded the average for night-time, when mysids are more dispersed. This may be a result of having to counter vertical transport in persistent turbulent flows during the day, perhaps to avoid being visible prey for fish. Opposing vertical transport may mean repeatedly swimming back toward the bottom and concurrent reduction in predation efficiency.

Nocturnal vertical migration has been hypothesized as a mechanism for avoiding visual predation (Zaret and Suffern, 1976), and sightless predation may be avoided in such migrations as well. Predation by individuals of *C. franciscorium* and *P. macrodactylus* is probably a sightless process since arthropod eyes are inferior in image formation (Goldsmith, 1973) and since individuals of both species prey at night and in darker regions during daytime. There is more time for predation at night since opposing vertical transport to avoid visibility is incon-

sequential. However, this sightless predation is avoided to some extent by N. mercedis through its dispersion in its nocturnal vertical migration.

Opposition of vertical transport during the day, and prey dispersion at night could keep the average number of mysids per foregut unchanged in most diel cycles. However, predation at night is more effective over some cycles for *C. franciscorum*. Also, another crangonid shrimp, *C. septemspinosa*, is indicated as feeding more at night from observations of greater volumes of stomach contents at night (Wilcox and Jeffries, 1974).

C. franciscorum and P. macrodactylus had their greatest impact on the standing crop of N. mercedis in September, and mysid recruitment was low in the following weeks, as indicated by the low abundance of 2 to 3 mm mysids in late November (Fig. 3). At a daily 8% decrease in N. mercedis standing crop, and with other factors unchanged in their effects on predation, only 1% of the September standing crop of N. mercedis would have been left by the time of the late November diel sampling. What probably prevented a portion of this decimation was the reduction in numbers of C. franciscorum and P. macrodactylus individuals, as indicated by the drop in their biomass (Fig. 1). C. franciscorum has been observed to move to greater salinities during cooler periods (Israel, 1936; Krygier and Horton, 1975). P. macrodactylus probably emmigrated also, perhaps seaward and to slower, shallower channels and marshes, for it is adapted for walking and climbing and has been found in such habitats (Newman, 1963; Little, 1969).

The similarities between C. franciscorum and P. macrodactylus raise the question of interspecific competition, both between themselves and between either of them and fish. C. franciscorum and P. macrodactylus specimens of similar size, coexist, undergo nocturnal vertical migrations, and have similar prey. Both have their greatest impact on the standing crop of N. mercedis in September, when their standing crops are at intermediate to high levels. It is during September that there is the greatest chance of interspecific competition for food (N. mercedis) between C. franciscorum and P. macrodactylus. The biomass of N. mercedis consumed by each predator population relative to its own standing crop was not low in September in comparison with other months (Table I) indicating that food supply was not limiting. Competition between C. franciscorum or P. macrodactylus and fish is possible but most likely only to occur in the fall, when N. mercedis is in relatively low abundance, but when the caridean shrimps are abundant. Unfortunately, no information was available on the biomass, distribution, and feeding of the fishes present.

Interspecific competition between C. franciscorum and P. macrodactylus may increase in the future. P. macrodactylus is an exotic species, thought to have been introduced into the Sacramento-San Joaquin Estuary in the first half of this century (Newman, 1963), and the relationship between the two species may not yet have stabilized. P. macrodactylus may have an important advantage over C. franciscorum in the study area, because only P. macrodactylus reproduces there, whereas C. franciscorum migrates seaward to reproduce. Data are still insufficient to speculate on the extent to which P. macrodactylus may displace C. franciscorum.

Changes in environment relative to conditions at the time and place of this

study may modify indications in these results. Drought in California in 1976 led to an intrusion of salinity unusually far upstream. Also, *N. mercedis* abundance during the same period was below average (Orsi and Knutson, in preparation).

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SUMMARY

- 1. Feeding studies were conducted on the caridean shrimps Crangon franciscorum and Palaemon macrodactylus of the Sacramento-San Joaquin Estuary, California. Foregut contents from 352 specimens of C. franciscorum and 198 specimens of P. macrodactylus collected over six diel cycles in 1976 were itemized.
- 2. C. franciscorum and P. macrodactylus are mainly carnivorous. Animal material always exceeded plant fragments in frequency of occurrence in foreguts, being respectively 46 to 86% and 7 to 61% in C. franciscorum and 74 to 92% and 0 to 59% in P. macrodactylus. The most frequent prey item identifiable in both predators was the mysid shrimp Neomysis mercedis. Both predators selected for N. mercedis of intermediate lengths (5 to 9 mm), and selected against those 2 mm or >10 mm long.
- 3. Day and night differences in the number of individuals of *N. mercedis* per foregut were significant only for *C. franciscorum*, and then only in late September and late November, with greater means at night in each case.
- 4. The percentages of N. mercedis standing crops consumed daily by C. franciscorum and P. macrodactylus respectively, ranged from 0.1 to 6.2% and 0.0 to 4.8% in terms of individuals, and from 0.1 to 5.1% and 0.0 to 3.7% for biomass. The percent of their respective population biomasses that specimens of C. franciscorum and P. macrodactylus respectively consumed daily as N. mercedis ranged from 1 to 3% and 1 to 4%. Similarities between these predators suggest the possibility of competition.

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