Trophic relations of *Crangon franciscorum* Stimpson and *Palaemon macrodactylus* Rathbun: predation on the opossum shrimp, *Neomysis mercedis* Holmes[1]

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Abstract

Crangon franciscorum and *Palaemon macrodactylus* are carnivorous shrimp in the Sacromento-San Joaquin River Delta. These shrimp prey primarily on the opossum shrimp, *Neomysis mercedis.* Behavioral and morphological differences result in *P. macrodactylus* stomachs containing a greater number of prey, on the average, than *C. franciscorum.* Dietary overlap and similarity were high (>80%) throughout the study. *C. franciscorum* is generally larger than *P. macrodactylus* and is able to ingest larger prey. This results in some size-related resource partitioning.

Introduction

The franciscan bay shrimp, *Crangon franciscorum,* and the oriental shrimp, *Palaemon macrodactylus,* are the dominant decapods of the Sacramento-San Joaquin River Delta. *C. franciscorum* is a common inhabitant of the continental shelf and estuaries from southeastern Alaska to southern California (Schmitt 1921). *P. macrodactylus* is a recent introduction to the Bay-Delta system, presumably from water ballast tanks of ships returning from Korea in the early 1950s (Newman 1963).

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). *Crangon* spp. are generally considered omnivorous, but animal tissues usually comprise the main food items (Lloyd & Yongue 1947; Allen 1960; Wilcox & Jeffries 1974). *Palaemon* spp. are also reported to be omnivorous, feeding on algae, moss, and small arthropods and debris (Patwardham 1937; Berglund 1980). Preliminary reports of the diets of these shrimp in the Delta indicated mostly carnivorous habits, with the bulk of the diets comprised of crustacean prey, especially *N. mercedis* (Siegfried *et al.* 1978; Sitts & Knight 1979). The distributions of *C. franciscorum* and *P. macrodactylus* show a high degree of overlap in the Delta and have been related, in part, to *N. mercedis* abundance (Siegfried 1980). This study compares the diets and presents information on dietary overlap between these two decapod shrimp collected from throughout the Delta between January 1976 and October 1978. Dietary overlap and similarity were high throughout the study period although some size-based trophic resource partitioning does occur.

Materials and methods

Decapod shrimp and the opossum shrimp, *Neomysis mercedis,* were collected at approximately bi-weekly intervals from 32 stations in Suisun Bay and the Sacramento and San Joaquin Rivers (Fig. 1) from December 1977 through October 1978. From January 1976 through July 1977 shrimp were collected for stomach content analysis only from Sacramento River stations. The 32 stations were sampled over four consecutive days, with stations

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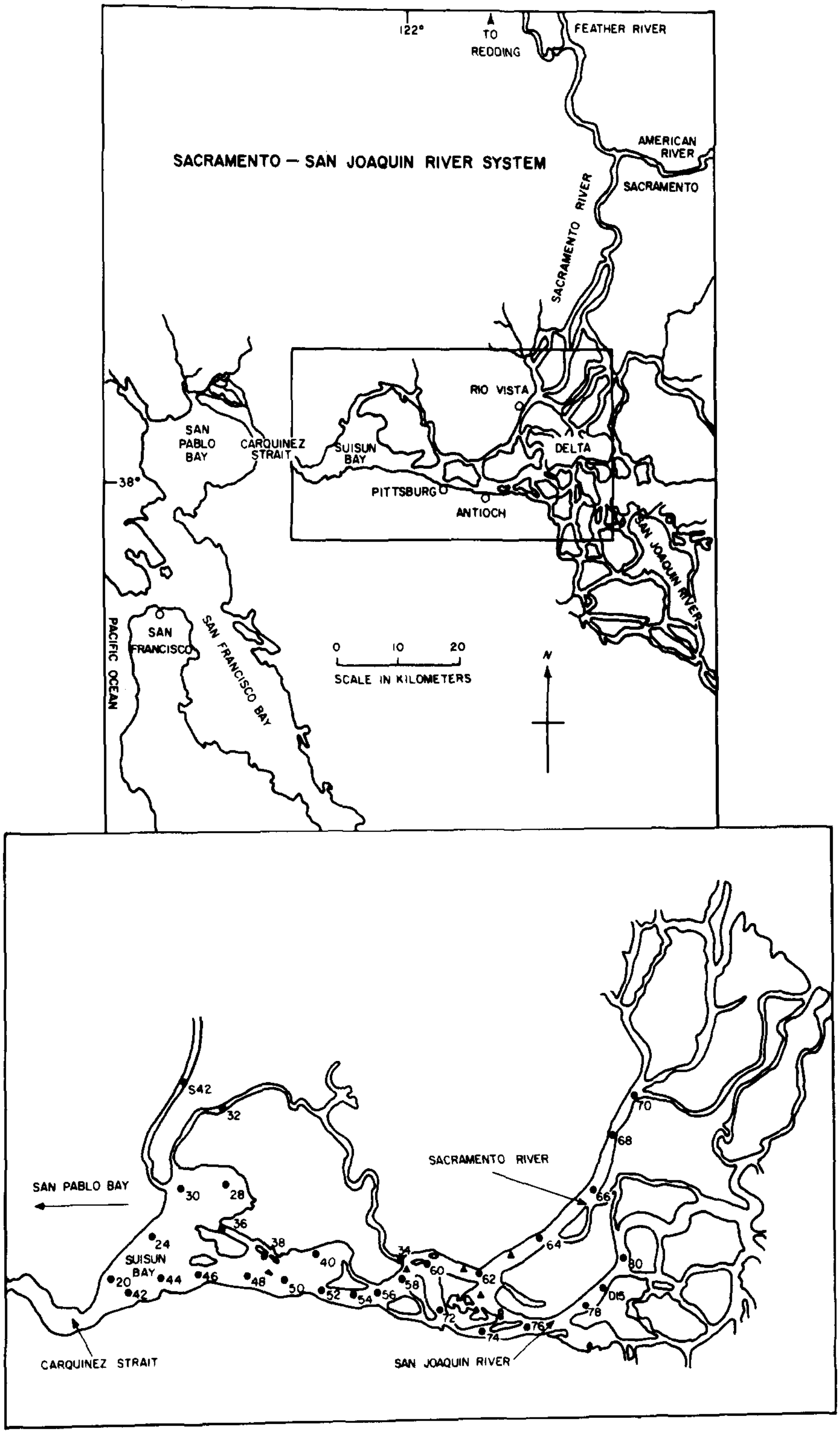

Fig. 1. Location of study area and collection sites in Sacramento-San Joaquin River Delta.

20-40, 42-60, 62-70, and 72-80 sampled on separate days. Sampling at stations 20-40 and 42-60 required ~4 h to complete while the river stations 62-70 and 72-80 could be sampled in 1 h. Each day's sampling began at the downstream station and proceeded upstream. Almost all collections were completed by noon each day. All shrimp collected were placed in 10% buffered formalin and later transferred to 70% ethanol. Each shrimp was measured from the anterior edge of the carapace (excluding the rostrum) to the distal tip of the telson prior to analysis of stomach contents.

Stomachs from total of 1245 specimens of *C. franciscorum* and 562 specimens of *P. macrodactylus* were examined in 1978. Stomachs from an additional 349 specimens of *C. franciscorum* and 205 specimens of *P. macrodactylus* were examined in 1976-1977. The number of shrimp examined each month varied with their abundance in the study area. Neither shrimp is abundant in the Delta during the winter months (December-March) and less than 10 of each species were examined in these months. From 100-300 specimens of *Crangon* and 50-100 specimens of *Palaemon* were examined each month from May through October 1978. The shrimp examined ranged in size from 21-70 mm for specimens of *C. franciscorum* and 10-44 mm for specimens of *P. macrodactylus*. For stomach analysis the carapace of each shrimp was lifted and split with forceps to expose the internal organs. The stomach was removed and teased open in a gridded petri dish. The contents were examined with a dissecting microscope (7-40X) and identified. Crustacean prey were measured and assigned to the nearest mm length class.

Results

Stomach contents

Table 1 lists the items found in the shrimp stomachs and their frequency of occurrence in

Table 1. Stomach contents of *Crangon franciscorum* and *Palaemon macrodactylus* collected from the Sacramento-San Joaquin Delta, January 1976 – October 1978.

Food item	% occurrence		Average no. organisms in stomachs containing prey item		Average no. organisms in stomachs of all shrimp containing prey		% total prey in stomachs containing prey	
	1976–77	1978	1976–77	1978	1976–77	1978	1976–77	1978
Crangon franciscorum								
Neomysis mercedis	74	61	1.68	1.47	1.23	0.90	62	84
Corophium spp.	31	3	1.15	1.50	0.36	0.04	18	4
Isopoda		2	1.00	1.00	0.02	0.02		
Miscell. and undet. crustacea	19	10					19	8
Neanthes spp.	1	4	1.00	1.00	0.02	0.04	1	4
Bivalves	1	<1	1.00		0.02		1	
Inorganic material	26	<						
Vascular plant material	42	1						
Unrecogn. debris	44	19						
Palaemon macrodactylus								
Neomysis mercedis	67	68	1.91	2.15	0.63	1.56	76	94
Corophium	9	5	1.67	1.00	0.71	0.05	9	3
Isopoda		<1		1.00		<0.01		
Miscell. and undet. Crustacea	34	8					11	2
Neanthes spp.	2	2	1.00	1.00	0.01	0.02	1	1
Bivalves	2						3	
Inorganic material	2	2						
Vascular plant material	51	2						
Unrecogn. debris	16	15						

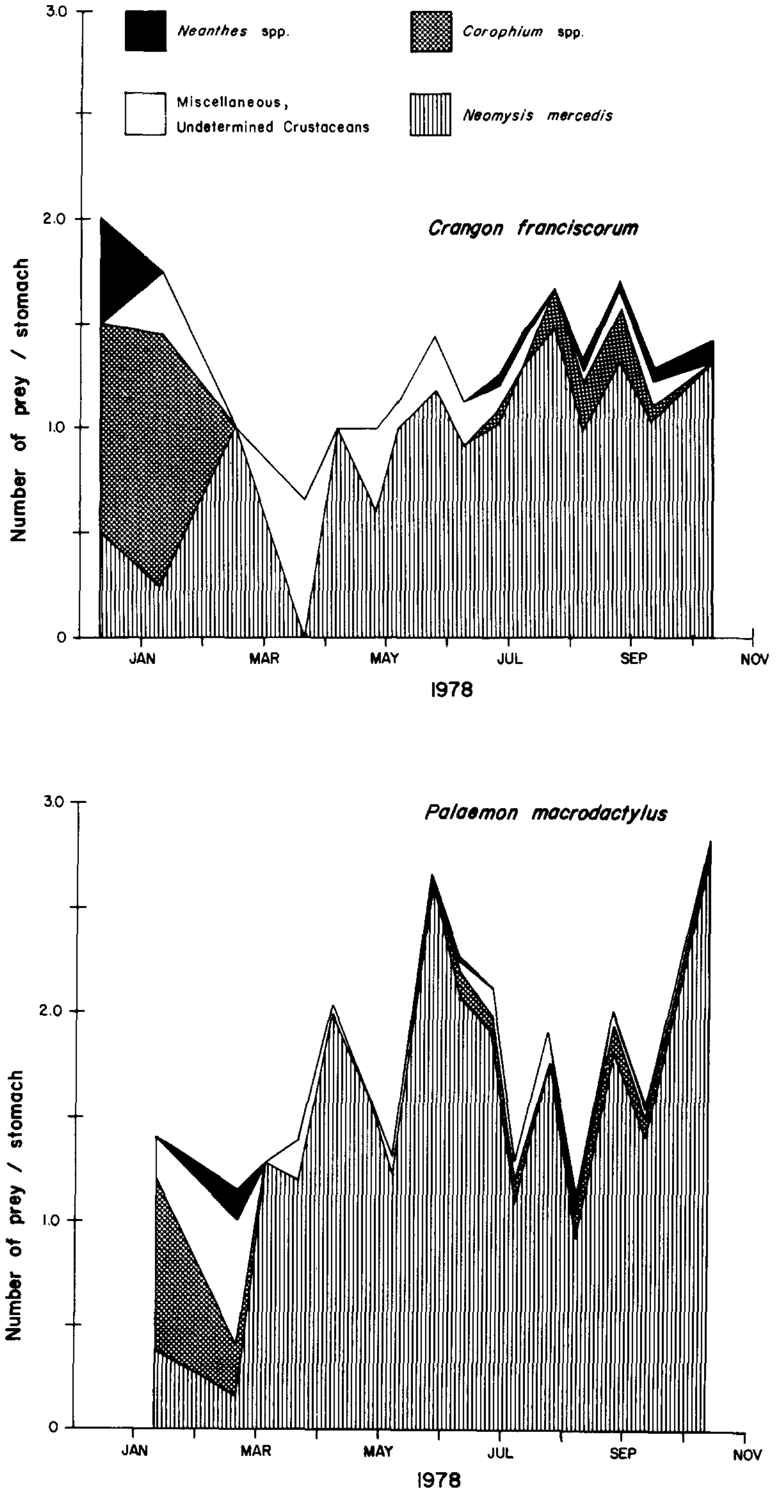

Fig. 2. Mean composition and number of prey items in stomach contents of *Crangon franciscorum* and *Palaemon macrodactylus*, December 1977 - October 1978.

stomachs containing food items. Table 1 also shows the mean number of each prey organism and their percentage of the total prey organisms identified from the stomachs of the decapod shrimp. *N. mercedis* was the most important and amphipods of the genus *Corophium* the second most important prey of both caridean shrimp. Three species of *Corophium* were identified: *C. stimpsoni, C. spinicorne,* and *C. ascherusicum.* An additional amphipod, *Paraphoxus milleri,* was identified on a single occasion in the stomach of a specimen of *C. franciscorum. Gnorimosphaeroma* spp. were the isopods most frequently ingested, but small specimens of *Synidotea* were occasionally ingested by *C. franciscorum.* Miscellaneous Crustacea ingested include copepods (*Eurytemora hirundoides* and harpacticoids), ostracods, crab larvae (*Rhithropaneopus harrissi*) and megalops, and *P. macrodactylus* larvae. Unidentified fragments of crustacean exoskeletons were common in the stomach contents. Crustacean prey accounted for more than 95% of the prey organisms identified from the stomachs of specimens of both *C. franciscorum* and *P. macrodactylus.* The only non-crustacean prey observed in the stomachs of these decapod shrimp were polychaetes (*Neanthes* spp.) and an occasional bivalve.

The decapod stomachs often contained several copepods or crustacean larvae but in cases in which a macro-prey item other than *N. mercedis* or *Corophium* spp. was ingested, only a single such item was present in the stomach (Table 1). The stomachs of specimens of *P. macrodactylus* generally contained more *N. mercedis* prey than did specimens of *C. franciscorum.* Often more than five and as many as thirteen mysids were found in a single stomach of a *P. macrodactylus* specimen. Stomachs of *C. franciscorum* specimens rarely contained more than two or three mysids, with six being the maximum.

Vascular plant materials were frequently encountered in the stomachs of the decapod shrimp in 1976-1977 but not in 1978 (Table 1). Vascular plant materials never filled the stomach; generally only a

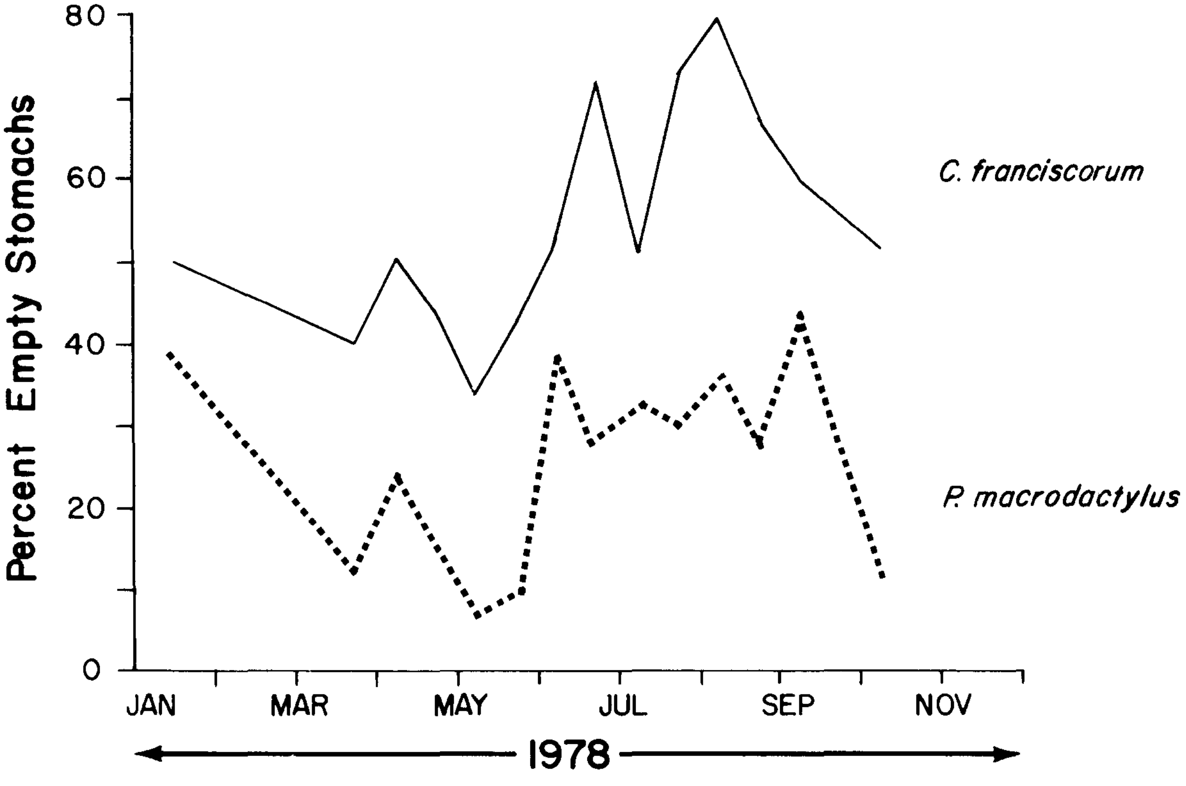

Fig. 3. Frequency of empty stomachs of *Crangon franciscorum* and *Palaemon macrodactylus* collected from Sacramento-San Joaquin River Delta, December 1977 - October 1978.

few bits or strands were evident. Inorganic material, i.e. sand, was frequently in the gastric mills of specimens of *C. franciscorum* in 1976–1977 but not in 1978. In 1976–1977 *Corophium stimpsoni*, an inhabitant of sandy substrates, was a frequent prey of *C. franciscorum* and much of the sand observed in the gastric mills may have been taken incidental to the capture of an amphipod. Sand grains may have a coating of bacteria and provide some nutrition but it's unlikely that active 'grazing' on sand grains occurs among these caridean shrimp. Unrecognizable debris (Table 1) includes all organic materials of 'undeterminable origin'. Most of the debris is probably derived from animal prey.

Temporal and geographic patterns

The variation of the diets of specimens of *C. franciscorum* and *P. macrodactylus* throughout the 1978 study period is illustrated in Fig. 2. In winter, polychaetes and *Corophium* spp. were important components of the diets of the few caridean shrimp collected in the study area. Winter marks the annual minimum in *N. mercedis* abundance and this is reflected in the diets of the caridean shrimp. The composition of the diets was fairly consistent throughout the study area except that polychaetes were more prevalent at downstream stations and amphipods were most often in stomachs of shrimp collected from upstream stations.

Of the 1245 stomachs of *C. franciscorum* specimens examined in 1978, 756 or 61% were empty. Only 27% of the 562 stomachs of *P. macrodactylus* specimens examined in 1978 were empty. The frequency of empty stomachs of *C. franciscorum* dropped below 40% only in early May (Fig. 3). Less than 10% of the stomachs of *P. macrodactylus* specimens examined at this time were empty. Geographic variability was much greater than temporal variability (both diel and seasonal) in frequency of empty stomachs. During the summer 80–100% of the caridean shrimp collected at stations near the downstream limit of the study area had empty stomachs, but less than 40% of those collected near the upstream limit of their distribution were empty.

Overlap

The diets of *C. franciscorum* and *P. macrodactylus* specimens are very similar throughout the year. Dietary overlap, $C_m = 2\Sigma(p_{xi}\,p_{yi})/(\Sigma p_{xi}^2 + \Sigma p_{yi}^2)$ (Horn 1966), and similarity, $C_{xy} = 1 - \frac{1}{2}(\Sigma|P_{xi} - P_{yi}|)$ (Renkonen 1938), respectively exceeded 90% and 80% on almost every sample date (Table 2). However, size-related trophic resource partitioning occurs. Figure 4 illustrates the size frequency distribution of mysids ingested by various sizes of caridean shrimp. More than 60% of the mysids ingested by specimens of *P. macrodactylus* were $\leqslant 4$ mm long while only 23% of those ingested by specimens of *C. franciscorum* were $\leqslant 4$ mm long. Correspondingly, only 7% of the mysids ingested by specimens of *P. macrodactylus* were $\geqslant 8$ mm long while 35% of those ingested by specimens of *C. franciscorum* were $\geqslant 8$ mm long. The median size of mysid ingested increased as specimens of *C. franciscorum* increased in size, from 4 mm for 21–25 mm long crangonids to 8 mm for crangonids > 40 mm long. The median size of mysid ingested by specimens of *P. macrodactylus* was 3-4 mm for all *Palaemon* size groups.

Table 2. Dietary overlap (Horn 1966) and similarity (Renkonen 1938) between diets of *Crangon franciscorum* and *Palaemon macrodactylus* specimens collected in the Sacramento-San Joaquin River Delta, 1978.

Survey	Dietary overlap	Similarity	Overlap of mysid prey ingested[a]
April II	0.79	0.60	
May I	0.99	0.95	
May II	0.97	0.83	0.82
June I	0.98	0.85	0.60
June II	0.98	0.89	0.38
July I	0.99	0.91	–
July II	0.93	0.74	0.57
August I	0.97	0.80	–
August II	0.99	0.88	0.58
September I	0.91	0.91	0.54
October I	0.93	0.93	0.51

[a] Surveys with no overlap values reported indicate dates on which insufficient numbers of mysids were sizable in stomach contents of the decapod shrimp.

Discussion

Both *C. franciscorum* and *P. macrodactylus* are basically carnivorous. This is true of many crangonids, including *C. crangon*, *C. septemspinosa*, and

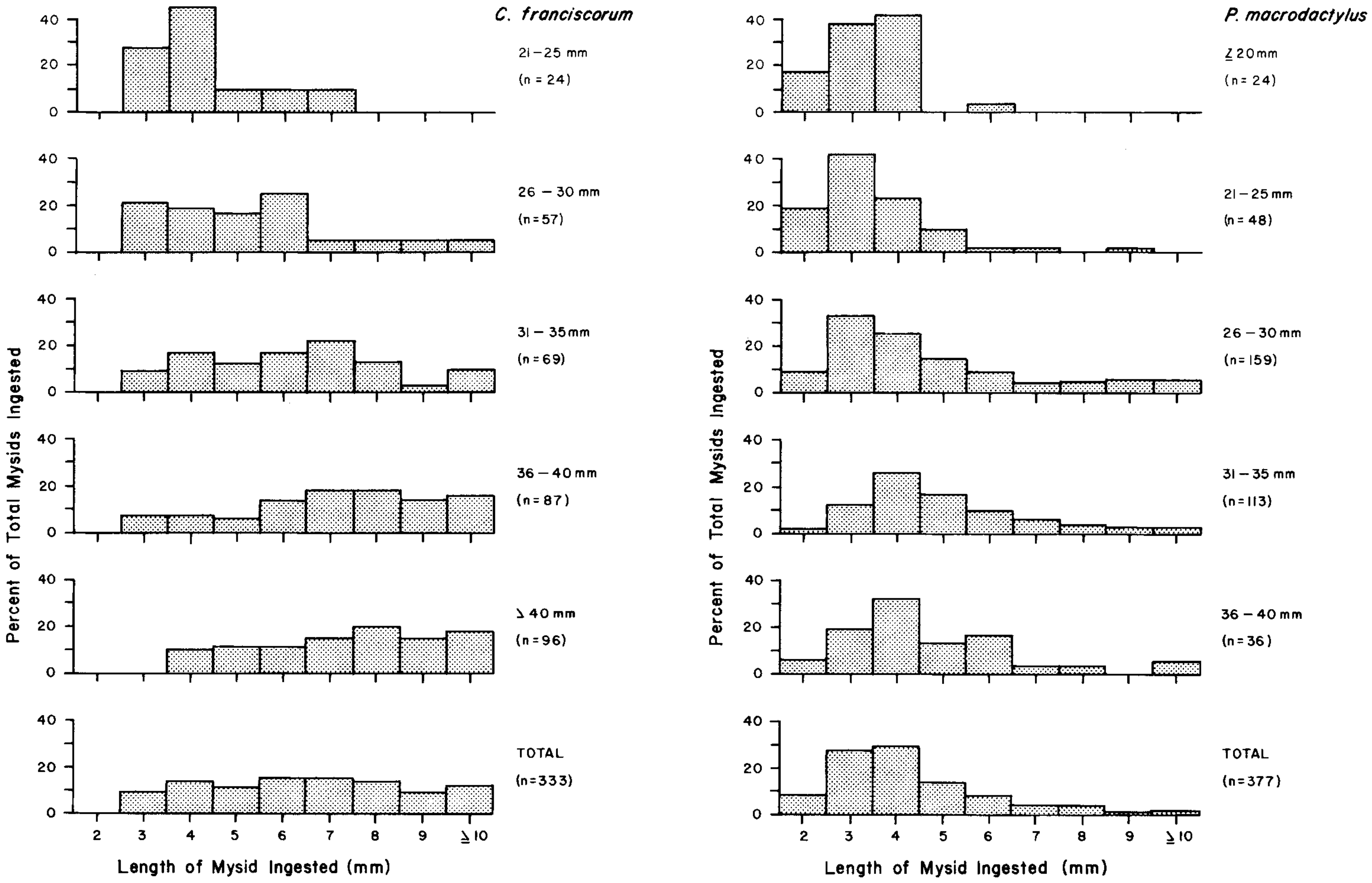

Fig. 4. Size frequency distribution of *N. mercedis* found in stomachs of various size groups of *Crangon franciscorum* and *Palaemon macrodactylus*, 1978. Number in parentheses indicates number of mysids measured.

C. affinis (Lloyd & Yongue 1947; Allen 1960; Price 1962; Kosaka 1970; Wilcox & Jeffries 1974) and other caridean shrimp (Williams 1955; Dahl 1968). The diets reported here are basically similar to those reported by Sitts & Knight (1979), although they did not report the occurrence of isopods in the diets of these caridean shrimp. Both shrimp were found, in this study, to ingest *Gnorimosphaeroma* and specimens of *Crangon* ingested *Synidotea.* Sitts and Knight reported *Corophium* included as one of the gammarids ingested by *C. franciscorum* and *P. macrodactylus* but did not indicate what other gammarid amphipods were found. The only amphipods found in the shrimp diets reported here were three species of *Corophium* and a single specimen of *Paraphoxus milleri.* Copepods were the second most numerous prey in the stomachs of both *C. franciscorum* and *P. macrodactylus* specimens examined by Sitts & Knight (1979). Specimens of *P. macrodactylus* examined in this study did occasionally contain a large number of copepods but few specimens of *C. franciscorum* had ingested large numbers of copepod prey. The contribution of copepods to the overall diets was minimal.

The dominance of crustacean remains in decapod stomachs may be a reflection of their resistance to trituration. Soft body organisms such as oligochaetes, which were abundant in the benthos of many Delta stations, would be rapidly triturated and unrecognizable. Specimens of both *C. franciscorum* and *P. macrodactylus* will ingest tubificid oligochaetes in the laboratory (Nelson *et al.* 1979) but have not been observed to do so in the field.

Polychaetes were determined to be the most frequently ingested prey of *C. septemspinosa* from Delaware Bay, but mysid shrimp were the most prevalent crustacean identified in their gastric mills (Price 1962). The diversity of materials found in the digestive tracts of *Crangon* spp. led Wilcox & Jeffries (1974) to suggest that they ingest anything encountered. The low diversity of the diets of shrimp collected in this study reflects the low diversity of the fauna in the study area.

Both *C. franciscorum* and *P. macrodactylus* are nocturnal, dispersing into the water column during darkness (Siegfried *et al.* 1978; Sitts 1978). This nocturnal activity is thought to be associated with active feeding. However, seven 1976 diel studies of *C. franciscorum* and *P. macrodactylus* stomach contents indicated no significant temporal difference in numbers of prey/stomach in 5 of the 7 studies (Sitts & Knight 1979; Siegfried, unpublished). Examination of shrimp collected in the present study revealed no significant effect of time of collection on number of prey/stomach or frequency of empty stomachs on any collection date. *C. septemspinosa* has been shown to feed primarily during darkness (Wilcox & Jeffries 1974), its movement into the water column linked to the presence of *Neomysis americanas* (Welch 1970). When *N. americanas* was absent from laboratory observation chambers, *C. septemspinosa* remained in the substrate but when mysids were present the crangonid entered the water column to feed. *C. franciscorum* is sometimes abundant in the water column during daylight at locations coinciding with high *N. mercedis* densities (Ganssle 1966; Siegfried *et al.* 1978). The presence of *C. franciscorum* in the water column and the lack of any strong diel feeding pattern may indicate active feeding throughout the diel cycle in the study area. This may be related to the low density and abundance of prey populations in the study area (Siegfried *et al.* 1980). A more distinct feeding periodicity might be expected in downstream areas where prey is more plentiful. High turbidity in the study area (depth of 1% surface light generally <2 m) may also contribute to greater diurnal activity.

Specimens of *P. macrodactylus* almost always contained a greater number of prey, on the average, than did specimens of *C. franciscorum.* This difference can be related to the behavioral and morphological characteristics of the shrimp. *C. franciscorum* is dorsally-ventrally flattened and, in the laboratory, prefers to bury itself in depressions in sandy substrates during daylight. *P. macrodactylus* is more robust and does not bury itself. The substrate at most study sites is sandy and would thus allow *C. franciscorum* to bury itself while *P. macrodactylus* remained on the substrate surface. This may mean that during daylight *P. macrodactylus* would be more likely to encounter prey and thus have more opportunity to capture prey than would *C. franciscorum.*

The cardiac stomach of *C. franciscorum* is modified to form an efficient food-crushing apparatus known as the gastric mill. *P. macrodactylus* lacks a gastric mill and, therefore, no mastication of food occurs in the cardiac stomach of

P. macrodactylus. The churning digestive action of the cardiac stomach of *P. macrodactylus* may not be as efficient as the gastric mill of *C. franciscorum*. This may account for the greater number of prey recognized in the stomachs of specimens of *P. macrodactylus* and the greater frequency of empty stomachs of specimens of *C. franciscorum*.

Geographic differences reported above correspond to differences in *N. mercedis* abundance; during the summer, mysids were abundant at the upstream end of the study area and relatively rare downstream. This affects the geographic distribution of *C. franciscorum* and *P. macrodactylus* (Siegfried 1980). The maximum abundance of both caridean shrimp generally coincides with the maximum abundance of *N. mercedis* at salinities above ~1%. The concentration of the decapod shrimp at a few stations and the almost complete dominance of *N. mercedis* in their diets precludes a detailed examination of geographic variation in the study area. However, limited collections of crangonids from San Francisco Bay (downstream from the study area) found much more diversity in their diet (personal observation).

Sitts & Knight (1979) found both shrimp to exhibit similar prey size selection patterns. Both selected mysids of intermediate sizes while selecting against smaller or larger mysids. The results of this study indicate differences in sizes of mysids ingested. Specimens of *P. macrodactylus* generally ingested mysids ⩽4 mm in length and specimens of *C. franciscorum* ingested larger sized mysids. This difference can be related to life history differences which tend to enhance size-related partitioning of resources. *C. franciscorum* attains a larger size and begins recruitment earlier in the year than does *P. macrodactylus* (Siegfried 1980). The mean size of *C. franciscorum* collected in the Delta is thus larger than that of *P. macrodactylus* for almost the entire year. May, a time of recruitment of juvenile crangonids to the Delta, is the only month in which populations of the two caridean shrimp had similar mean sizes. Size differences increase after May as juvenile crangonids mature and *P. macrodactylus* recruitment begins. This is reflected in the overlap co-efficients calculated for mysid prey ingested by the two caridean shrimp (Table 2). In May overlap was high, indicating that the two caridean shrimp were ingesting a similar size distribution of mysids, and then declined through October.

Observations of handling time of various size groups of *C. franciscorum* and *P. macrodactylus* preying on various sizes of *N. mercedis* indicates little difference between similar sizes of predator (C. Siegfried, unpubl.). Mean handling times of these decapod shrimp preying on mysids ⩽4 mm in length range from <1 s for shrimp >40 mm long to ~8 s for smaller (⩽25 mm long) specimens of *P. macrodactylus*. The largest individuals of either predator are capable of ingesting even the largest mysid without difficulty (handling time <20 s) and tend to ingest larger prey in the field. Laboratory observations indicate that the smaller individuals (<30 mm long) generally could not handle mysids >6 mm long. Attacks occurred but large mysids usually escape from the chelipeds of the small predators. Sometimes a small caridean shrimp killed a large mysid after several attacks but was not able to completely ingest the mysid.

The smallest size classes of mysids are not necessarily 'selected' against, as electivity indices suggest (Sitts & Knight, 1979). Availability of prey to the predator must also be considered. Smaller mysids are generally higher in the water column than are larger mysids (Siegfried *et al.* 1979), making them less likely to be encountered by bottom dwelling predators.

Sitts & Knight (1979) speculate that predation by caridean shrimp on intermediate sizes of mysids affects not only the population structure but also the abundance of the mysids of the Delta. Their analysis was based on data from a single Delta station and cannot represent the dynamics of a system as large as the Delta. Vertical and geographic distributional differences among mysid size classes along with differential downstream and upstream transport rates for the various mysid size classes (Siegfried *et al.* 1979) precludes extrapolation of predation dynamics from a single station to the entire Delta. Calculation of consumption rates and extrapolation to daily removal of prey biomass from data collected at a single station is likewise unwarranted unless recruitment and emmigration of both predators and prey are considered. The bulk of the mysid population is located upstream of the $1^0/00$ salinity level (Orsi & Knutson, Calif. Dept. Fish and Game, unpubl. ms), the upstream limit of *C. franciscorum* and *P. macrodactylus* distribution (Siegfried 1980). Thus much of the mysid population is unavailable to these predators. The total Delta-wide abundance of predators and prey differed by at least three orders of magnitude even in 1977 when mysid abundance was at their lowest recorded levels (Siegfried 1980; Orsi & Knutson, unpubl. ms). Predation by these shrimp on *N. mercedis* may have some localized impact on the mysid population but does not appear to be significant in terms of the overall population of the Bay-Delta. Predation by fish is probably more important in this respect.

The association between *C. franciscorum* and *P. macrodactylus* is recent in the San Francisco Bay system. There is no quantitative data available to evaluate the effect, if any, of the introduction of *P. macrodactylus* on native shrimp populations. Although there is some temporal separation of populations of *C. franciscorum* and *P. macrodactylus* in the Delta, spatial overlap is great (Siegfried 1980). Trophic overlap is also very high. If trophic resources become limiting, e.g. during severe droughts, competition may be intense. Continued study of these shrimp, both in the Delta and in San Pablo and San Francisco Bays, should provide important information on competitive interactions between these shrimp.

Summary

The diets of the native caridean shrimp, *Crangon franciscorum*, and the introduced oriental shrimp, *Palaemon macrodactylus*, from the Sacramento-San Joaquin River Delta were investigated from January 1976 through October 1978. Both shrimp are carnivorous, preying primarily on the opossum shrimp, *Neomysis mercedis*, but ingesting representatives of nearly all macroinvertebrates known to be present in the study area. Detritus was not a significant part of the diets. Specimens of *P. macrodactylus* almost always contained a greater number of prey, on the average, than did specimens of *C. franciscorum*. This difference is related to behavioral and morphological characteristics of the two shrimp.

The diets of *C. franciscorum* and *P. macrodactylus* are very similar throughout the year. Dietary overlap (Horn 1966) and similarity (Renkonen 1938), respectively, exceeded 90% and 80% on almost every sample date. However, size-related trophic resource partitioning occurs. Specimens of *C. franciscorum* are generally larger than specimens of *P. macrodactylus* and ingest larger mysids than do specimens of *P. macrodactylus*. More than 60% of the mysids ingested by specimens of *P. macrodactylus* were ≤4 mm long while only 23% of those ingested by specimens of *C. franciscorum* were ≤4 mm long. Correspondingly, only 7% of the mysids ingested by specimens of *P. macrodactylus* were ≥ 8 mm long while 35% of those ingested by specimens of *C. franciscorum* were ≥8 mm long. The association between *C. franciscorum* and *P. macrodactylus* is still relatively recent and no quantitative data is available to evaluate the effect of the introduction of *P. macrodactylus* into the Delta. However, since spatial and trophic overlap is great, competition may become severe when trophic resources are limiting, e.g., during droughts.

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